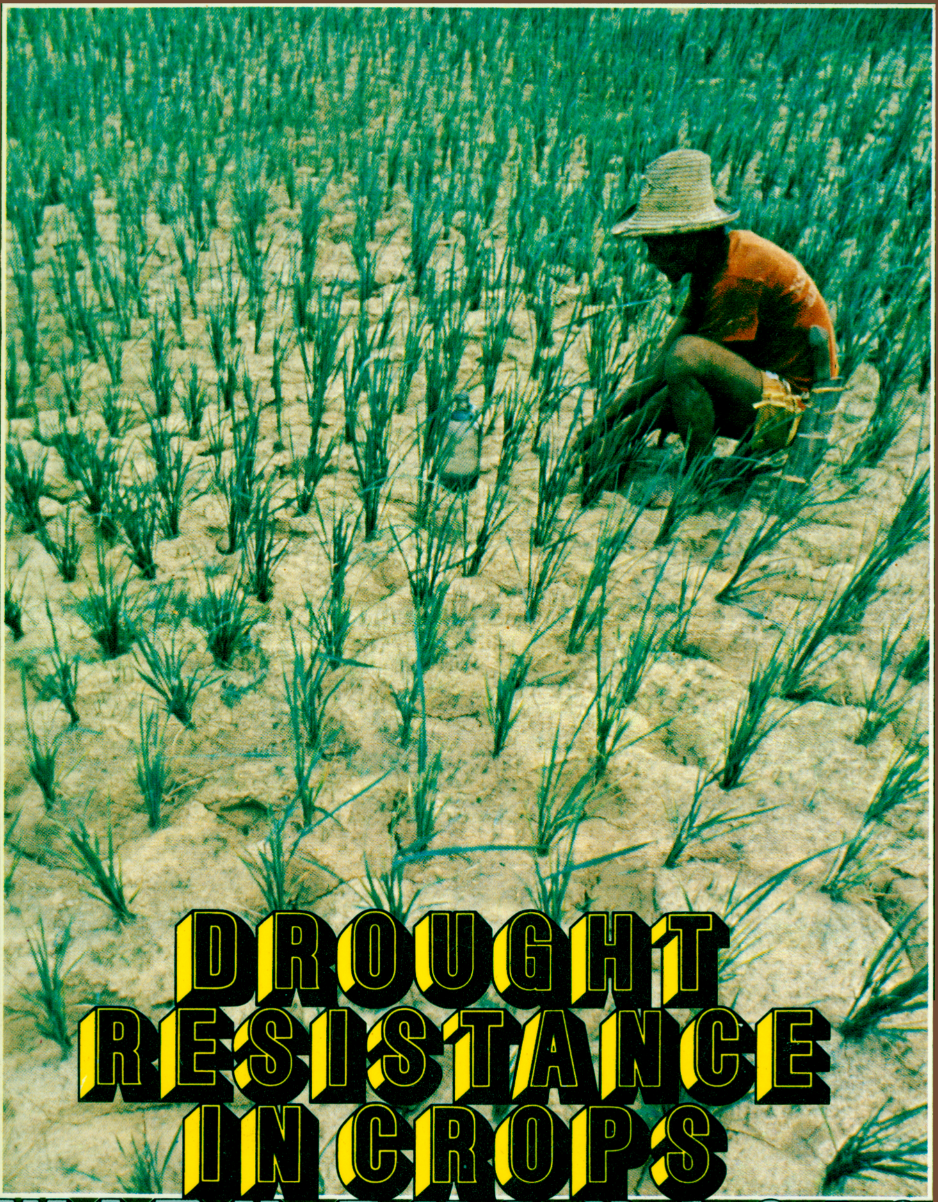


# DROUGHT RESISTANCE IN CROPS WITH EMPHASIS ON RICE

INTERNATIONAL RICE RESEARCH INSTITUTE

# DROUGHT RESISTANCE IN CROPS WITH EMPHASIS ON RICE

---

1982
INTERNATIONAL RICE RESEARCH INSTITUTE
LOS BAÑOS, LAGUNA, PHILIPPINES
P.O. BOX 933, MANILA, PHILIPPINES

The International Rice Research Institute (IRRI) is one of 13 nonprofit international research and training centers supported by the Consultative Group for International Agricultural Research (CGIAR). The CGIAR is sponsored by the Food and Agriculture Organization (FAO) of the United Nations, the International Bank for Reconstruction and Development (World Bank), and the United Nations Development Programme (UNDP). About 50 countries, international and regional organizations, and private foundations comprise the CGIAR.

IRRI receives support, through the CGIAR, from a number of donors including:

the Asian Development Bank
the European Economic Community
the Ford Foundation
the International Fund for Agricultural Development
the OPEC Special Fund
the Rockefeller Foundation
the United Nations Development Programme

and the international aid agencies of the following governments:

Australia
Belgium
Brazil
Canada
Denmark
Federal Republic of Germany
India
Japan
Mexico
Netherlands
New Zealand
Philippines
Spain
Sweden
Switzerland
United Kingdom
United States

The responsibility for this publication rests with the International Rice Research Institute.

**ISBN 971-104-078-6**

# CONTENTS

**COMPONENTS OF DROUGHT RESISTANCE**

**BREEDING AND SELECTION APPROACHES FOR DROUGHT-PRONE AREAS - RICE**

## BREEDING AND SELECTION APPROACHES FOR DROUGHT-PRONE AREAS - OTHER CROPS

# FOREWORD

The interactions of soil, water, climate, and plant are key elements in the production of cereal grains. Water, more than any other factor, controls development of field crops at crucial growth stages.

Irrigation and water management are possible only with a dependable and controllable water supply. But in many countries, this stable water supply does not exist. Nearly one-sixth of all rice land is rainfed.

In Asia, 30-40% of all rice lands are subject to monsoon floods. Monsoon rainfalls fluctuate drastically, from heavy downpours in eastern India to intermittent showers in the Philippines. Fluctuations occur within all countries throughout the region.

The papers presented 4-8 May 1981 during the IRRI symposium on drought resistance attempt to explain drought stress across a range of environmental, agroclimatic, and genetic conditions in grain cereals. The hoped-for result is that rice scientists in particular will gain insight to advance their studies of water stress resistance in the rice plant. These proceedings will serve as an important reference.

At the end of 3 days of paper presentations and discussions, participant working groups analyzed specific questions and developed specific recommendations for future work in improving drought resistance in crops. Those reports are included at the end of the proceedings.

IRRI appreciates the time and effort of speakers and participants and of all those who made the symposium possible. Special recognition goes to coordinator Dr. John C. O'Toole, IRRI agronomist, and to the Information Services Department staff who edited the proceedings.

Marcos R. Vega
Acting director general

# WELCOME ADDRESS

Welcome to the International Rice Research Institute. To those of you who were with us for the International Rice Research Conference last week, we appreciate your staying on for this symposium. We thank all of you for coming to share your knowledge and your experience on a subject that has always been a constraint to crop production — drought. In the effort to produce more food, you naturally focus on how to overcome that constraint by improving drought resistance in crops. Because our institute is devoted to rice, we of course want the knowledge and experience that will lead to the improvement of drought resistance in rice.

In the tropics, rice normally is grown during periods of high rainfall, the time of year commonly referred to as the rainy season. But the rice crop often is subjected to periods of severe moisture stress because of the marked variation in time and intensity of rainfall.

The ability of the crop to withstand drought is essential in most tropical rice-growing areas. Although drought-resistant rice varieties are needed most by dryland rice farmers, the drought-resistance character also is very important in rainfed wetland rice. Rice yields from rainfed areas are limited by unseasonal drought. In fact, deepwater rices also must possess drought resistance, because they normally are direct-seeded into dry soil and are likely to experience moisture stress before flooding occurs. Rices that grow in water up to 3 meters deep still must possess the ability to withstand moisture stress at early stages.

There is growing concern over the plight of rice farmers in the rainfed areas. This concern intensifies when all of us, including the farmers, see how science has been able to improve rice yields in irrigated areas, particularly where water control is fairly good. We do not have the same high-yielding technology for the drought-prone areas and there is a dearth of research to develop such technology.

Responses to a recent survey of 35 Asian rice breeders illustrate this point. When asked what they perceive as the important factors limiting rice production, the breeders indicated that drought is a close second to insects and diseases. Yet, if we consider the time and the effort those scientists have devoted to breeding for insect and disease resistance, we find they were not doing much breeding for drought resistance.

If this observation reflects a fair picture of the real situation, we should ask “why?” Is it because we do not understand the environment we call rainfed areas of drought-prone regions? Is it because we do not understand the components of drought resistance and, as a consequence, do not know what to measure and have not developed suitable screening techniques for this characteristic?

I may be raising the wrong questions. But we must certainly do something about the development of appropriate technology for the drought-prone rice areas.

IRRI’s objective in convening this conference — Principles and Methods in Crop Improvement for Drought Resistance with Emphasis on Rice — is to provide an opportunity to survey the art and the science of crop improvement for drought resistance. In inviting participants and papers to be discussed, emphasis was placed on integrating the principles of climatology, soil science, soil and plant water relationships, and manipulation of genetic variability for traits associated with drought resistance. In recognition of what we feel are apparent gaps, sessions on components of drought resistance and breeding and on selection approaches for drought-prone areas have been included.

But we are counting on the outcome of the panel discussions and the working group discussions to call attention to what needs to be done, to how those things that need to be done should be done, and to how we should organize to get the work done effectively and efficiently within the shortest time possible. We are counting on you.

Once again, on behalf of my colleagues at IRRI, I welcome all of you. We hope you find your stay both professionally and personally rewarding. Let us know if there is anything we can do to ensure that your visit to IRRI will be remembered as a pleasant and fruitful one.

M. R. Vega
Deputy director general

# ASPECTS OF DROUGHT FROM AN AGROCLIMATIC PERSPECTIVE

**HENRY A. NIX**

Definitions of drought mirror a growing understanding of water in the soil-plant-atmosphere continuum. A brief review of possible adjustments to drought emphasizes the wide range of strategies for drought mitigation that exist. Breeding and selection of crops for drought resistance is an important response, but it should be considered within the broader context.

Development of research strategies for improving drought resistance in crops requires discussion within the broad framework. A systems approach is seen as the only effective strategy currently available for coping with the enormous complexity of crop production systems and their adjustment to complex patterns of water deficits. Development of operational models, with an integrated resource data base, is an essential prerequisite for continuing analysis of the complex interactions in site-soil-crop-weather management of crop systems in general and of rice production systems in particular.

Such a system can be used to identify appropriate goals in crop improvement for drought resistance; to develop an understanding of crop response to water deficits; to provide a firm basis for development, evaluation, and testing of new and modified technologies; and to aid in the development of optimum networks for field experimentation.

## A DROUGHT DEFINITION

That there is no generally accepted definition of drought should not be surprising, since human perception of the phenomenon and its effects tends to be location and land use specific. Agricultural drought, for example, can have different threshold

---

CSIRO Division of Land Use Research, Canberra, Australia.

conditions and criteria than hydrological drought and need not be concurrent. At its simplest level, drought is a shortage of water in the system concerned. Lack of precipitation usually is seen as the primary cause, but careful distinction is made between those situations where lack of precipitation is a quasi-permanent feature (arid regions) and those where it is a period of below normal rainfall. The very concept of departure from normal conditions emphasizes the location-specific character of such definitions. Problems remain in specifying the extent of the departure from normal precipitation and the duration of the period.

My intention is not to canvass the very extensive list of definitions of drought, save to draw attention to the comprehensive reviews by Hounam (1971, 1976). The historical development of definitions for drought reflects the growing understanding of the dynamic role of water in the soil-plant-atmosphere continuum. Early definitions were based entirely on precipitation criteria. Later recognition of the importance of evaporation in precipitation effectiveness led to incorporation of temperature as a surrogate parameter (Lang 1915, De Martonne 1926, Koppen 1931). The continuing use of such definitions reflects the limited availability of evaporation data and the much greater availability of precipitation and temperature data rather than exhibiting any particular scientific value.

A significant advance in defining drought on a more realistic basis was the concept of a generalized water balance (Thornthwaite 1948) that involved recording transfers of water in six categories — precipitation, potential evapotranspiration, actual evapotranspiration, soil moisture storage, soil moisture deficit, and soil moisture surplus. Concurrently, Penman (1948) contributed a seminal concept to the estimation of potential evaporation. Much of the vast literature on soil-plant water relations since can be regarded as contributing to refining the terms in the water-balance equation and to quantifying transfer functions. While much of the earlier research focused on soil water status as a predictor of crop performance, recognition of plant water status as the operative variable followed rapidly from the pioneering work of R. H. Shaw and colleagues (Denmead and Shaw 1962, Dale 1964, Dale and Shaw 1965).

Continuing development of water balance models has permitted dynamic simulation of soil and plant water status at acceptable levels of accuracy for crop yield prediction for a wide range of crops in an equally wide range of environments. The estimation of plant water status at any time, coupled with a knowledge of crop sensitivity to water deficits during defined development stages, for important development processes, or both, has enhanced our ability to predict the consequences of drought. Rather than attempting to provide a static, empirical definition of drought, we can use crop modeling procedures that provide a direct measure of drought severity in terms of yield loss.

This does not imply that all of our problems are solved. Application of such methods demands certain minimum inputs of meteorological, soil physical, crop physiological, and management data and further research is necessary to develop general functional relationships.

Given the objectives of this conference, it is clear that agricultural drought is our sole concern. While catastrophic drought leading to crop death is part of a continuum of water stress and must be considered in any agroclimatic analysis of drought and its consequences, it seems clear that our primary concern is with the ability of crop plants to avoid, tolerate, or resist episodes of water deficits that significantly reduce growth and yield. While the emphasis remains on modification of the plant through breeding, we should not forget that other components of the production system also can be manipulated to minimize such effects.

## DROUGHT MITIGATION

Although sound land use planning can fit crops to specific environments to minimize the incidence of agricultural drought, some drought-induced loss is inevitable. Increasing population pressures on a limited land resource often lead to cropping strategies that carry a higher burden of risk and that lead to degradation of the basic land resource. Urban populations must carry some responsibility for such pressure and it would seem reasonable that they share in adjustments to drought stresses. Of course, they do this through such mechanisms as higher food prices, but this tends to benefit traders and those farmers who have a crop. Adjustment to drought loss can take place at the farm, in the village, at the governmental level of province or nation, or ultimately at the international level. While our primary concern is with mitigation of agricultural drought at the farm level, we must recognize that this can only be a partial solution to the total problem and that other forms of adjustment and mitigation of loss must not be neglected.

A very wide range of possible adjustments to drought can be recognized. Each represents a valid response and, given the complex character of farming systems, any one of the adjustments might be an appropriate response for a particular drought situation. While breeding and selection for drought escape, tolerance, and resistance of component crops might seem an obvious goal, it does have a cost. More important, in a time of scarce research resources, breeding has an opportunity cost. Could other avenues of research in drought mitigation produce a better return?

Kaltenhauser (1972) provides a broad classification of the wide range of possible adjustments to drought. This will be used as a basis to review alternatives for drought mitigation.

### Bearing the loss

Where a farmer has reserves of food or capital or both, those reserves may be an appropriate element in a longer-term strategy. Acceptance of higher levels of risk can lead to higher levels of yield averaged over a period. Acceptance of very low levels of risk to minimize year-to-year variation in yield can lead to substantial loss in the form of potential yield forgone. Stability is achieved but at a cost.

One very powerful application of crop modeling lies in evaluating alternative strategies for crop production that involve differing levels of risk. For example, in much of the Australian wheat belt, crop timing has been progressively adjusted to minimize the risk of frost at ear initiation and anthesis. However, at any location, with a decreasing probability of frost there is a rapidly increasing probability of severe water deficits during grain filling. Because frost is an event that can lead to almost total crop loss while water deficits usually produce a graduated yield loss, perception of risk is strongly biased toward frost avoidance. Simulation studies of alternative strategies that increase the frost risk (but decrease the risk of severe water deficits during grain filling) on varying proportions of the total cropped area suggest that very considerable gains in total grain production are possible without any other changes in existing crop system.

While higher risk strategies may lead to greater production on a time-averaged basis, they offer little to the farmer who does not have substantial capital backing. For the poorer subsistence farmer facing major crop loss, alternatives are few. He may be forced to use the limited reserves of food or capital or both he has available, to seek credit from the village moneylender, or perhaps even to sell property. Too often, these are the only adjustments possible. They inevitably lead to the emergence of a tenant farmer class. While acceptance of an occasional crop loss as part of a total cropping strategy may be appropriate for the capital-intensive farmer, it is unlikely to be part of the cropping strategy of the subsistence farmer.

## Spreading the loss

In this situation, adjustments are made by sharing the loss, either with the extended family (relatives), with an insurance company, or with the wider community through government relief and assistance. Government assistance has become a major factor internationally through famine relief and food aid programs. In terms of total expenditure, this may be the single most important mode of adjustment to drought. Although massive food aid programs may appear undesirable in the long term, they are a fact of life. Relevant research and development to improve the efficiency of such programs could yield positive benefits in mitigating the effects of drought.

Crop insurance systems operate successfully in a number of countries but premiums tend to be impossibly high where the risk and the need are greatest. In some cases, such insurance schemes are underwritten and subsidized by the central government. Insurance systems also are likely to work best in a commercially-based agricultural economy rather than in a subsistence economy where the need is for food rather than cash. Nevertheless, it would seem worthwhile to expend some research and development effort on exploring nationwide insurance schemes.

## Modifying the cause

Here we leave the socioeconomic modes of adjustment and enter those of the technological. Basically, the alternatives are to increase precipitation input through some form of weather modification or to reduce the demand for water through appropriate agronomic techniques, including drought-resistant species or cultivars or both.

Weather modification, through such activities as cloud seeding for rainmaking, has commanded considerable attention and research resources for more than two decades. Major difficulties in statistical analysis of rainmaking experiments arise because of the uncontrolled nature of the system under study. However, rainmaking is feasible and practical under certain rigorously defined conditions. But direct application of rainmaking to agricultural areas could create more problems than it solves, particularly in a complex terrain with diverse cropping patterns such as much of Southeast Asia. However, rainmaking could prove beneficial if used in drought-affected, nonagricultural catchment areas for major irrigation storages. Experiments in progress in the USA and Australia are evaluating such an application.

While prospects for increasing precipitation input through weather modification do not seem encouraging, there are a number of cropping adjustments that can decrease evaporative demand and make more efficient use of the water transpired. These include such well-known technologies as bare-fallowing, stubble-mulching, effective weed control, skip-row or wide-row planting, and the choice of better-adapted crop species or cultivars. Either singly or in combination, these technologies aim at using limited water resources more effectively. The major part of the research aimed at crop improvement for drought resistance falls within this broad category.

## Diversifying

This time-honored mode of adjustment to drought might involve a change in the crop species grown or in the mix of crop species grown or from crop only to a mixed crop-livestock system. For wealthier farmers with capital, the acquisition of additional land in a wider geographical area or occupying different positions along a hydrological toposequence might be an option. A combination of farm and off-farm enterprises or the development of cottage industry might be other alternatives. These are techniques for minimizing extreme variations in year-to-year food production and income and for lessening risk of total loss.

Many of these options are simply not available to poorer subsistence farmers. One option that is available is diversification of the crop base through the introduction of additional crops. Available techniques include serial cropping, intercropping, relay cropping, and ratoon cropping, particularly in situations where stored soil water is available following the major crop. The addition of dryland crops to wetland rainfed rice crop systems may be viewed as production intensification, but it also provides a hedge against yield losses due to drought in the primary rice crop.

The purpose of reviewing these major groups of adjustment to drought is to emphasize that many solutions to a common problem are possible. While breeding and selection for drought resistance may seem an obvious technological response, it should be considered within the broader context of drought and its effects on crop systems. Each broad category of drought adjustment has validity and elements of each may be incorporated into an individual farmer's responses. But the central problem remains — how to design, evaluate, and test an appropriate strategy relevant for an individual farmer and his farm. This returns us to the question of a general research and development strategy and the particular role that crop improvement for drought resistance might play within it.

## RESEARCH STRATEGIES

Specific research needs relating to crop improvement for drought resistance must be considered within the broader context of a total agricultural research and extension strategy. At the simplest, the goals of such a strategy are to develop appropriate technologies for increasing the efficiency of food and fiber production while maintaining the long-term stability of the land resource. Whatever the goals, implementation of new technologies ultimately rests with millions of individual farmers. Each farmer and his farm is unique. How do we prescribe a technology that is relevant to the land, labor, capital, and management resources of each individual?

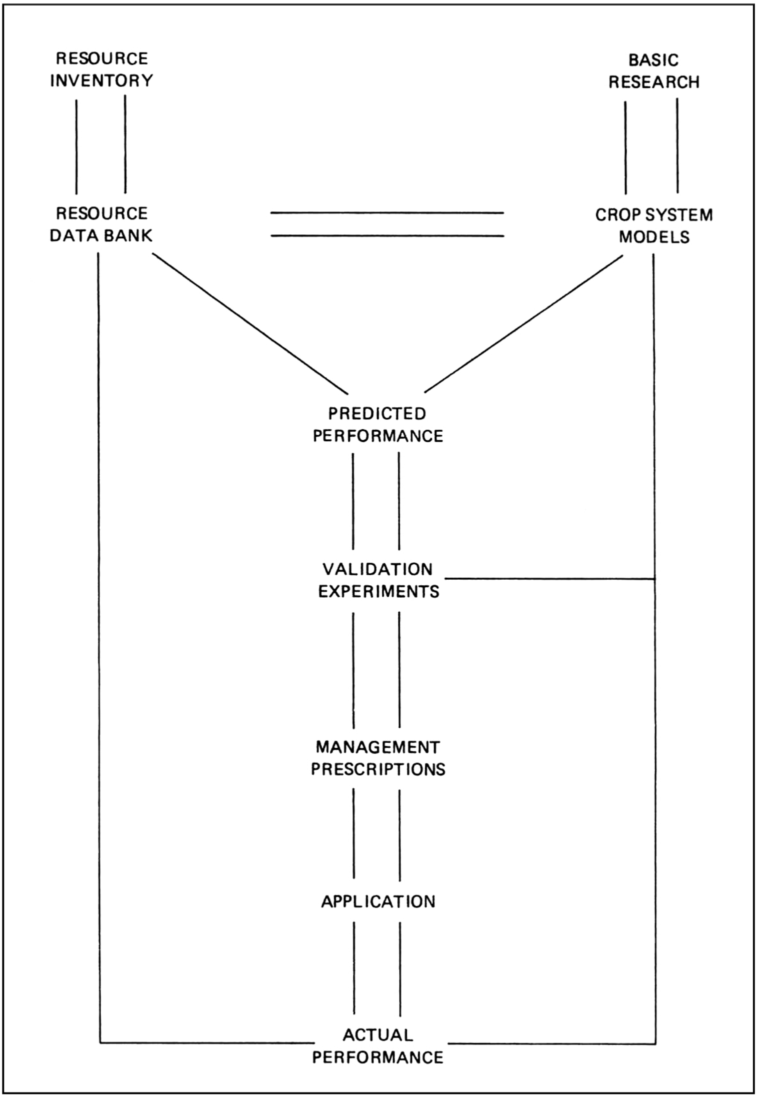
If, given a specified minimum set of soil-crop-weather and management data, it were possible to predict the performance of a particular crop system at a particular location, then it would be possible to predict an appropriate technology. This is an attainable objective, but it requires major shifts in the prevailing logic and methods of agricultural research (Nix 1968, 1976, 1979). Basically it requires a shift in emphasis away from the currently dominant reductionist or analytical approaches to holistic or synthesizing approaches. These two approaches are complementary rather than competitive.

Adopting a systems approach emphasizes the need for interdisciplinary teamwork. Knowledge and insight from the range of biological, physical, social, and economic disciplines become necessary. It formalizes what is known about crop production systems — their more important components, processes, and feedback mechanisms — and helps to identify significant, subtle constraints. Most importantly, the possible consequences (ecological, agronomic, economic) of introducing a new technology can be evaluated by using modeling and simulation techniques and field experiments designed to test model predictions.

A research strategy based firmly upon the systems approach would center on the balanced development of two interactive components (Fig. 1):

- crop production system models — fully operational and accessible at all times, but structured so that continuous improvement in logical structure and function is possible.
- resource data base — including only the physical, biological, social, and economic data necessary to implement the crop production system models. The special requirement for comprehensive files of climate and weather data should be apparent, since these are the primary inputs that drive the biophysical processes of the crop system.

A simple flow chart (Fig. 1) represents the functional analysis of major linkages in a systems-based research strategy. All components of this network rarely are contained within one institution, yet the free flow of information between components is vital. While different institutions may claim special responsibility for one or other components of the network (as subject specialists, you look for your own place within it), it is not intended to be viewed in that light. Rather than viewing the core interactive components of resource data base and crop production system models as the particular province of any one group, they should be seen as common property — as means, not ends. They are tools in the same sense a



**1.** Components of a system research strategy.

controlled environment facility, a chemical laboratory, or a field experiment is a tool. The basic currency is not so much the flow of matter and energy, but the flow of information.

The models should represent the current state of knowledge, organized hierarchically to cope with differences in level of organization and complexity. All models need not be complete, since partial models of particular processes can be useful. The object is to couple a particular model with a matching data base in order to make predictions about postulated changes in one or more variables that control the system's performance.

Sensitivity analysis can reveal important sources of potential variation and can permit a closer focus on those variables that make a major contribution to variation. This often raises fundamental questions about the model structure or functions, which leads directly to additional discipline-oriented research. At the same time, it can indicate points in the total production system that are amenable to more applied research and technology. The whole process is one of continuous repetition aimed at improving the model structure and function.

For large-scale evaluation of potential technologies, the models can be coupled with a climatic data base and standardized or actual terrain, soil, hydraulic, and management variables can be specified. Selected parameters from model runs can be used to classify zones in terms of similar responses to the new technology. This can aid in rationalizing and streamlining the next phase, field validation through carefully designed experiments. Given the prevailing research strategies, test sites would be centrally located in representative areas defined by the classification. An alternative systems-based strategy would use fewer but more closely monitored sites at nodal points in the classification, at or near major junction points of the classified zones.

Usually there will be considerable feedback between field validation and testing and model development. Only when this process has resulted in a robust model with realistic predictions will the next step — management prescription — be taken. Eventually this could take the form of specific prescriptions tailored for the specific combination of physical, social, and economic factors on a single farm. Elements of such a system already exist in some highly capital-intensive cropping systems in developed nations.

The process should not end with the application of new technology on farms. In addition to disseminating new technologies, the extension service also should systematically monitor production performance. Few technologies survive farmer adoption unchanged. Farmer innovation often is an important source of new technology. Monitoring farm management practices, productivity, social, and economic conditions also provides vital feedback to the resource data base as inputs that specify the current state of the system. This also can provide direct feedback to the model development and basic research components.

## Model development

Operational models of crop production systems can be developed only by close and constant interaction between:

- basic, process-oriented research
- conceptualization and programming
- directed experimentation
- data base development
- testing and validation
- integration with existing information systems

Conceptualization of such an integrated program is easier than its successful implementation because of institutional and disciplinary barriers between components. However, in structure at least, many international agricultural research institutes seem ideally suited for such development.

Any program of model development must answer a vital question at the outset: What is the purpose and the scale of operation of the models to be developed?

Evaluation and yield predictions are required at a range of levels of precision and accuracy. This can require a number of models. A hierarchy of models could be envisaged, ranging from those with the greatest precision and least generality to those with the greatest generality and least precision. In each case, the structural complexity of a model will be constrained by the current or potential availability of input data or both. It is easy to agree with Passioura (1973) that models should be simple; be readily testable, both in terms of predicting final yield and in the intermediate calculation steps; and be capable of improvement after testing.

Initially, model development may be confined to a restricted set of functions that relate to major, known factors influencing crop production in the particular environment under study. Such models can be useful, but they are location specific, season specific, and crop specific. Development of more general models capable of operating in a wide range of conditions demands that each model be based on a developmental template. All processes are functions of crop time, physiological time, or phenological time, rather than of calendar time. The ability to extrapolate a model to other sites, seasons, cultivars, and management conditions depends on the quality of the phenological simulation. Phenological data from field experiments are a vital requirement.

The most significant internal subroutine in crop models is water balance. It is difficult to envisage a general crop production model that is not firmly based on a water balance routine. Even in irrigated systems, water deficits are not unknown. And, while the crop evapotranspiration term may not be of particular interest, such terms as lateral flow, deep drainage, groundwater table movements in the water balance will be. For dryland and rainfed wetland crops and cropping patterns, the availability of water is of major significance and incorporation of a water balance is essential.

To come to terms with the problem of crop improvement for drought resistance, we must first be able to characterize the whole array of possible responses to water deficits by crops in diverse environments. O'Toole and Chang (1979) conclude that any attempt to improve the drought resistance of rice must be based on a thorough knowledge of and appreciation for the locational and temporal specificity that characterizes a particular drought condition. They also conclude that more research on soil-plant-water relationships of the rice crop should be encouraged.

If there is a single, unifying concept in crop improvement for drought resistance, it is the soil-plant atmosphere continuum. A water-balance model is a concrete expression of that concept. It can provide a flexible framework for specialized research into various terms within the water-balance equation. Each term can be modified and manipulated. Each has particular significance for crop physiologists, agronomists, hydrologists, civil engineers, and other specialists.

The soil-plant-atmosphere continuum can provide a vehicle for analysis of spatial and temporal patterns in water availability to crops, for exploration of alternate management strategies that seek to minimize water deficits at critical periods in the crop cycle, for optimizing the location and design of field experiments, and for analyzing the alternatives available (including that of modified physiology through breeding) to minimize water stress in the crop system.

Agricultural drought can result from any combination of the terms in the water-balance equation that produces sufficient internal water stress in plants to limit productivity. Major effects include delayed, impeded, or totally inhibited germination and establishment; reduced tillering or branching; reduced plant growth rates; reduced quantity and quality of harvested product, and increased predisposition to pest and pathogen attack. Water-stress effects can be particularly severe if they occur at a particularly sensitive or critical stage of crop development. Salter and Goode (1967) identify known critical periods for a wide range of crop species.

Plant-water relationships are vital to understanding crop growth and development. Begg and Turner (1976) point out that all plants undergoing transpiration can experience some degree of daily water deficit at any given time. Stress is viewed as an excess deficit that develops more slowly over a period of days and that significantly reduces plant growth and productivity. McMichael (1980) shows evidence for intraspecific as well as interspecific differences in the ability of plants to cope with severe plant water stress and to maintain plant turgor and photosynthetic capacity. Chang et a1 (1979) leave no doubt that such variation exists in both dryland and wetland rice cultivars. They also recognize the need to characterize or diagnose the location-specific parameters of drought.

## Data base development

Adoption of systems research strategies and their application demand that models have matching data bases. A particular model will identify the minimum data set necessary for its successful implementation. In the research and development phase of model building and testing, it is necessary to have matching input data that span a wide range of environmental conditions. Specific experiments may be devised to acquire these minimum data in the shortest time possible with the least expenditure, but most model building and testing have had to rely on a fortuitous assembly of data from a range of sources.

Very few experiments meet the need for balanced crop, soil, weather, and management data. In developing and implementing any system of standardized data collection, it is essential that all disciplines involved be a party to the identification of the data set. While recognizing the different objectives of field experiments and the different scales of facilities available, it is possible to erect a hierarchy of minimum data sets with increasing range, precision, accuracy, and frequency of measurement and observation. At all levels, the emphasis remains on maintaining a balanced monitoring of the whole crop system (Nix 1979). A proposed three-level system might have:

*Field trials remote from laboratory facilities.* Rainfall data are measured at the site, with regional values for temperature, evaporation, and solar radiation available. In a complex terrain, interpolation routines may be used to estimate these data. Weekly time step Soil water content at or near seeding and at harvest and, in a paddy situation, observations of water level are recorded. Crop data are limited to dates of emergence, flowering, and harvest. Floral initiation and physiological maturity data are desirable but not essential. Components of yield are recorded. These data are just sufficient to calculate semi-empirical indices and to verify simpler models.

*Field experiments conducted at or near regional research centers.* More frequent and more comprehensive soil, crop, weather, and management measurements and observations permit the use of model functions with a more explicit physiological or process basis. While retaining simplicity, this provides a sounder basis for the analysis of major environmental constraints and permits measurement of development and yield. Angus and Zandstra (1979) describe a simple model of the growth and development of wetland rainfed rice that accounts for the effects of radiation, temperature, water supply, and nitrogen nutrition. Angus (1979) details the minimum data set needed to implement this model. Despite its simplicity and acknowledged deficiencies, this model could provide the basis for regional evaluations of postulated cropping patterns and aid materially in reducing the complexity of agricultural drought to manageable proportions. Daily or weekly time step.

*Major data-logging and data-processing facilities available.* Greatly increased frequency of sampling and monitoring of the soil-plant-atmosphere continuum permits a more detailed analysis of component subsystems and processes. This is the level at which many subject specialists will want to operate. Sampling and monitoring frequency may be hourly or less for parts of the day for some processes, but the basic model could integrate and update on a daily basis. At this level, the consequences of different root geometry, osmotic regulation, or stomatal response mechanisms could be examined. The crop model used as the basic vehicle would incorporate explicit representation of major processes in the system.

The emphasis throughout must be on an absolute minimum data set at each level of complexity. Standardized data collection sheets and crop phenological charts would ensure comparability of data and common access to developed models and would permit more comprehensive analyses of crop experiments at widely spaced locations. Such a development would benefit the development and transfer of technology. It is essential for the systems approach.

Climate and weather data occupy a primary position in the hierarchy of data acquisition, processing, and analysis. In the past, the most attention has been directed toward the soil component of the physical data base. Efforts have been mounted to map and describe soil patterns, but attention to mapping and describing climate and weather patterns has been minimal. Part of the difficulty has been the dispersed sources of such data. Sophisticated mathematical techniques now becoming available hold promise of an ability to predict weekly mean values of primary climate elements at any point, given limited positional information. With such a potential, it is likely that soil data will once more become limiting. Before running any water balance simulations, we will require specified terrain and soil hydrological data.

The historical climate record is a priceless asset for any nation, but few have given it the attention it deserves. In the first instance, it is essential for agricultural applications that research and extension workers have ready access to an integrated data file with at least weekly means of the primary climatic elements across the widest possible network. While long-term weekly mean data are acceptable for the more stable elements such as solar radiation, temperature, and potential evaporation, a historical sequence of actual weekly rainfall totals is desirable. We have developed such files for over 1,000 stations in Australia and are currently developing a global file that ultimately will document some 10,000 stations. An example of such an integrated climatic data file for Southeast Asia is that of Angus and Manalo (1979) for the Philippines.

Coupling appropriate models with such integrated data files can yield useful insights into the relative importance of drought for differing cropping patterns and across a wide range of sites and seasons. This approach was adopted in an analysis of the Australian environment and its influence on wheat yield and quality (Nix 1975) and in a study of climatic factors and wetland rainfed rice cropping in the Philippines (Angus 1979). Such interactive systems of model and matching data base can play an important role in:

- locational analysis (which crops grow best, where);
- development, testing, and application of new and modified management strategies and tactics;
- development of optimum networks for research and other activities; and
- development of an understanding of complex crop systems and their component processes.

The ultimate utility of such a system depends on its availability to users. It should not be regarded as the particular province of yet another group of specialists, but as a common utility. The development of small, inexpensive, programmable calculators should soon make this a reality.

## CONCLUSIONS

Drought in general and agricultural drought in particular is a complex phenomenon, involving dynamic interchanges within the soil-plant-atmosphere continuum. Fitting a crop production system to a particular environment to minimize significant water stress at critical periods requires an understanding of site, soil, crop, weather, and management factors and their interactions. Analysis of this process of adaptation and manipulation demands, at the very least, a water balance modeling approach, ideally one that includes growth, development, and yield of the crop as well. While such an approach will not solve the specific problems of screening, selecting, and breeding for drought resistance, it can aid in asking the right questions in the first place.

## REFERENCES CITED

Angus, J. F. 1979. Minimum data requirements in rice experiments. Pages 95-99 *in* World Meteorological Organization and the International Rice Research Institute. Proceedings of a symposium on the agrometeorology of the rice crop. International Rice Research Institute, Los Baños, Philippines.

Angus, J. F., and H. G. Zandstra. 1979. Climatic factors and the modeling of rice growth and yield. Pages 189-199 *in* World Meteorological Organization and International Rice Research Institute. Proceedings of a symposium on the agrometeorology of the rice crop. International Rice Research Institute, Los Baños, Philippines.

Angus, J. F., and E. B. Manalo. 1979. Weather and climate data for Philippine rice research. IRRI Res. Pap. Ser. 41. 14 p.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. *In* N. C. Brady, ed. Advances in agronomy. Academic Press, New York.

Chang, T. T., B. Somrith, and J. C. O'Toole. 1979. Potential for improving drought resistance in rainfed lowland rice. Pages 149-164 *in* International Rice Research Institute. Rainfed lowland rice: selected papers from the 1978 international rice research conference. Los Baños, Philippines.

Dale, R. F. 1964. Weather effects on experimental plot corn yields: climatology of selected favorable and unfavorable conditions. Unpublished Ph D thesis, Iowa State University, Ames, Iowa.

Dale, R. F., and R. H. Shaw. 1965. The climatology of soil moisture, atmospheric demand and resulting moisture stress days for corn at Ames, Iowa. J. Appl. Meteorol. 4:661-669.

De Martonne, E. 1965. L'indice d'aridité. Bull. Assoc. Geogr. Fr. 9.

Denmead, O. T., and R. H. Shaw. 1962. Availability of soil water to plants as affected by soil moisture content and meteorological conditions. Agron. J. 45:385-390.

Hounam, C. E. 1971. Assessment of drought. Report of WMO Working Group (Part A, Part B). Bureau of Meteorology, Melbourne.

Hounam, C. E. 1976. Drought. Australian UNESCO Seminar A.G.P.S., Canberra.

Kaltenhauser, J. 1972. Global summary of human response to natural hazards: drought. 22nd International Geographical Congress, Calgary, Canada.

Koppen, W. 1931. Die klimate der Erde. Walter de Gruyter, Berlin.

Lang, R. 1915. Versuch einer exakten klassifikation der Boden in klimatischer and geologischer hinsicht. Int. Mitt. Bodenkd. 5.

McMichael, B. L. 1980. Water stress adaptation. *In* J. D. Hesketh and J. W. Jones, eds. Predicting photosynthesis for ecosystem models. CRC Press, Boca Baton.

Nix, H. A. 1968. The assessment of biological productivity. *In* G. A. Stewart, ed. Land evaluation. McMillan, Melbourne.

Nix, H. A. 1975. The Australian environment and its influence on grain yield and quality. *In* A. Lazenby and E. M. Matheson, eds. Australian field crops: I. Wheat and other temperate cereals. Angus and Robertson, Sydney.

Nix, H. A. 1976. Climate and crop productivity in Australia. Pages 495-500 *in* International Rice Research Institute. Proceedings of the symposium on climate and rice. Los Baños, Philippines.

Nix, H. A. 1979. Agroclimatic analogues in transfer of technology. *In* International Crops Research Institute for Semi-Arid Tropics. International symposium on development and transfer of technology for rainfed agriculture and the SAT farmer. Hyderabad, India.

O'Toole, J. C., and T. T. Chang. 1979. Drought resistance in cereals. Rice: a case study. *In* Stress physiology in crop plants. John Wiley and Sons, New York.

Passioura, J. P. 1973. Sense and nonsense in crop simulation. J. Aust. Inst. Sci. 39:181-183.

Penman, H. L. 1948. Natural evaporation from open water, bare soil and grass. Proc. R. Soc. London. Ser. A, 193:120-149.

Salter, P. J., and J. E. Goode. 1967. Crop responses to water at different stages of growth. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geogr. Rev. 38:55-94.

# VARIABILITY OF RICE PRODUCTION IN TROPICAL ASIA

H. FUKUI

Variability is an inherent characteristic of agricultural production. Rice production in tropical Asia is no exception. But the degree of variability is not the same throughout the region. Production, stable in some areas, varies violently in others. This paper shows the degree of year-to-year rice production variability in different areas, discusses the causes of such differences in variability, attempts to identify an area within which bumper and lean harvests tend to occur in the same year, and gives a future perspective on variability of rice production.

## STATISTICAL DATA AND COMPUTATIONAL PROCEDURES

### Statistical materials

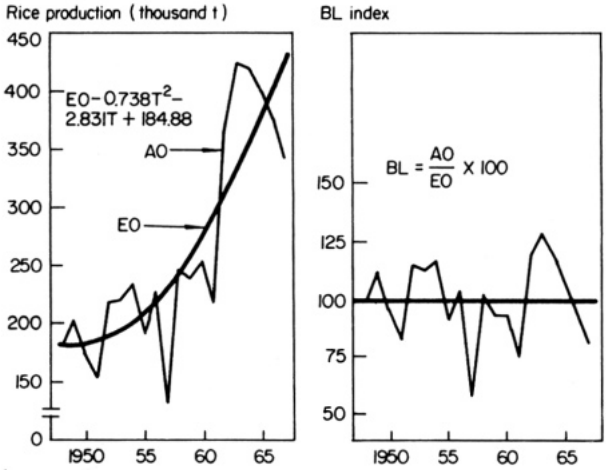
To statistically express variability or stability of production in a district requires statistical data of a long time span. If the purpose of a variability analysis is to assess the relationship between production variability and natural phenomena, it is best to examine a period during which no dramatic socioeconomic disturbance occurred. This study took these aspects into account and, restricted by availability of consistent time-series data, used the periods summarized in Table 1. Statistics on rice area and production were collected for six countries — Sri Lanka, India, Bangladesh, Burma, Thailand, and Philippines.

---

The Center for Southeast Asian Studies, Kyoto University, 46 Shimoadachi Yoshida, Sakyo-ku, Kyoto, Japan. Computation work, S. Yasuda; graphics, S. Hayakawa and A. Yamamoto.

**Table 1. Summary of rice production statistics.**

| Country | Units (no.) | | Year (no.) | | | Remarks |
|---|---|---|---|---|---|---|
| Sri Lanka | 20 | districts | 1960-61 | 1971-72 | 12 | The production of the dry season crop in the year of (*n/n* + 1) and that of the wet season crop in the year of (*n*) were summed, making the total production in the year of (*n*). |
| India | 103 | districts | 1948-49 | 1967-68 | 20 | The year of (*n/n* + 1) was read as the year of (*n*). |
| Bangladesh | 17 | districts | 194748 | 1971-72 | 25 | |
| Burma | 29 | districts | 1949-50 | 1966-67 | 18 | |
| Thailand | 69 | changwats | 1948 | 1968 | 21 | |
| Philippines | 9 | regions | 1947-48 | 1974-75 | 28 | |

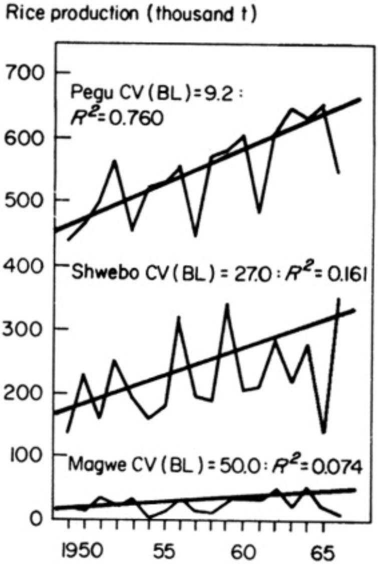


**1.** The computation procedure of bumper-lean index (BL) for W. Dinajpur, India.

## Computational procedures

To determine a bumper-lean index (BL), a quadratic equation was fitted to the actual production (AO). The curve obtained showed the trend of production over the study period (Fig. 1). The trend line indicates the expected production (EO) without a year-to-year variation.

An AO-EO ratio was computed for each year and multiplied by 100 to give the BL. A set of BL data was obtained for each set of original production data. The mean BL for a district was 100 (Fig. 1). The standard deviation gave a coefficient of variation of BL = CV (BL). The extent of relative variability or stability of rice production was compared in terms of CV(BL).

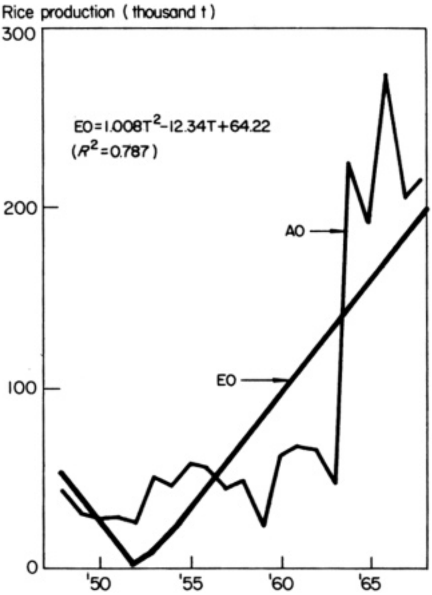


**2.** Relation among AO, EO, and CV (BL) at 3 districts in Burma.

## Computational procedure problems

A quadratic equation may not necessarily be adequate. An illustration is the AO and the trend line (EO) for three districts in Burma (Fig. 2). The trend lines are nearly straight, as is the case for most districts in countries for which the quadratic fit appears adequate. (Adequacy of the trend line cannot be judged by $R^2$, which is itself an indicator of variability.) However, the quadratic equation is questionable in a changwat in Thailand (Fig. 3), where production jumped from less than 50,000 t/ha to 200,000 t/ha in 1963-64. But such a case is rare.

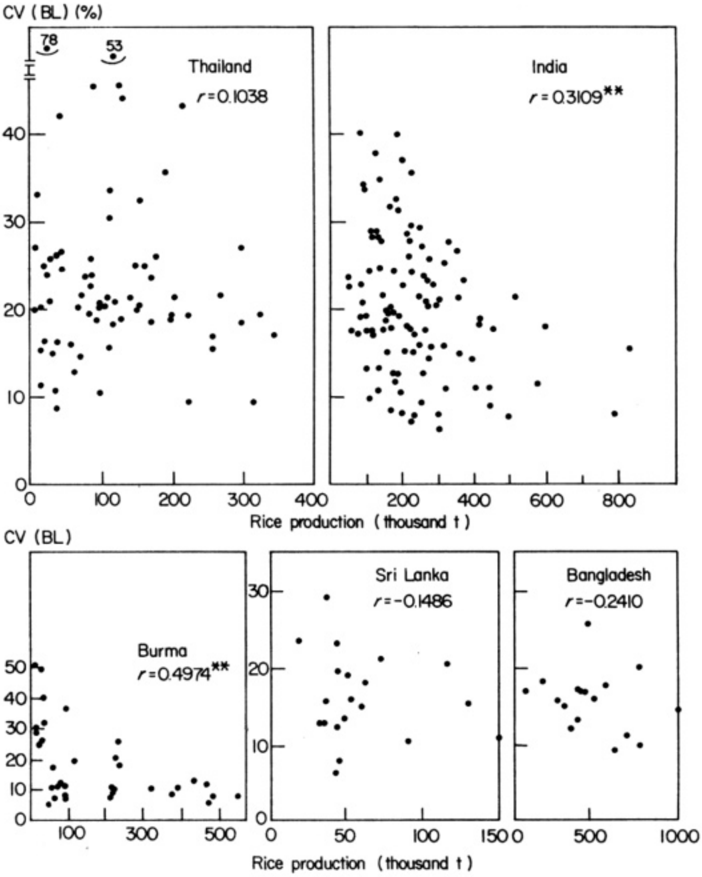
Deviation from EO is not expressed in tons of rice. In Pegu District, Burma, production in the lean years was nearly 100,000 t/ha below normal. Such lean years occurred 3-4 times during 1949-66. The CV(BL) for this district was 9.2%. The two other districts in Figure 2 had much smaller rice productions than Pegu. Deviation from the trend line of a few tens of thousand t/ha resulted in a large CV(BL).



**3.** Example of inadequate fitting of trend line to AO. Thailand.

A harvest may be good in one part of a district and poor in another. This within-district compensation will result in an apparent stability in the district as a whole. Since it may occur more often in a large district than in a small one, CV(BL) values among districts of similar size should be compared.

The relation between the size of districts and CV(BL) is shown in Figure 4. The size of districts is expressed in the means of rice production over the period studied. The correlation between means tended to be significantly negative in some countries. Large districts rarely had great variability. Production also was stable in some small districts; however, it is true that the great variability was mainly in the small districts.



**4.** Correlation between CV (BL) and size of district (in terms of rice production).

Small rice production districts tended to be in marginal areas. Large ones were in a center of the rice bowl. Therefore the within-district compensation should not be regarded as the only cause of the negative correlation between CV(BL) and the size of district.

## Determinants of rice production variability

In this study, the trend and the year-to-year variability were separated to demonstrate yearly variability and its geographical pattern and to discuss its possible causes. Only those factors that fluctuate yearly, thus affecting the year-to-year variability of production, are discussed.

Changes in production are caused by changes in area and in yield per area unit. Various natural and socioeconomic factors affect production through their influence on changes in area and in yield.

Generally, the factors determining production can be divided into two groups.

One group consists of natural factors, including soil, climate (the means of various climatic indicators), topography, and hydrology. The other group consists of social and economic factors, including capital, labor, technology, the marketing system, and the prices of inputs and output. In group 2, some factors vary significantly from year to year, others change gradually during a long period. Factors in group 1 are more major determinants of yearly variability of production. Factors in group 2 are determinants of the trend of production.

Yearly variability of area planted to rice could be caused by changes in cropping patterns for socioeconomic reasons, as well as by drought and flood before planting. Socioeconomic causes may be likely only where the land is suitable for crops other than rice and where rice production is so commercialized that farmers react to yearly changes in the economic situation. Yearly fluctuations of yield per unit area might be caused by fluctuations of the relative prices of produce and inputs. Prices may be determined under free market conditions or affected by a public agency through such measures as a price support and subsidy scheme.

Perhaps the most important factor affecting the yearly variability of rice yield is the year-to-year variability of climate, especially rainfall. Where irrigation is perfect, yield is not affected by rainfall shortage. But it is affected by solar radiation. Since rainfall and solar radiation are negatively correlated, the correlation coefficient between yield and rainfall becomes negative, as in Japan where all the rice fields are adequately irrigated.

Climate may indirectly affect the yield fluctuation by affecting biological damage to rice plants. There could be other factors and other ways of affecting yearly variability.

## GEOGRAPHICAL PATTERN OF YEAR-TO-YEAR VARIABILITY

Variability in CV(BL) for each district is summarized by country in Table 2. Production in Burma appears to be the most stable, followed by that in Bangladesh. Sri Lanka and the Philippines have intermediate production stability. The variability range in India is wide. Variability is small in a substantial number of districts but at the same time rice is produced in unstable conditions in other districts. This reflects the extent of India’s rice-growing regions, which cover diverse natural conditions. Among the six countries, Thailand has the greatest variability. Burma and Thailand, the most stable and the most unstable, are rice-exporting countries.

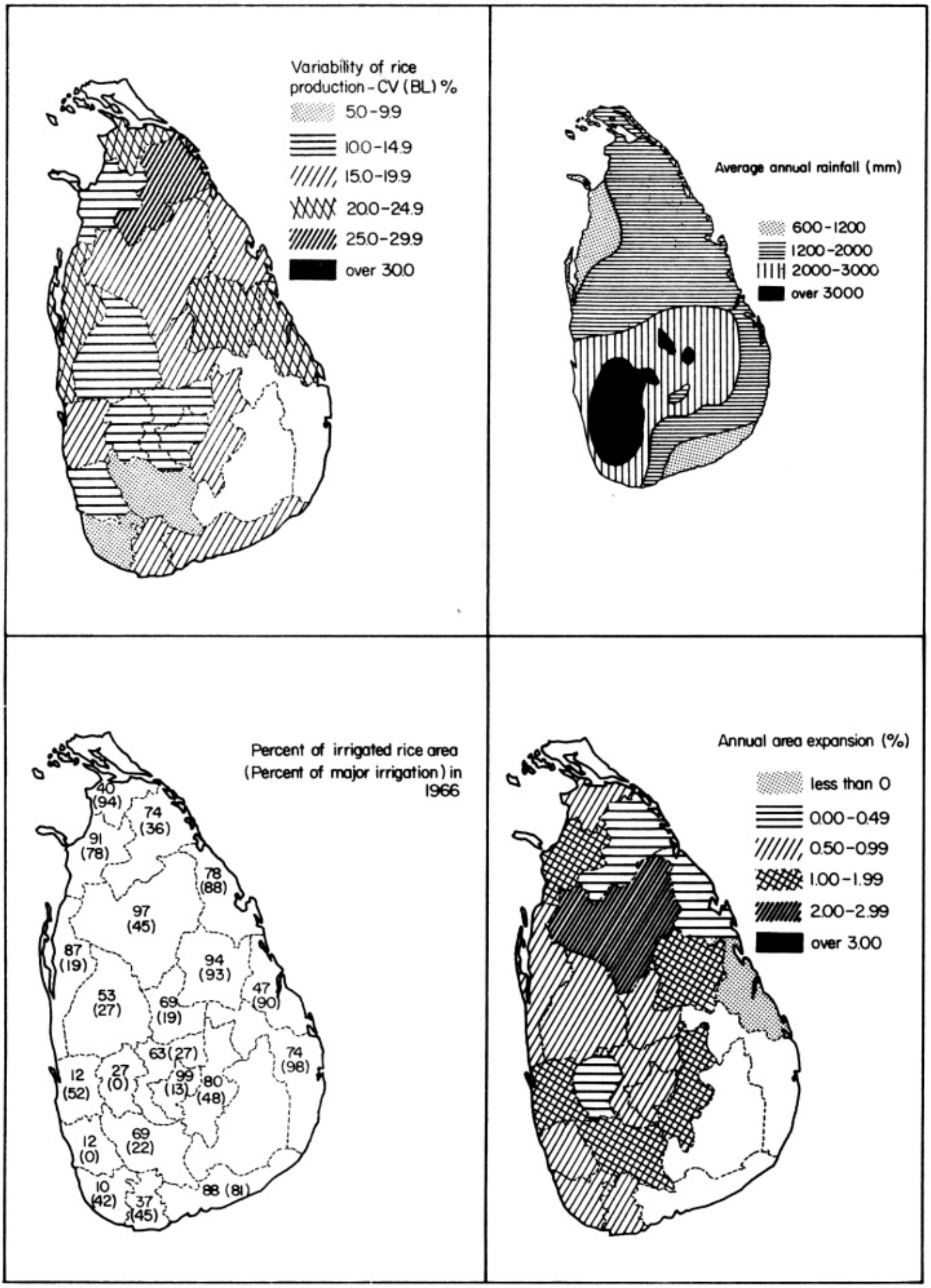
### Sri Lanka

Production is more stable in the southern and western portions than in the northern and eastern areas. This geographical pattern of variability roughly coincides with rainfall. In the districts receiving more than 2,000 mm annual rainfall, CV(BL) is less than 15%. Two districts with less than 10% variability are situated within the zone having over 3,000 mm annual rainfall. Although annual rainfall might explain some of the production variability, it could not explain all of it. CV(BL) ranges from 10-15% to 25-30% within the dry zone. Such difference in variability within the dry zone could be related partly to the percentage of irrigated

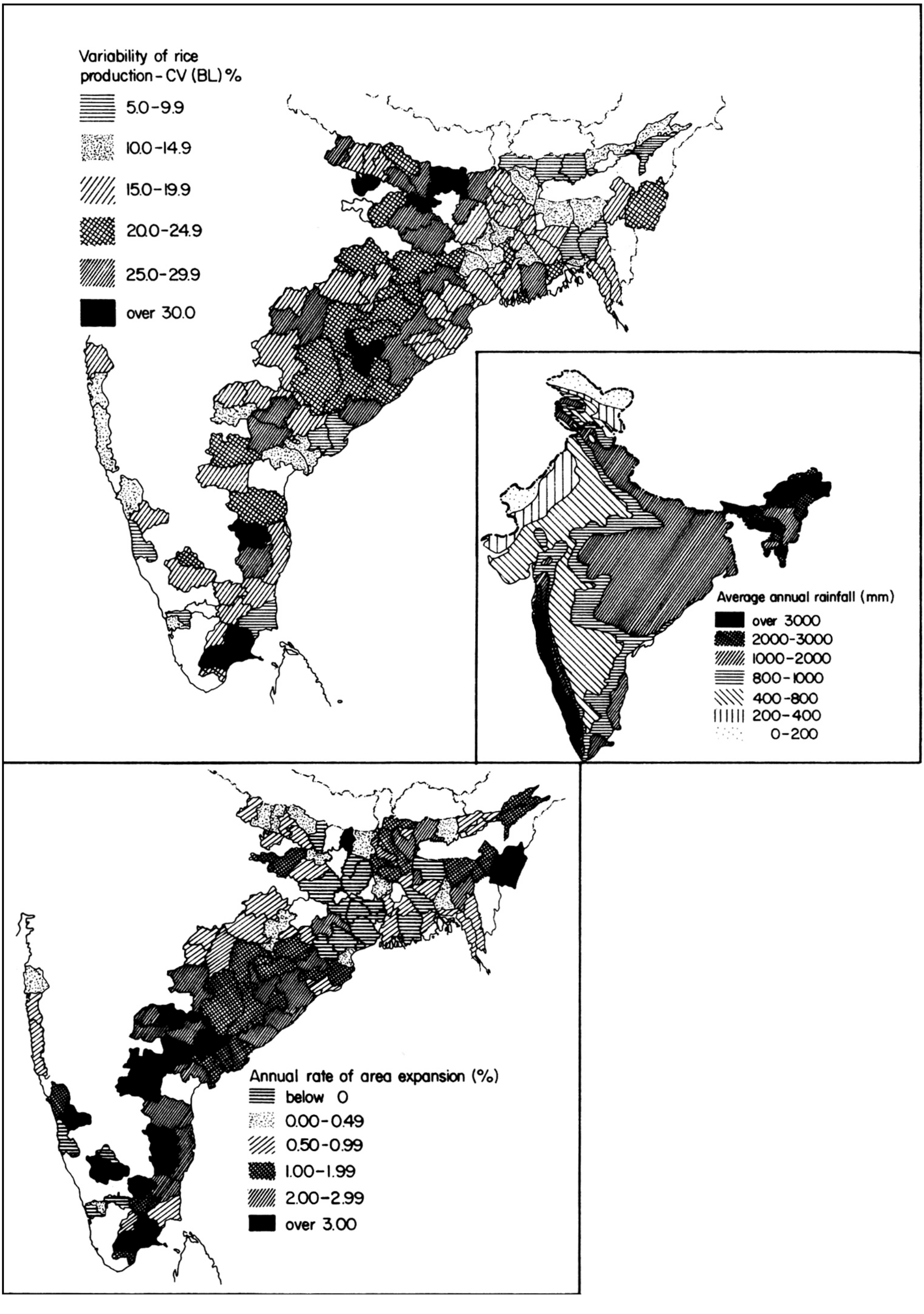
**Table 2. Summary of variability in rice production in 6 countries.**

| BL[a] (%) | | Sri Lanka | India | Bangladesh | Burma | Thailand | Philippines | Total |
|---|---|---|---|---|---|---|---|---|
| 5.0- 9.9 | Districts (no.) | 2 | 10 | 1 | 9 | 3 | 1 | 26 |
| | Production | 88 | 3.363 | 660 | 2,359 | 567 | 466 | 7,503 |
| | (%) | (7.3) | (14.2) | (7.7) | (39.6) | (7.9) | (12.2) | (14.6) |
| 10.0-14.9 | Districts (no.) | 6 | 15 | 5 | 11 | 5 | 2 | 44 |
| | Production | 401 | 3,789 | 3,369 | 2,512 | 267 | 1,492 | 11,830 |
| | (%) | (33.2) | (16.0) | (39.5) | (42.1) | (3.3) | (38.9) | (23.1) |
| 15.0-19.9 | Districts (no.) | 7 | 30 | 9 | 3 | 19 | 3 | 71 |
| | Production | 433 | 7.111 | 3,239 | 392 | 2.91 0 | 1,135 | 15,220 |
| | (%) | (35.9) | (30.0) | (38.0) | (6.6) | (36.1) | (29.7) | (29.7) |
| 20.0-24.5 | Districts (no.) | 4 | 22 | 1 | 1 | 21 | 2 | 51 |
| | Production | 249 | 4,764 | 786 | 222 | 2,052 | 524 | 8,597 |
| | (%) | (20.6) | (20.1) | (9.2) | (3.7) | (25.5) | (13.7) | (16.8) |
| 25.0-29.9 | Districts (no.) | 1 | 15 | 1 | 5 | 10 | 1 | 33 |
| | Production | 36 | 3.211 | 473 | 293 | 969 | 216 | 5,198 |
| | (%) | (3.0) | (13.5) | (5.5) | (4.9) | (12.0) | (5.6) | (10.1) |
| 30.0 | Districts (no.) | 0 | 10 | 0 | 5 | 12 | 0 | 27 |
| | Production | 0 | 1,490 | 0 | 186 | 1,291 | 0 | 2,967 |
| | (%) | (0.0) | (6.3) | (0.0) | (3.1) | (16.0) | (0.0) | (5.8) |
| Total | Districts (no.) | 20 | 102 | 17 | 34 | 70 | 9 | 252 |
| | Production | 1,207 | 23,728 | 8,527 | 5,964 | 8,056 | 3,833 | 51,315 |
| | (%) | (100) | (100) | (100) | (100) | (100) | (100) | (100) |

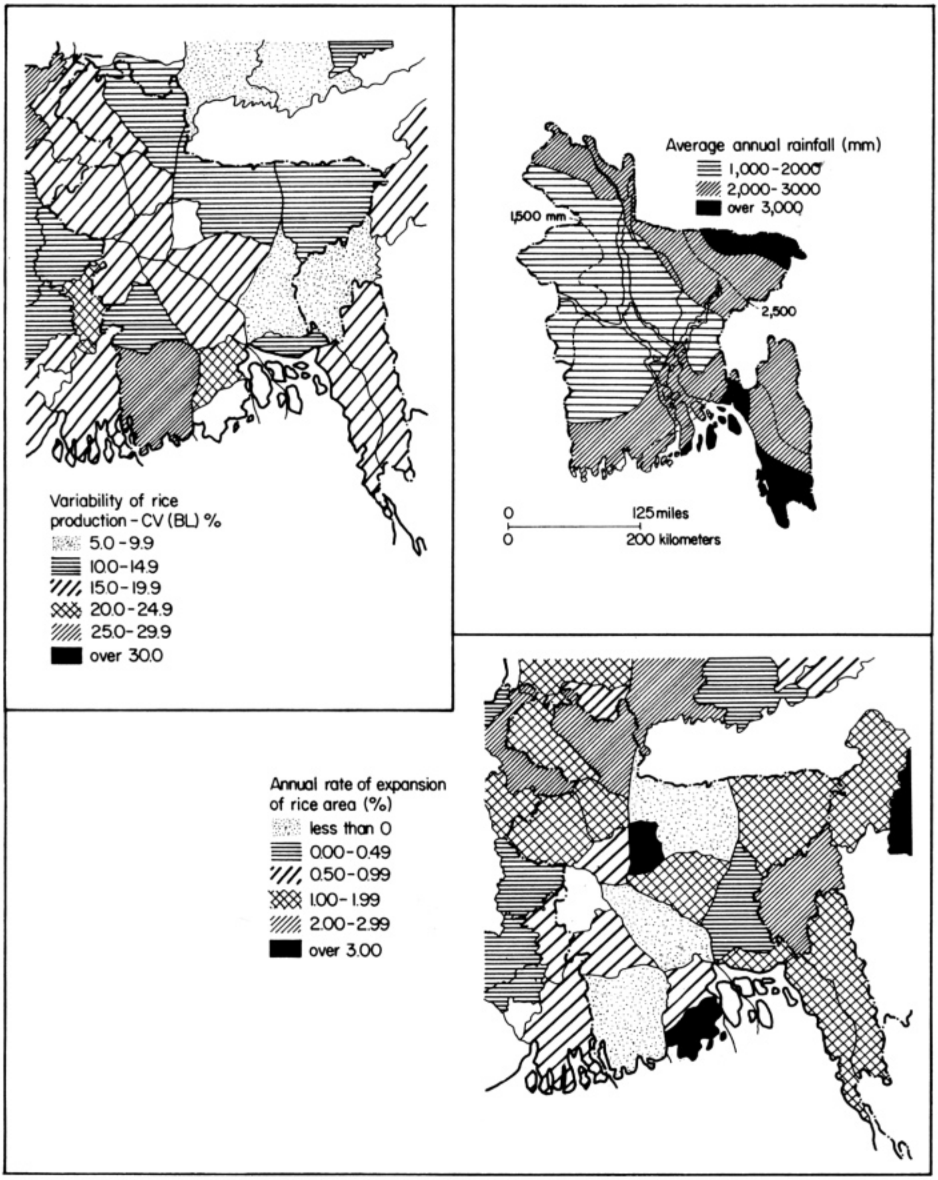
[a] Bumper - lean index.



**5.** Variability of rice production, annual rainfall, irrigated area, and rate of expansion of rice area in Sri Lanka.

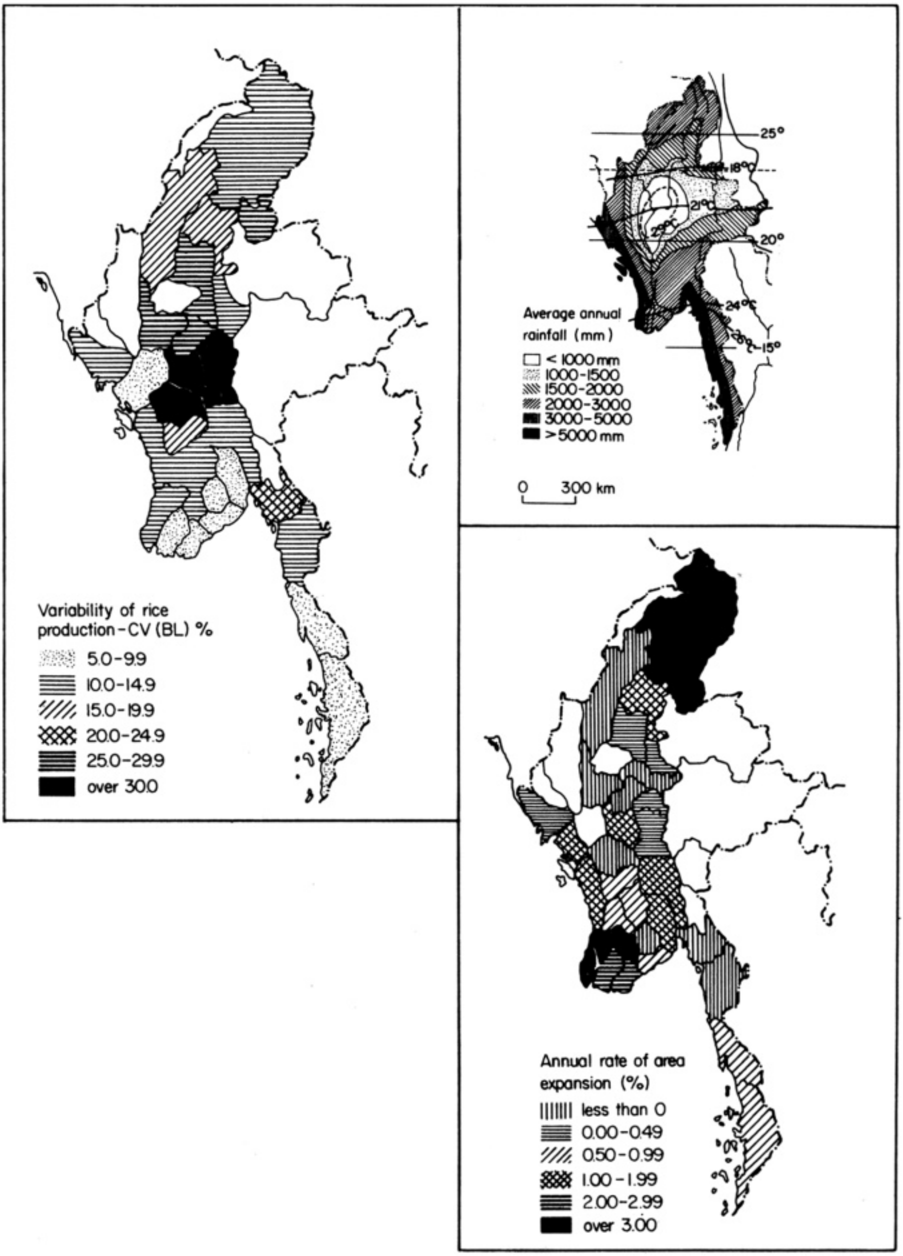


**6.** Variability of rice production, annual rainfall, and rate of expansion of rice area in India.



**7.** Variability of rice production, annual rainfall, and rate of expansion of rice area in Bangladesh.

rice area and the quality of the irrigation systems. As seen in the lower left of Figure 5, the districts of great variability of production are characterized by relatively low percentage of either irrigated rice area or major irrigation. It should also be noted that the stable production of the high-rainfall districts appears to be due primarily to high rainfall itself. In these districts, only small portions of rice areas are irrigated.



**8.** Variability of rice production, annual rainfall, and rate of expansion of rice area in Burma.

## India

In four areas in India production is stable and the CV(BL) is less than 15% (Fig. 6). Two areas have over 2,000 mm annual rainfall. These are coastal areas facing the Arabian Sea and the Assam valley. The two other areas of stable production receive an annual rainfall of less than 2,000 mm. They are in the eastern coastal area region and in West Bengal, both located in large alluvial plains developed along the Ganges, Mahanadi, Godavari, Krishna, and Couveri Rivers.

The districts where rice production is most unstable are found mainly in Bihar and the Eastern Ghats. The annual rainfall in these districts ranges from 1,000 to 2,000 mm. However, although the annual rainfall is less than 1,000 mm in the southern part of the Eastern Ghats, production is not necessarily less stable than in the northern half of the Eastern Ghats. The reason appears to be the higher percentage of irrigated rice area in the drier zone.

## Bangladesh

In the area where annual rainfall exceeds 2,000 mm, production is stable and CV(BL) is less than 15% (Fig. 7). However, a few coastal districts are exceptions. The production is unstable regardless of the high rainfall, probably because of flood damage by high tide.

Where annual rainfall is less than 2,000 mm, production is less stable. Yet, CV(BL) is not below 20% because the whole country is within the two gigantic alluvial plains of the Ganges and Brahmaputra.

## Burma

Production is stable, i.e. CV(BL) is less than 15%, where annual rainfall is over 2,000 mm. When annual rainfall is less than 2,000 mm, CV(BL) is over 25% and production is unstable (Fig. 8).

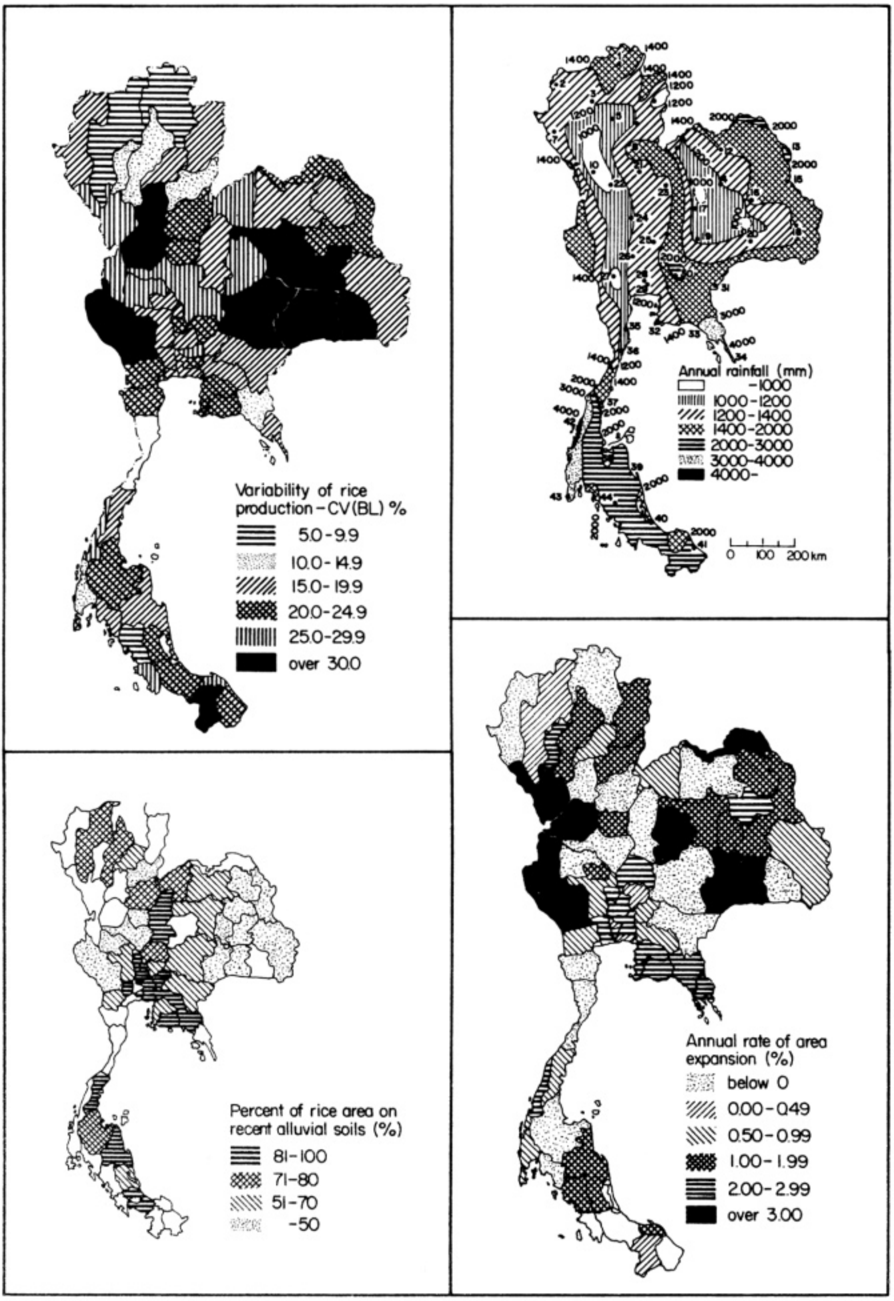
In the dry zone, production is stable in three districts — Mandalay, Kyaukse, and Minbu. These three districts are famous for well-developed irrigation systems hundreds of years old. All three districts are close to the vast mountainous area, the Shan Plateau, and the Arakan mountains. Run-of-the-river irrigation can be easily installed. In the districts situated in the middle of the dry zone, the only source of water is the scanty rain and local reservoirs or tank irrigation.

## Thailand

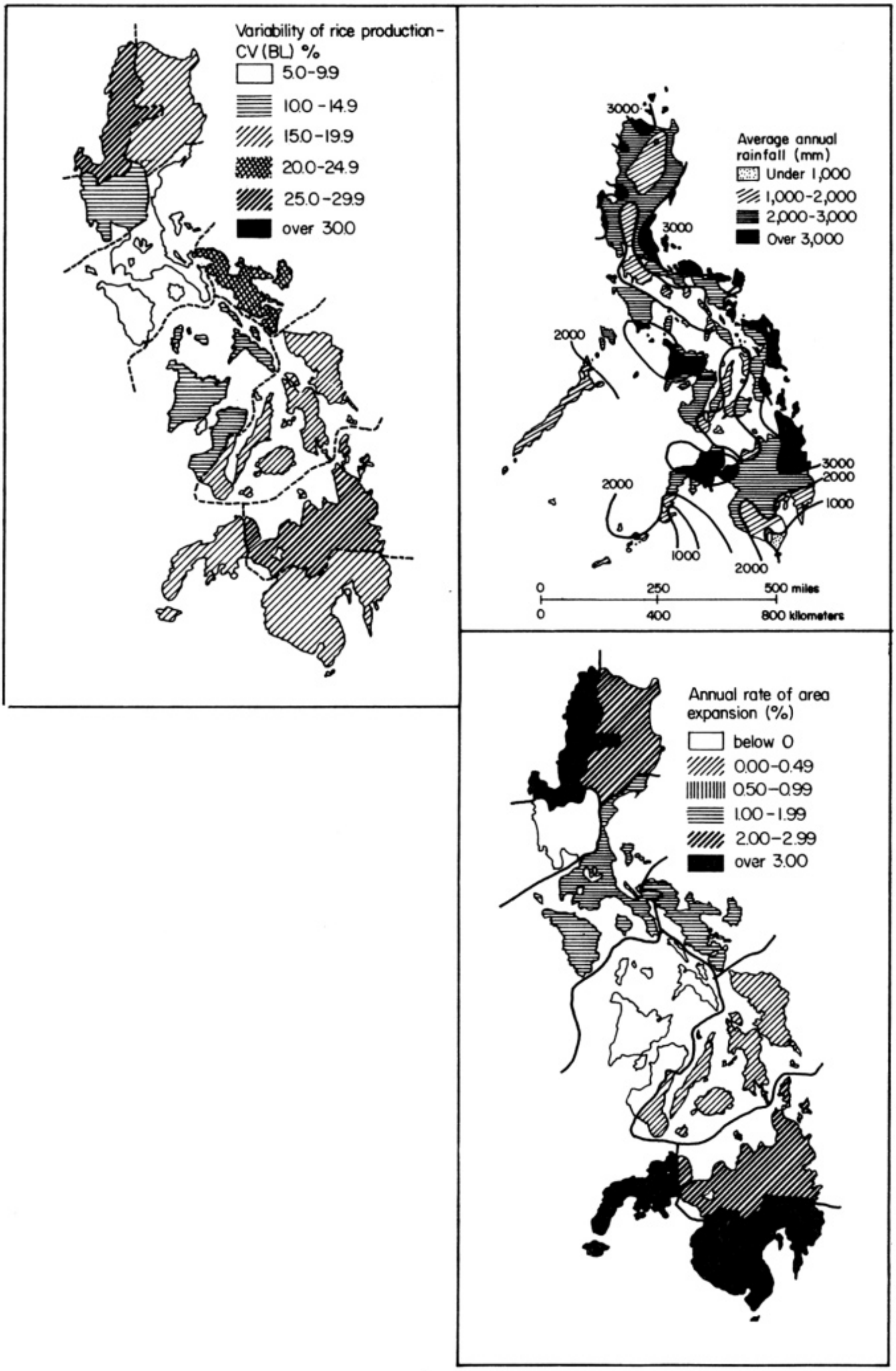
Northeastern Thailand is famous as a drought-prone area. However, not all parts suffer from chronic drought (Fig. 9). The most unstable production is restricted to seven changwats in the southwestern part. The changwats on the northern and western periphery of the Central Plain also have unstable production. The CV(BL) exceeds 25% and, in many cases, 30%. The geographical pattern of these areas of high instability corresponds to that of an area of less than 1,400 mm annual rainfall.

Changwats where production is stable — CV(BL) values of less than 15% — are limited. Stability in some changwats in the southern and southeastern parts can be explained by the high (more than 2,000 mm) annual rainfall. However, stability in the northern districts is not related to high rainfall but is attributable to irrigation systems in the intermountain basins.

The rice bowl of Thailand is the alluvial plain of the Chao Phraya River. Rice production there is not particularly stable — CV(BL) values between 15 and 25% — probably because annual rainfall is less than 1,400 mm. Production in the



**9.** Variability of rice production, annual rainfall, landform and rate of expansion of rice area in Thailand.



**10.** Variability of rice production, annual rainfall, and rate of expansion of rice area in the Philippines.

northeastern part of the northeast is as stable as in the Central Plain, but the annual rainfall exceeds 1,400 mm.

In the peninsular part of Thailand, variability in production differs among changwats. Such a patchwork pattern may be due to diverse climatic conditions within short distances.

## Philippines

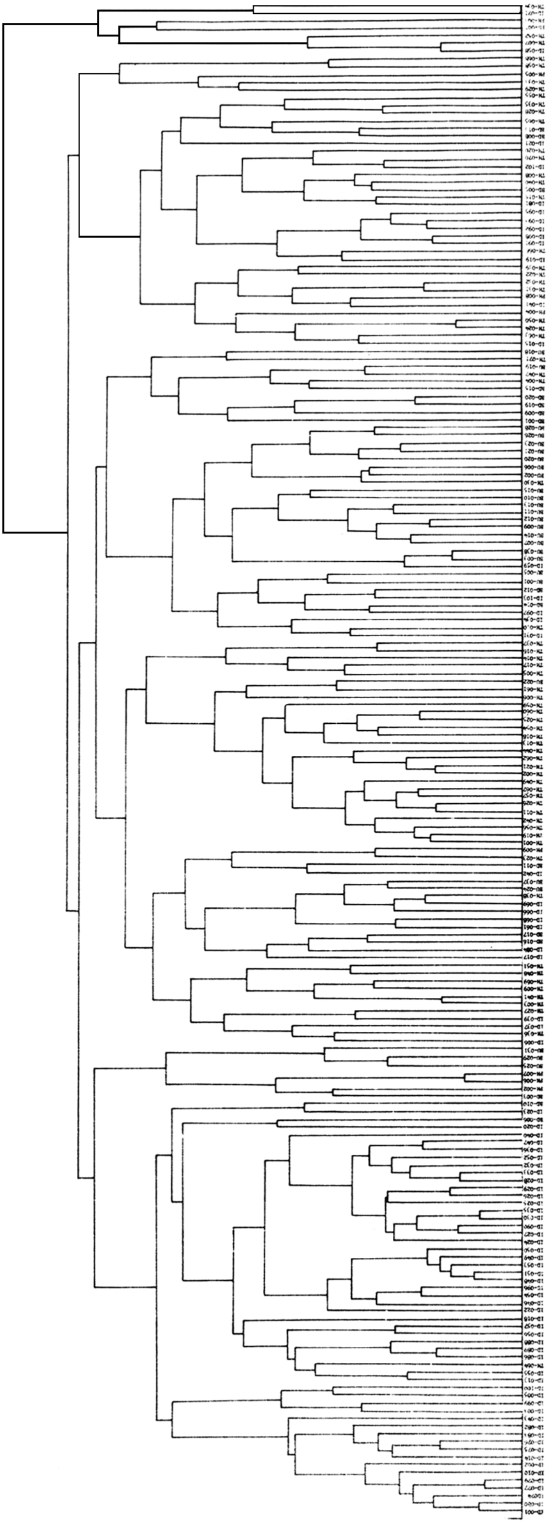
In the Philippines production tends to be more stable in the middle than in the extreme north and south, and in the west than in the east (Fig. 10). Such geographical patterns of production variability could hardly be related to rainfall distribution. The rainfall distribution pattern is so complex that the statistical unit used in this study appears to be too large to relate to climatic conditions.

## Conclusions

- Where annual rainfall exceeds 2,000 mm, variability in rice production is generally stable — CV(BL) below 15%. This low variability is not due to irrigation. The percentage of irrigated area is low in the high rainfall zone, which includes the wet zone of Sri Lanka, the western coast and the Assam Valley of India, the northeastern part of Bangladesh, most of Lower Burma, and the southeastern part of Thailand. An exception is the coastal area of Bangladesh, where production is probably unstable because of flood damage.
- Rice production in the huge alluvial plains is more stable than in other landforms under the same rainfall conditions. CV(BL) is less than 15% in the alluvial plains of the Ganges, Krishna, Godavar, and Couveri Rivers, where the annual rainfall is less than 2,000 mm and in some places less than 1,000 mm. In other alluvial plains, CV(BL) is not as low as in the Indian plains, although rainfall is not less than in India. In the alluvial plains of Thailand, CV(BL) is between 15 to 20% where annual rainfall is less than 1,200 mm.
- The most unstable production of rice — CV(BL) over 25% — is found where annual rainfall is less than 1,500 mm and the dominant landform is such that run-of-the-river type irrigation is impossible. The Himalayan piedmont, Bihar, the eastern Ghats, the dry zone of Burma, and northeast Thailand are examples. In these areas, run-of-the-river irrigation is difficult because of excessive permeability, limited catchment area, or rivers too large for water diversion.
- Where run-of-the-river type of irrigation is possible, production is stable regardless of rainfall. Such is the case in the intermountain basins of Thailand and the three districts in the dry zone of Burma.
- Generally, production in the plateau type landform is unstable. However, it can be stabilized by tank irrigation. The dry zone of Sri Lanka and the southern part of the eastern Ghats appear to be such cases.

## AREAS OF SIMULTANEOUS PRODUCTION FLUCTUATION

This section studies in which year a bumper or lean harvest took place. Districts are grouped according to simultaneous production fluctuation. The degree of variability, CV(BL), does not affect grouping.



11. Cluster analysis of 197 districts by correlation of BL indices in 1949-66.

**Table 3. Summary of cluster analysis, by country.**

| Cluster | India | Bangladesh | Burma | Thailand | Philippines | Total |
|---|---|---|---|---|---|---|
| A | 17 | 0 | 0 | 0 | 0 | 17 |
| B | 34 | 2 | 0 | 1 | 0 | 37 |
| C | 0 | 1 | 3 | 0 | 3 | 7 |
| D | 10 | 3 | 2 | 10 | 1 | 26 |
| E | 0 | 0 | 1 | 26 | 0 | 27 |
| F | 5 | 2 | 19 | 2 | 0 | 28 |
| G | 0 | 5 | 2 | 3 | 0 | 10 |
| H | 2 | 0 | 0 | 7 | 2 | 11 |
| I | 9 | 3 | 0 | 10 | 0 | 22 |
| J | 0 | 0 | 0 | 4 | 1 | 5 |
| K | 2 | 0 | 0 | 3 | 2 | 7 |
| Total | 79 | 16 | 27 | 66 | 9 | 197 |

## Method of analysis

Districts whose production data were available continuously from 1949 to 1966 were selected. The bumper-lean indices for each district for each year, 197 districts × 18 years, were computed. The simple correlation coefficients of BL between every possible pair of 197 districts were computed. The districts were grouped according to the values of the correlation coefficients. This became the cluster analysis by simple correlation. Results are shown in a dendrogram (Fig. 11).

## Discussion

Eleven clusters (A-K) are identified. A cluster consists of from 5 to 37 districts. The districts in one cluster may or may not be distributed across countries (Table 3). All districts in A are in India. Most of those in B are in India and those in E in Thailand. Nineteen out of 27 districts in Burma are in cluster F. The districts of other clusters are scattered over more than two countries.

The years in which relatively bumper or lean harvests were recorded are shown for those districts belonging to A (Table 4). The districts are characterized by 4 successive lean years, from 1949 to 1952, and a bumper year, 1964. The number of districts that had either a bumper or a lean harvest in each year was counted for every cluster (Table 5).

Figure 12 shows the geographical distribution of the districts belonging to the 11 clusters. The districts in B, for instance, are found in the western coast and the Assam Valley of India, where variability of rice production is lowest, and in Bihar and the eastern Ghats, where production is most unstable. That means that a factor or factors affecting the yearly fluctuation in these districts were identical but resulted in a bumper or lean harvest of different degrees because of differences in resilience of production in each district.

Cluster A consists of districts in southeastern India. The northeast monsoon seems to be a reason for the concentration of districts in this cluster.

Most of the districts in lower Burma are grouped in F. Several districts in northern Bihar and West Bengal also belong to this cluster. The similarity, if any,

**Table 4. Occurrences of bumper and lean years[a] in cluster A.**

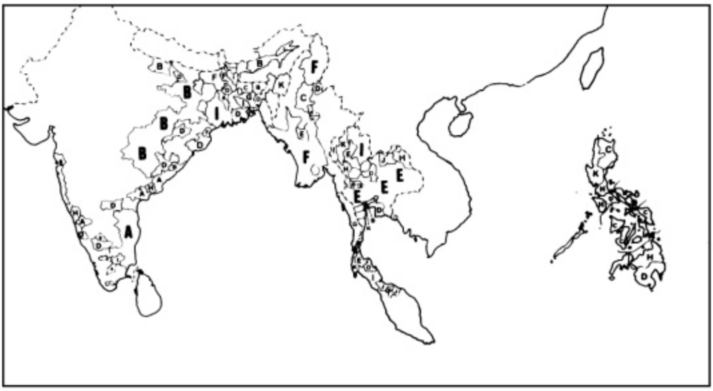
| District | CV (BL) | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ID-1 | 32.4 | – |  |  | – |  |  |  | + |  |  |  |  | + | + |  | + |  |  |
| ID-80 | 19.7 | – | – | – | – |  |  |  | + |  | + |  |  |  |  |  | + |  |  |
| ID-74 | 16.0 | – | – | – | – | – |  |  |  |  |  | + |  |  |  |  |  |  |  |
| ID-77 | 25.4 | – | – | – | – |  |  | + | + |  |  |  |  |  |  |  |  |  |  |
| ID-79 | 15.1 | – | – | – | – |  |  | + |  |  |  |  |  |  |  |  |  |  |  |
| ID-10 | 21.5 |  | – | – |  |  |  |  | + | + |  |  |  | + |  | + |  |  |  |
| ID-2 | 9.1 | – |  |  | – |  |  |  | + |  |  |  |  | + | + |  | + |  |  |
| ID-14 | 28.0 |  |  |  | – |  |  |  |  |  |  | + |  |  | + |  | + | – | – |
| ID-76 | 15.1 | – | – | – | – |  |  |  |  |  |  |  |  | + |  |  |  | – |  |
| ID-83 | 8.2 |  |  |  | – |  |  | – | – |  |  |  |  |  |  |  |  |  | – |
| ID-82 | 24.4 | – |  |  | – |  |  |  |  |  |  |  |  | + |  | + | – | – | – |
| ID-43 | 17.2 |  | – |  | – |  |  |  |  |  | + | + |  |  |  |  | + | – |  |
| ID-3 | 10.9 |  | – | – | – | + |  |  |  |  | + |  | + |  | – | – | + |  |  |
| ID-99 | 14.6 | – |  | – |  | + | + |  | – |  |  | – | + |  |  |  | + |  |  |
| ID-5 | 11.2 |  |  |  | – |  | + |  |  |  | – |  | + | + |  |  | + |  |  |
| ID-100 | 20.3 |  | – | – | – |  |  |  | – | – | – |  | + |  |  |  | + |  |  |
| Districts (no.) with bumper harvest (+) |  | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 5 | 1 | 3 | 3 | 4 | 5 | 4 | 2 | 9 | 0 | 0 |
| Districts (no.) with lean harvest (–) |  | 9 | 9 | 9 | 14 | 1 | 0 | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 4 | 3 |

[a] The years in which bumper-lean index was BL > 100 + SD (+) or BL < 100 - SD (—).

**Table 5. Number of districts that recorded relatively bumper or lean harvest [a] in each cluster, 1949-66.**

| Cluster (no. of districts) | | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | BP (+) | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 5 | 1 | 3 | 3 | 4 | 5 | 4 | 2 | 9 | 0 | 0 |
| (17) | Ln (–) | 9 | 9 | 9 | 14 | 1 | 0 | 1 | 3 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 4 | 3 |
| B | BP (+) | 8 | 0 | 1 | 5 | 13 | 5 | 11 | 7 | 2 | 16 | 7 | 16 | 11 | 4 | 8 | 7 | 0 | 0 |
| (37) | Ln (–) | 3 | 20 | 10 | 2 | 1 | 8 | 0 | 3 | 13 | 0 | 3 | 1 | 1 | 8 | 0 | 0 | 15 | 32 |
| C | BP (+) | 0 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 7 | 3 | 1 | 0 | 0 | 0 | 0 | 1 |
| (7) | Ln (–) | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 5 | 1 |
| D | BP (+) | 5 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 6 | 4 | 9 | 3 | 14 | 11 | 2 | 6 |
| (26) | Ln (–) | 2 | 5 | 4 | 4 | 5 | 3 | 4 | 1 | 18 | 8 | 4 | 2 | 0 | 1 | 1 | 1 | 6 | 1 |
| E | BP (+) | 4 | 3 | 7 | 3 | 20 | 0 | 2 | 10 | 2 | 0 | 2 | 2 | 2 | 6 | 9 | 3 | 2 | 10 |
| (27) | Ln (–) | 2 | 2 | 0 | 5 | 0 | 22 | 2 | 0 | 15 | 8 | 8 | 6 | 1 | 1 | 1 | 2 | 5 | 1 |
| F | BP (+) | 2 | 3 | 5 | 6 | 3 | 1 | 1 | 3 | 0 | 3 | 3 | 2 | 1 | 4 | 10 | 13 | 8 | 0 |
| (28) | Ln (–) | 5 | 1 | 2 | 0 | 3 | 6 | 5 | 1 | 22 | 5 | 1 | 1 | 7 | 3 | 1 | 0 | 0 | 19 |
| G | BP (+) | 2 | 5 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 3 | 3 | 2 | 0 | 3 | 2 | 1 | 1 |
| (10) | Ln (–) | 0 | 0 | 1 | 1 | 2 | 4 | 5 | 1 | 0 | 4 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 |
| H | BP (+) | 0 | 0 | 2 | 1 | 10 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 3 | 1 | 0 | 2 |
| (11) | Ln (–) | 3 | 0 | 0 | 1 | 0 | 1 | 0 | 3 | 4 | 0 | 7 | 4 | 2 | 2 | 1 | 0 | 4 | 1 |
| I | BP (+) | 3 | 6 | 1 | 4 | 20 | 3 | 1 | 11 | 8 | 0 | 0 | 4 | 1 | 0 | 1 | 2 | 1 | 0 |
| (22) | Ln (–) | 2 | 2 | 5 | 5 | 0 | 4 | 6 | 0 | 0 | 10 | 6 | 1 | 4 | 8 | 3 | 2 | 3 | 3 |
| J | BP (+) | 2 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 |
| (5) | Ln (–) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| K | BP (+) | 1 | 1 | 1 | 1 | 1 | 5 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 2 |
| (7) | Ln (–) | 0 | 0 | 1 | 1 | 3 | 0 | 2 | 1 | 1 | 1 | 5 | 2 | 2 | 2 | 3 | 0 | 0 | 0 |
| Total | BP (+) | 27 | 20 | 19 | 23 | 74 | 22 | 21 | 42 | 14 | 28 | 31 | 38 | 34 | 22 | 50 | 49 | 18 | 22 |
| (197) | Ln (–) | 27 | 40 | 32 | 33 | 15 | 50 | 27 | 13 | 79 | 41 | 38 | 18 | 17 | 28 | 13 | 8 | 42 | 62 |

[a] Bumper-lean index (BL) > 100 + SD or BL < 100 – SD.



**12.** Geographical distribution of districts in 11 clusters.

in the rainfall pattern in these widely separated areas has yet to be examined.

Cluster E consists of districts in central and northeast Thailand. Variability of production in these districts differs substantially. The districts of I distribute across West Bengal and north of Thailand. It is not known whether this can be explained climatologically or is merely incidental.

Dominance of a certain cluster in one country or a large region (F in Burma, E in Thailand, B in the eastern Ghats, and A in southern India) indicates that a bumper or lean harvest in a particular year covers an extensive area. These countries and regions have more disadvantages than others where simultaneous fluctuation covers a smaller area. A food shortage would be widespread in a lean year while an extreme bumper harvest over a large area would lower prices so that farmers would not benefit so much from such harvest. In areas where fluctuation covers a smaller area, a local food shortage could easily be remedied by transporting rice a relatively short distance. That seems to be the case in the insular part of Southeast Asia.

Table 5 indicates that a bumper or lean harvest in certain years spreads over a few clusters. For instance, a lean harvest was experienced in clusters A and B in 1950 and 1951. The year 1957 was lean in B, C, D, E, and F clusters. Many districts belonging to E, H, and I clusters had bumper crops in 1953. In 1956, however, only those of E and I enjoyed high production. These features suggest that the yearly fluctuation of rice production is governed partly by a factor affecting an extensive area and partly by a factor affecting a smaller area. The fluctuation is a synthesis of the large- and small-scale phenomena.

## CONCLUSION

The year-to-year variability of rice production was compared at the district level and its geographical distribution pattern was shown. Areas of stable and unstable production were identified on a map. Those districts in which rice production fluctuated simultaneously were grouped on a map by the cluster analysis method. The two maps were compared with maps showing the annual rainfall. Interpretation of the maps of production variability also was attempted from the viewpoints of irrigation and landform.

These maps and their interpretation suggest that drought is one of the most significant causes of year-to-year fluctuation in rice production in the six countries studied. However, no direct correlation of production data to climatic data was attempted. Therefore, significance of drought has yet to be compared with significance of the other factors.

Whether yearly variability of production is increasing or decreasing was not studied. The possible causes of stabilization include improvement of water control. The expansion of rice area would adversely affect stabilization.

The rate of increase of the rice area was computed for all districts (Fig. 5-10). In India, Thailand, and Philippines, the rate is generally high in districts where variability in production is also high. This means that rice production would not be easily stabilized in those districts, at least for now. In Burma, however, the expansion is concentrated mainly in the delta area where production is stable. In this case, area increase would not result in greater variability in production.

Construction and improvement of irrigation facilities would more or less improve production in several parts oftropical Asia. In the dry zone, where annual rainfall is below 1,000 mm, farmers tend to prefer to grow upland crops unless irrigation water is available. Expansion of the irrigated area in this zone would bring about an increase in irrigated rice area. This seems to be the case in Sri Lanka's dry zone. The same could be said for the southern part of the eastern Ghats.

Where annual rainfall exceeds 2,000 mm, rice production is stable without irrigation. Need for irrigation in those areas would be more for double-cropping than for stabilization of the existing rice crop. This is the case in most of insular Southeast Asia.

The zone where annual rainfall is between 1,000-2,000 mm is most problematic. Except in the alluvial plains developed at the lowest reach of giant rivers and the run-of-the-river irrigation areas close to mountains, production is very unstable. Yet, rainfall is sufficient for growing rice, at least in the rainy years. The prospect of irrigation is dim for several reasons. One is the technical difficulty of obtaining a good source of water. The other is the low economic benefit expected from irrigation because it will only stabilize production without a dramatic change in land use or land use intensity. As long as the benefit-cost ratio remains a criterion of feasibility for an irrigation project, this zone will remain unirrigated.

## SOURCES OF STATISTICAL DATA

Sri Lanka: Department of Census and Statistics, Department of Agriculture and Department of Agrarian Services.

India: Ministry of Agriculture, Directorate of Economics and Statistics. Bulletin of Rice Statistics in India (District-wise). 1974.

Bangladesh: Statistics Division. Agricultural Production Levels in Bangladesh (1947-1972).

Burma: Season and crop report.

Thailand: Ministry of Agriculture and Co-operatives, Department of Rice. Annual Report on the Rice Production in Thailand.

Philippines: Anden, Teresa L., and Adelita C. Palacpac. Data series on rice statistics, Philippines. The International Rice Research Institute, Department of Agricultural Economics, and Philippine Council for Agriculture and Resources Research. Revised, December 1976.

# THE SOIL-PLANT-ATMOSPHERE CONTINUUM IN RELATION TO DROUGHT AND CROP PRODUCTION

**THEODORE C. HSIAO**

Plants form part of the water transport pathway linking soil and the atmosphere. The basic aspect of water transport through this continuum is discussed with special attention to the balance between plant inflow and outflow, as this balance determines the extent of plant water deficit or stress. A conceptual hydraulic tank model describing most of the key features of the soil-plant-atmosphere system is reviewed. The relatively simple model, when used to analyze plant water balance and crop use of soil water, permits consideration of rooting depth and intensity, soil moisture release characteristics, conductances of the pathway segments, stomatal control of transpirations, and the lower limits of plant water potential for the maintenance of productivity.

Mechanisms of drought resistance in crop plants are outlined by classifying them functionally according to their role in the soil-plant-atmosphere continuum. Costs, in terms of growth and productivity associated with each mechanism, as well as benefits are listed. A partially new perspective of yield and seasonal patterns of biomass production as influenced by water stress is provided. This perspective is based on considerations of carbon assimilation and assimilate partition and emphasizes quantification, timing and severity of stresses, and key physiological parameters known to have direct impact on biomass production and yield. The need to differentiate various growth stages with respect to their sensitivity and physiological responses is made obvious.

---

Department of Land, Air and Water Resources, University of California, Davis, Ca 95616, USA.

Crop water deficit or stress is the result of complex interactions among factors in the rhizosphere, the plant, and the atmosphere. To improve drought resistance of crops, it is important to know how these factors interact to lead to water stress in plant tissue and how the plant responds and adapts to the stress in terms of growth and productivity. This paper first describes how plant water status is determined by the balance between water uptake from the soil and loss through transpiration to the atmosphere. Drought resistance mechanisms relevant to crop species are outlined within the context of this soil-plant-atmosphere continuum, together with benefits and costs to the plant of each mechanism. Discussed last are some general principles of crop productivity as related to plant water stress.

## THE SOIL-PLANT-ATMOSPHERE CONTINUUM

### Transpiration, water uptake, and water balance

Water exists as a liquid continuum from the soil through the roots and stem to the leaves, then as a vapor continuum from the intercellular spaces in the leaves across the leaf epidermis and through the air boundary layer to the atmosphere above. Water loss from the plant by transpiration is the inevitable consequence of the need to open stomata to facilitate carbon dioxide assimilation. Because the heat needed to vaporize water is so high, transpiration is determined largely by the energy supply to the leaves when stomata are open. Most of that energy comes directly from solar radiation and from air of a higher temperature than the leaves.

Absorption and transport of water by plants are passive movements, downhill in terms of the free energy status of the water or water potential (Y). Leaf and shoot Y must be lower than root and soil Y for water absorption and transport to the shoot. Other things being equal, the steeper the Y gradient, the faster the uptake. In fact, the driving force of the Y gradient and the conductance (the inverse of resistance) of the water pathway jointly determine the rate of water transport. Transpiration, by reducing the leaf water content and Y, gives rise to the Y gradient for uptake. Because uptake is the consequence of loss, higher evaporative demands from the atmosphere and consequent higher transpiration mean a lower leaf Y, even though uptake is raised to balance the high transpiration. Thus, crops can suffer water stress on hot sunny days when transpiration is high, even in moist soil.

The fact that the crop water status or Y is jointly determined by soil, plant, and atmospheric factors can be better appreciated by examining a simplified transport equation commonly used to describe water flow in the soil-plant-atmosphere continuum. The equation was arranged (Hsiao et al 1980) to express leaf Y as a function of soil Y, rate of transpiration (T), and resistances (R) of soil, root, and shoot to liquid water flow:

$$\Psi^{\mathrm{leaf}} = \Psi^{\mathrm{soil}} - T\,(R^{\mathrm{soil}} + R^{\mathrm{root}} + R^{\mathrm{shoot}}) \qquad (1)$$

This expression emphasizes that there is no unique relationship between leaf Y and soil Y. For a given leaf Y, soil Y must be more positive by a factor of the transpiration rate times the sum of liquid phase resistances in the soil-plant pathway. Excessively low leaf Y can be caused by soil drying (low soil Y), high transpiration, high soil resistance, or high plant resistances or a combination of two or more of these factors.

The water storage capacity of crop plants is very small relative to the rates of water uptake and loss. Consequently, a careful balance must be struck between uptake and loss to avoid an excessive water deficit in the tissue. Plants have evolved various means to maintain this balance (Table 1). Two of these are stomatal control of transpiration and root development for water absorption from deeper soil layers or new soil volume.

Species differ in stomatal responses to water parameters. With many herbaceous crop plants, much of the response is confined to changes in the bulk water status of the leaf. During the day and when there is no substantial water deficiency in leaves, stomata of such species are wide open and transpiration proceeds at a pace largely determined by the atmospheric conditions, particularly by the energy supply to evaporate water. At the same time, the open stomata ensure adequate inward passage of carbon dioxide for photosynthesis. Leaf У can vary within a certain range with no noticeable effect on transpiration and $CO_2$ assimilation. When water deficit in the leaves goes beyond a threshold level and becomes excessive, stomata respond by closing (at least partially) to slow down transpiration. The concurrent reduction in carbon dioxide movement and photosynthesis is unavoidable. Thus, stomata in these species operate as safety valves to check water loss when tissue water status becomes too low or unfavorable, minimizing the development of severe water deficiency in the plant. The tradeoff is that dry-matter production (photosynthesis) is slowed. The threshold water status for stomatal closure falls generally in the range where bulk turgor pressure of the leaf tissue is near zero (Turner 1974, reviewed by Hsiao and Bradford 1982).

The other water parameter to which stomata respond is humidity. This response is common in tree and wild species, is observed infrequently in herbaceous crops, and usually is in addition to response to the bulk water status of the leaf. When the absolute humidity gradient from the leaf to the air is large, as it is on days of low humidity or high temperature, stomata of these plants partly close, even though leaf У and water content remain high. In anticipation of water stress to come, such stomata conserve water in the rhizosphere on days of high evaporative demand despite a leaf bulk turgor pressure well above zero. Needless to say, $CO_2$ assimilation is restricted on such days, although the soil may be fully charged with water.

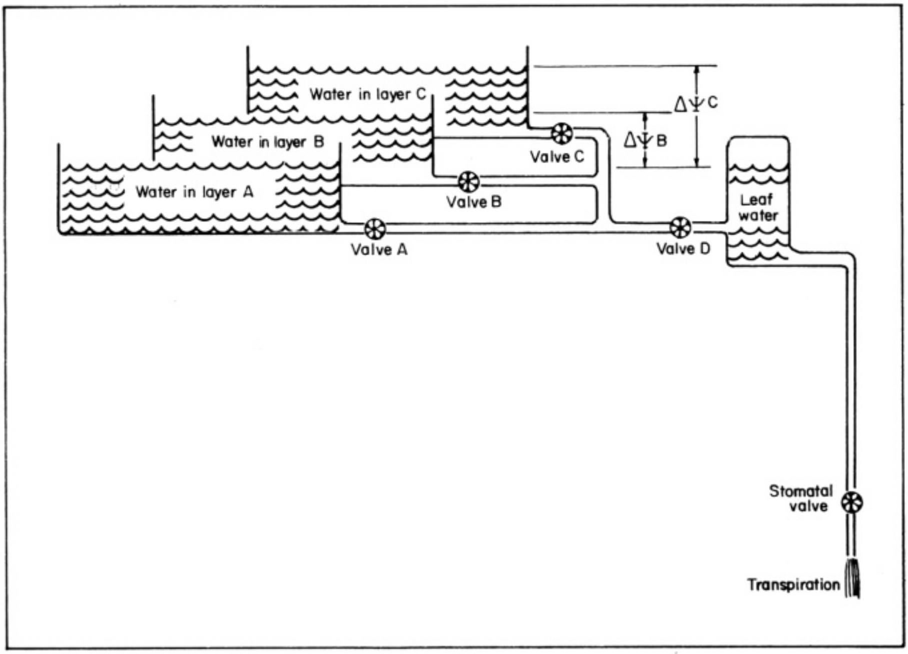
In addition to controlling loss, plant water balance can be improved by enhancing the water supply through better root development. Root growth often is favored over shoot growth when water becomes limiting. Such growth is confined largely to the wetter parts of the soil (Bradford and Hsiao 1982). This new growth taps the water in the heretofore unexplored soil volume and can be an effective means ofensuring an adequate water supply under the right conditions (Hsiao et al 1976).

## A hydraulic tank model

The concept of plant water balance in the soil-plant-atmosphere continuum, as it is influenced by rooting depth and controlled by stomata, has been depicted in a

**Table 1. Drought-resistance characteristics classified according to their role in the soil-plant-atmosphere continuum, and the associated growth and productivity benefits and costs to the plant.**

| Function or location in soil-plant-atmosphere continuum | Drought resistance characteristic | Benefits arising from the characteristic | Costs associated with the characteristic |
|---|---|---|---|
| Middle reservoir (tissue water balance) | Osmotic adjustment or buildup of tissue solutes | Ability to retain much of water and tissue volume in spite of low tissue y | Energy and carbon to generate solutes or energy for solute uptake |
| Supply reservoir and uptake resistances | More extensive rooting, vertically and horizontally | Enlarged supply reservoir volume and probably lower soil and radial root resistance | More carbon for root structure and more energy for root maintenance |
| Uptake resistances | More intensive rooting (higher root length density) | Lower root and soil resistances | More carbon for root structure and more energy for root maintenance |
| | More or larger xylems in roots and stems | Lower axial resistances in roots and stems | More carbon for xylem walls and higher probability of widespread cavitation under water stress |
| Loss resistance | Temporary or permanent smaller total opening of stomata | Higher stomatal resistance to transpiration | Higher stomatal resistance to $CO_2$ assimilation |
| | Thicker and tighter cuticles | Higher leaf resistance to transpiration when stomata are mostly closed | More carbon for cuticles |
| Loss surface and evaporative demand | Leaf rolling, smaller and fewer leaves, or leaf senescence and abscission | Smaller loss surface and less radiation absorbed for transpiration | Less photosynthetically active radiation (PARI absorption, less photosynthetic area, and carbon loss through leaf loss |
| Evaporative demand | Leaf pubescence or awns on small grains | Higher reflectivity and hence less radiation absorbed for transpiration | Less PAR absorbed for photosynthesis and more carbon for hairs or awns |
| | Paraheliotropic leaf orientation or leaf drooping under water stress | Less radiation absorbed for transpiration | Less PAR absorbed for photosynthesis |



**1.** A hydraulic tank model depicting a soil profile divided into depth layers as a series of reservoir tanks supplying water to a crop. Water levels in the tanks represent y as well as the extent of filling. Differences in levels between the tanks for each soil layer and the leaf tank represent the driving force (Dy's) for uptake. The extent of valve opening reflects the magnitude of conductance between the tanks. The stomatal valve controls the outflow and should be visualized as linked to the level of water in the leaf tank via a float such that the stomatal valve begins to close when leaf water drops to a critical level. Note that the soil profile may be divided into shells instead of layers and may be represented by as many tanks as is appropriate. Size and shape of tanks also can be varied to reflect the layer storage capacity and the moisture release characteristics of the soil (based on Hsiao et al).

simple hydraulic tank model by Hsiao et al (1980). The depiction highlights the roles played by 1) soil water-holding capacity, 2) rooting depth, 3) soil y, 4) conductance or resistance of the soil and the plant, and 5) the minimum plant water status that must be maintained to avoid significant detrimental effects on the crop.

In the model, different soil volume shells or depth layers are depicted as a series of tanks, each serving as a water reservoir (Fig. 1). The soil tanks are connected through regulating valves to a tank representing plant (more specifically, leaf) water. The valves (A, B, and C) connected directly to the soil tanks represent soil and root conductance (or resistance) in each soil layer. Valve D, connecting the other valves to the leaf water tank, represents plant shoot conductance.

An increase in conductance (or a decrease in resistance) is thought of as some opening turns of a valve and a decrease as some closing turns. The volume of soil water accessible to the crop depends on the storage capacity (tank size) of each depth layer, its fullness, and the number of layers (soil tanks) explored by the roots. The levels of water in the tanks reflect not only the volumes of water stored, but also soil y and leaf y. The difference in water levels between the soil and leaf tanks is the y gradient that drives the water flow from a soil layer to the leaves through the valves or across the series of resistances.

Transpiration or outflow from the leaf tank is shown to be controlled by the stomatal valve. The difference in elevations of the water level in the leaf tank and at the end of the outflow pipe represents evaporative demand. To visualize stomatal response to bulk leaf water status, the stomatal valve can be thought of as being linked to a float in the leaftank such that, when the water level in the tank drops to a threshold level, the valve is triggered to close, reducing outflow from the tank. Above that threshold, the water level in the leaf tank can fluctuate without any effect on the stomatal valve.

To minimize cluttering, the feedback via the float is not shown explicitly in Figure 1. To represent the stomatal response to humidity, one may imagine that the stomatal valve is linked to the elevation at the end of the outflow pipe (evaporative demand or the gradient of absolute humidity), with the valve partly closing as the pipe is lengthened and its end lowered.

In crop species which show little or no direct stomatal response to humidity, transpiration continues unabated during a dry period as long as the stomatal valve remains fully open. This in turn gradually depletes the water in the reservoirs and soil y values (water levels in tanks) drop. At the same time, soil conductances (hydraulic conductivities) decrease because of soil drying (closing of valves A, B, and C). Yet water flow from the soil to the plant must remain about as before because transpiration remains the same and changes in tissue water content represent an insignificant quantity relative to the flow rate. The flow is maintained by leaf y (leaf tank level) dropping not only to a level to compensate for the drop in soil y (soil tank levels), but further, to a level to compensate for the decrease in conductances as well. In terms of equation 1, leaf y must drop more than soil y so that the difference in y increases to compensate for the increases in soil resistance. As the soil water depletes further, eventually leaf y drops to the threshold level for activation of stomatal closure (stomatal valve). The closure restricts water loss from the crop and slows the further depletion of soil water.

The model also illustrates the importance of rooting depth or volume in supplying water to the crop and permits the consideration of differential drying of different soil layers. Incremental exploration of larger and larger soil volumes or deeper and deeper layers means connections to more and more soil tanks (for example, increasing the tanks from three to six). Very restricted rooting means connection to only one tank. Connections to more tanks provide not only a larger total reservoir to draw on, but also smaller y gradients from the soil to the roots. Because the flow from each tank constitutes a smaller fraction of the total uptake, the y gradient needed to drive the flow from each tank would be smaller and leaf y can be kept higher for a given soil y and transpiration rate.

The tank model provides special insights for analyzing the amount of stored soil water usable to the crop and the limit for soil water depletion by the crop. Some water will flow from the soil to the leaf as long as the water level in the leaf tank is lower than the water level in one of the soil tanks. If plant or leaf y drops low enough, much of the soil water can be extracted, but at very slow rates. So the question becomes: How low can leaf or shoot water level drop before crop productivity is impaired?

It turned out that expansive growth is the physiological process most sensitive to water stress. Reduction in Y of 1 or 2 bars can slow expansive growth of leaves substantially (Hsiao et al 1976b). In my experience, the first indication of water deficiency in the field is often a reduction in plant size in the early vegetative phase. Because of inherent variability, the difference in leaf Y becomes readily measurable only later, when stress becomes more intensive. The high insensitivity of expansive growth to stress dictates that leaf Y should be kept as high as practical in the period of canopy development to ensure maximum productivity. This point is expanded later.

During other parts of the crop life cycle, expansive growth is less important and leaf water level can decline to some extent with no significant effect on productivity. But in all cases it is important to keep the leaf water level above the threshold for triggering closure of the stomatal valve, or at least high enough to minimize the duration of the closure so that there is no sustained restriction of $CO_2$ assimilation. The closure threshold, around the point of zero turgor, corresponds to leaf Y values of −12 to −16 bars for a number of crop species without a history of pronounced osmotic adjustment (Hsiao and Bradford 1982).

For a given lower limit of leaf water level or Y corresponding water levels in the soil tanks are dependent on the transpiration rate, the extent of the opening of the valves connecting soil tanks to the leaf tank, and the number of soil tanks connected (Fig. 1). Hence, there is no unique relationship between the lower limits of leaf Y and soil Y. The lower limits of allowable soil water depletion found in the literature were arrived at empirically and based on experience. The tank model provides a conceptual framework for improving the estimation of that limit for each soil-crop-climate combination.

The volume of soil water usable by a crop for high productivity is the sum of the volumes held by each soil tank between the upper limit (usually taken as field capacity) and the lower limit corresponding to the lower limit of leaf water status. Because of differences in their moisture release curves (which can be reflected in the size and shape of the tanks in the model), the volume between these two limits will differ among different soils as well.

## DROUGHT-RESISTANCE MECHANISMS: BENEFITS VS COSTS

An understanding of drought-resistance mechanisms is essential for breeding crops for drought-prone areas. Equally important is an appreciation of the costs to crop productivity associated with the various mechanisms. The known crop drought-resistance mechanisms are outlined here in the context of water transport through the soil-plant-atmosphere continuum. Considerations of the costs of mechanisms are conceptual, since experimental data are lacking in most cases.

Drought-resistance characteristics can arise at any point in the soil-plant-atmosphere continuum. In terms of the hydraulic tank model, resistance can be due to particular properties of the middle tank or reservoir (tissue water balance), the supply reservoirs (soil tanks), uptake resistance (supply valves), loss resistances (stomatal and other loss valves), or evaporative demand (outflow pipe length). The resistance characteristics are listed in Table 1, with brief outlines of the associated benefits and costs to the plant. Some extreme drought-resistance characteristics found in wild species (Evanari et al 1971) but not known for most crops were omitted. For brevity, some minor aspects of costs and benefits are not mentioned. The column for costs makes it clear that all adaptive features have some negative impact on growth and the ability to accumulate biomass. Thus, it comes as no surprise that, as a group, crops bred for high productivity are not highly drought resistant. An important task in the 1980s is to delineate in quantitative terms the costs and benefits of the various resistance mechanisms.

## CROP PRODUCTIVITY AS AFFECTED BY DROUGHT

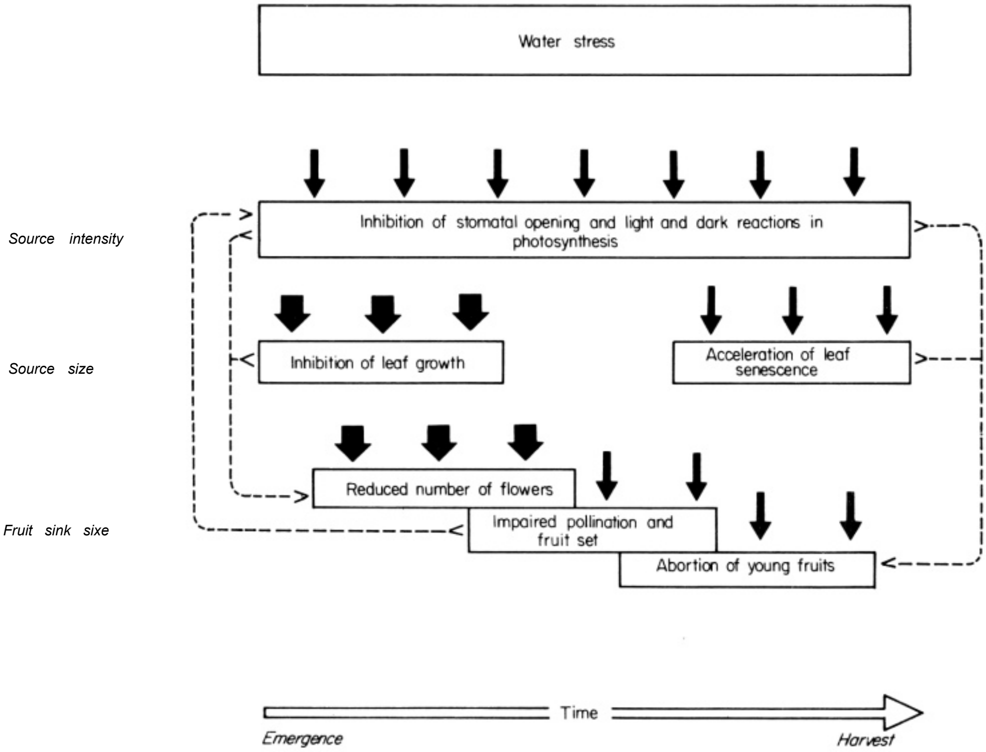
To improve crops for drought-prone environments systematically and analytically, it is necessary to have an appreciation of how crop growth and yield are altered by water deficits. Because of the dynamic nature of plant water balance, deficit effects on a crop are highly dependent on timing and duration as well as severity of the stress. From the viewpoint of cellular and metabolic physiology, stress effects are extremely complex and can involve numerous processes (Bradford and Hsiao 1982, Sinha et al, this vol). Fortunately, results of recent studies suggest that integrated plant and crop behavior under drought can be quantified reasonably well by a manageable number of parameters without a detailed knowledge of many of the underlying processes. Our reference frame is the concept that crop yield is the result of net carbon dioxide assimilation and the partition of assimilates to the harvestable part of the crop. Stated as an equation:

$$Y = HI \int_e^h A\, dt \qquad (2)$$

where $Y$ is the harvestable yield, $HI$ is the harvest index or the proportion of total biomass in $Y$, $A$ is the net assimilation rate per unit land area, and $t$ is time. The integration is from the time of emergence (e) to harvest (h). Depending on its timing and severity, water stress can reduce yield by reducing assimilation per unit of land area ($A$) and by altering the patterns of assimilate partition ($HI$).

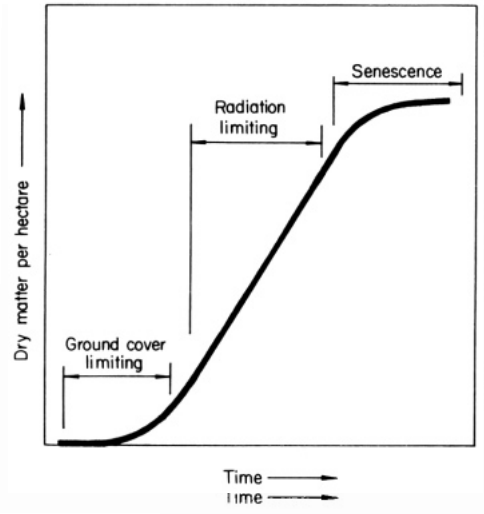
Assimilation and partition of assimilates may be viewed in terms of sources and sinks for assimilates. The effects of water stress at different times of crop development on these parameters are summarized for an annual grain or fruit crop in Figure 2. Source intensity is the rate of $CO_2$ assimilation per unit of effective leaf surface area, source size is the effective leaf area per unit of land area, and fruit sink size is the number of potential fruits per unit of land area. For simplicity and because of a lack of research data, sink strength is not considered in this depiction.

Overall assimilation is the product of source intensity times source size integrated over the time span in question. Reduction in sink size does not affect total assimilation directly, but by a feedback effect which inhibits source intensity. The most important effect of sink size is on the harvestable yield, through changes in the harvest index.



**2.** Effects of water stress on the physiological and morphological parameters underlying source intensity, source size and sink size for assimilation at various times of ontogeny, generalized for annual crops grown for grain or fruit. The time intervals within the crop ontogeny when water stress can cause physiological and morphological changes are indicated by the locations of the rectangles outlining the changes. Solid short arrows point to the changes. Arrow shaft widths indicate the sensitivity of the parameter to water stress. For example, leaf growth is the most sensitive to stress and flower number is the next most sensitive. Dashed arrows and lines indicate causal relations among the parameters. For example, inhibition of leaf growth, of stomatal opening, and of photosynthesis results in fewer flowers being differentiated, probably because the number of reproductive axes is determined by plant size and the amount of assimilates available. Another example of causal relations is that impaired fruit setting reduces the number of sinks for assimilates and usually leads to a reduction in stomatal opening and photosynthesis via feedback inhibition.

In the past, attention often has been directed at effects of stress on source intensity. However, as Figure 2 makes clear, the effects on source size are equally or even more critical. Source size is considerably more sensitive to water stress during the canopy development phase than is source intensity. Also, reductions in source size can be reversed only slowly, if at all, whereas source intensity usually recovers fully in a matter of one to a few days after water again becomes available. The literature leaves the impression that a crop is particularly sensitive to water stress at the reproductive phase, especially around the time of pollination and fruit setting. However, my recent results (unpubl.) indicate that stress has to be quite



**3.** Conceptual depiction of seasonal pattern of biomass accumulation for annual crops in a favorable environment in the absence of significant stress. The early phase is approximately exponential, representing the period when canopy is incomplete and photosynthetically active radiation (PAR) interception is approximately proportional to canopy size,.The middle phase is nearly linear and represents the period when the canopy intercepts almost all of the incident PAR and biomass production rate is highest. The last phase represents the period of maturation and senescence with declining rates of assimilation.

severe to significantly affect pollination. This is the basis for designating pollination and fruit setting as the least sensitive of all the parameters depicted in Figure 2. On the other hand, when stress in the tissue is severe enough to inhibit pollination markedly, the effect on yield can be drastic, as is exemplified below.

The seasonal pattern of biomass accumulation for annual crops (Fig. 3) is interpretable in the terms depicted in Figure 2. The early portion of the curve is approximately exponential and represents the stage when source size is limiting, prior to the stage when the crop canopy covers the ground, and when much of the incident photosynthetically active radiation (PAR) is not intercepted by the crop. This stage is sensitive even to very mild water stress because expansive growth of leaves is slowed by stress of such levels. A very mild stress persisting for a duration of weeks can have a noticeable effect on canopy development. A plausible explanation for this effect at this stage lies in its exponential nature.

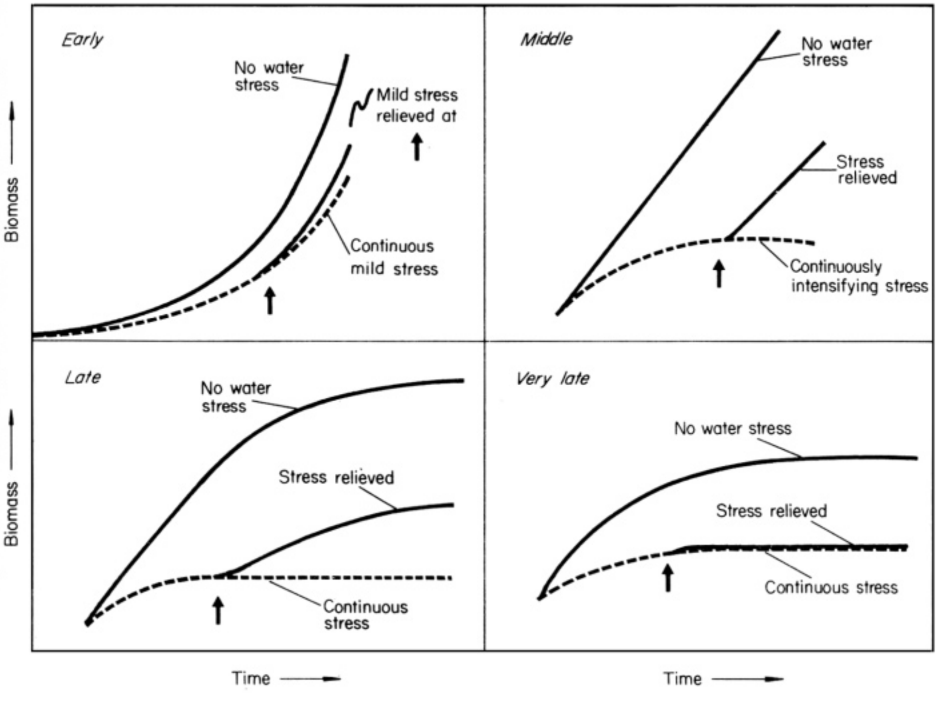
As a reasonable approximation, biomass production rates may follow first-order kinetics at this stage, with a rate of biomass increase proportionate to the existing biomass. The basis for this behavior may be that PAR absorption is approximately proportionate to the biomass or size of the plant. The integrated equation for first-order kinetics is:

$$m = m_0 e^{kt} \tag{3}$$

where $m$ is biomass per unit land area at time $t$, $m_0$ is $m$ at time zero, e is the base of natural logarithm, and $k$ is constant for a more or less stable environment when averaged over time periods of a number of days (e.g. 1 week). Because of the exponential dependence of $m$ on $k$ and $t$, small changes in $k$ have marked effects on $m$ when the time interval involved is long. Very mild water stress, by slightly slowing expansive growth of leaves, would cause small reductions in $k$. Compounded by time, such small changes in $k$ would have marked effects on biomass and canopy size. For example, in a field study of beans by Flavio Arruda in my group, a mild stress (reductions in midday leaf $\Psi$ of 1-2 bars) lasting about 20 days was found to retard canopy development substantially and to reduce PAR interception 36% (Bradford and Hsiao 1982).

During the exponential phase, a change in the partition of assimilates to leaves also will show up as a change in *k*. Thus, in theory, drought-resistance characteristics such as osmotic adjustment or a higher root-to-shoot ratio, by diverting slightly more assimilates to solutes or roots, would compound in time into substantial reductions in canopy size and biomass.

Once the canopy closes and the crop absorbs most of the radiation incident on the field, biomass accumulation should be proportionate to incident radiation. In environments where the average radiation over periods of several days or a week is more or less constant and other environmental factors are not limiting, biomass accumulation should be linear. This provides a reasonable explanation for the linear portion of Figure 3. During this phase, the crop should be less sensitive to water stress than during the exponential phase, as further leaf expansion and foliage development would not increase PAR interception significantly. However, when stress is sufficiently severe to cause significant stomatal closure and reduc-



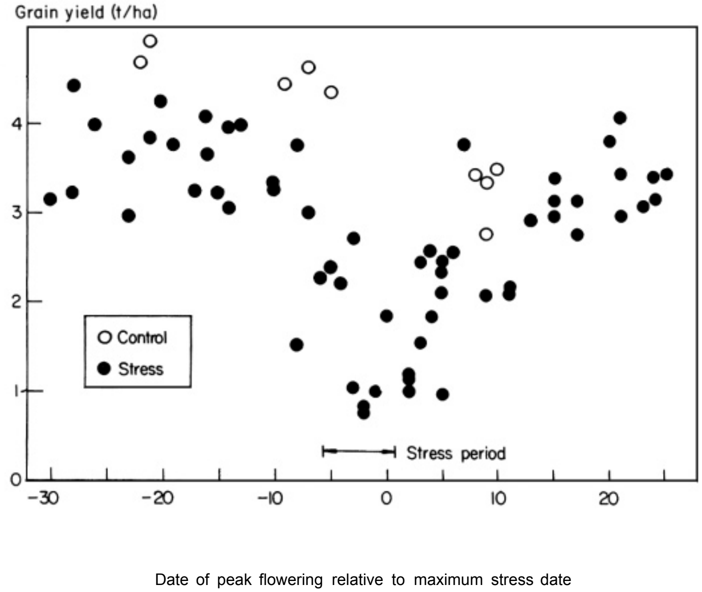
**4.** Hypothesized changes in patterns of biomass accumulation induced by water stress and stress relief within different phases of crop ontogeny. The early, middle, and late phase refer to those shown in Figure 3. Hence, the starting points for biomass are different for each phase. The shapes of the different portions of the biomass curve for the unstressed control are as discussed in Figure 3. Water stress is assumed to begin near the start of each time period. Arrows indicate the time of complete stress relief by irrigation or rain. Biomass curves are shown as dashed lines for the periods when tissue is stressed and as solid lines for periods when tissue is not stressed.

tion in assimilation per unit leaf area, biomass accumulation would be slowed.

The late phase of the biomass accumulation pattern is dominated by maturation and senescence. Here, declines in green leaf area and the associated reduction in assimilation per unit of remaining area account for the slowing and final cessation of biomass accumulation. When subjected to moderate stress during this period, leaf senescence usually is accelerated and final biomass is less but the crop matures earlier.

Data are scarce on the detailed dynamics of biomass accumulation during water stress and upon stress relief. The possible patterns of changes when stress occurs at various growth stages are hypothesized in Figure 4, but need to be verified and refined by intensive field experimentation of high precision.

With many crops, only a portion of the total biomass is harvested as yield. In many instances, the harvest indices either are not altered or are reduced only slightly by water stress at different growth phases. However, in extreme cases the index and hence the yield can be diminished markedly. This is due to failure of pollination or fruit setting, as is illustrated by some rice data (Fig. 5). Rice grown under dryland conditions is exceptionally susceptible to this damage because



**5.** Rice grain yield as affected by the time of maximum flowering in relation to the time of maximum water stress (date O). Negative dates indicate that peak flowering occurred prior to the date of maximum stress and positive dates indicate that peak flowering occurred afterwards. Rice cultivar IR36 was planted on 16 dates at the IRRI upland farm in 1979 and plots were stressed at the same time. Stress developed over a period of about 6 days, with the maximum stress (average midday leaf $\Psi_l$ of –24 bars) reached on 2 May. Stress was relieved by rain plus irrigation. Well-irrigated controls (O) were planted on only 3 dates and their declining yields reflect more cloudy weather after the stress period. Values are for single plots. (T. C. Hsiao, O. S. Namuco, and J. C. O'Toole, unpubl. data.)

severe water stress can develop suddenly due to the shallow root systems of the crop (Yoshida and Hasegawa, this volume). When such stresses coincide with the time of flowering, pollination is inhibited markedly and affected spikelets are sterile. In the study shown in Figure 5, the yield and harvest index were reduced by about 60%. Spikelet sterility increased from 30% to 75% when maximum stress occurred at the time of normal peak flowering (actual spikelet opening and anthesis were prevented by the stress). This accounted for most of the reduction in the yield. For this drastic effect, stress was very severe with average midday leaf y , staying at −20 bars or lower for 3 days and dropping to −24 bars on the last day. Leaves were tightly rolled in the last few days and stress-induced senescence of lower leaves was obvious. In a separate study on the same rice cultivar (unpubl.), midday y of −17 to −18 bars did not inhibit pollination significantly, although leaves were rolled and senescence of lower leaves was initiated.

The susceptibility of rice pollination to stress damage, although dramatic, is exceptional and does not indicate that other crops are similarly susceptible. In many practical agricultural situations, very severe water stress similar to that encountered in the rice study is rare because of better rooting. When stress does not develop so suddenly, crops tend to adjust their transpiring surface area through growth restrictions of leaves and canopy and senescence of older leaves to balance the loss against uptake and to avoid steep reductions in shoot y (Bradford and Hsiao 1982). Hence, values of −20 bars or lower for midday leaf y are not commonly encountered except in crops capable of substantial osmotic adjustment. In these cases, the adjustment presumably permits normal pollination in spite of the low y values. In studies with several crops not capable of substantial osmotic adjustment we were unable to induce significant sterility by withholding water in the field and had to artificially restrict rooting depth to 30 cm to effect stress sufficiently severe to inhibit pollination drastically (unpubl.). Overall, it appears that productivity and yield of many crop species are controlled more by source size and intensity than by sink size, even when there is substantial water stress.

The topic of soil-plant-atmosphere continuum in relation to drought resistance and crop productivity is wide-ranging. Hence, this discussion has been broad and general with minimal specifics. For more in-depth treatments, recent books and reviews (Hsiao et al 1976, Fischer and Turner 1978, Turner and Kramer 1980, Taylor et al 1982, Lange et al 1982) should be consulted.

## REFERENCES CITED

Bradford, K. J., and T. C. Hsiao. 1982. Physiological responses to moderate water stress. *In* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds. Encyclopedia of plant physiology, N. S., Physiological plant ecology B. Water relations and photosynthetic productivity. Springer-Verlag, Berlin/New York. (in press)

Evanari, M., L. Shanan, and N. Tadmor. 1971. The Negev: the challenge of a desert. Harvard University Press, Cambridge, Massachusetts. 345 p.

Hsiao, T. C., and K. J. Bradford. 1982. Physiological consequences of cellular water deficits. *In* H. M. Taylor, W. R. Jordan, and T. R. Sinclair, eds. Efficient water use in crop production. Agron. Soc. Am., Madison, Wisconsin. (in press)

Hsiao, T. C., E. Fereres, E. Acevedo, and D. W. Henderson. 1976. Water stress and dynamics of growth and yield of crop plants. Pages 281-305 *in* O. L. Lange, L. Kappen, and E. -D Schulze, eds. Water and plant life: problems and modern approaches. Springer-Verlag, Berlin.

Hsiao, T. C., J. C. O'Toole, and V. S. Tomar. 1980. Water stress as a constraint to crop production in the tropics. *In* International Rice Research Institute. Priorities for alleviating soil-related constraints to food production in the tropics. Los Baños, Philippines.

Lange, O. L., P. S. Nobel, C. B. Osmond, and H. Ziegler, eds. 1982. Encyclopedia of plant physiology, N. S., Physiological plant ecology B. Water relations and photosynthetic productivity. Springer-Verlag, Berlin/New York. (in press)

Sinha, K., R. Khanna-Chopra, P. K. Aggarwal, G. S. Chaturvedi, and K. R. Koundal. 1982. Effects of drought on shoot growth: significance of metabolism to growth and yield. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Laguna, Philippines.

Taylor, H. M., W. R. Jordan, and T. R. Sinclair, eds. 1982. Limitations to efficient water use in crop production. Am. Soc. Agron., Madison, Wisconsin. (in press)

Turner, N. C. 1974. Stomatal behavior and water status of maize, sorghum, and tobacco under field conditions. Plant Physiol. 53:360-365.

Turner, N. C., and P. J. Kramer, eds. 1980. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York. 382 p.

Yoshida, S., and S. Hasegawa. 1982. The rice root system: its development and function. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Laguna, Philippines.

# EVIDENCE FOR GENETIC VARIABILITY IN DROUGHT RESISTANCE AND ITS IMPLICATIONS FOR PLANT BREEDING

A. BLUM

An agronomic definition of drought resistance uses a stability analysis of yield performance over an array of water regimes. A physiological definition of drought resistance is formulated in terms of dehydration tolerance.

Dehydration avoidance and its physiological components — leaf area and morphology, stomatal activity, epicuticular wax content and configuration, root growth and function, and osmotic adjustment — are genetically variable in several crop species.

Genetic variation exists in dehydration tolerance as measured by plant or organ growth rates, cell membrane stability, proline accumulation, and translocation of stored assimilates.

The measurement of the components of drought resistance and their application to breeding programs are discussed.

## DEFINITIONS OF DROUGHT RESISTANCE

### Agronomic

The agronomic definition of drought resistance is related to yield as a major economic consideration and as an integrator of the effects of plant drought stress in time and space.

The absolute plant yield under stress, although a breeding target, is a poor estimate of drought resistance. Yield under stress is affected by the genotype's yield potential (Mederski and Jeffers 1973, Fischer and Maurer 1978, Blum 1980b). It may be affected by any given nonstress environmental factor, masking

---

Agricultural Research Organization, The Volcani Center, P.O.B. 6, Bet Dagan Israel.

the genotype-stress interaction, a major interest in this context. Yield under stress is not a reliable selection criterion because the genetic component of variation relative to the environmental component of variation in yield is usually low under stress (Frey 1964, Johnson and Frey 1967, Daday et al 1973).

Controlled experiments allow a comparison between yield under drought stress and potential yield under nonstress conditions. Drought resistance then may be defined in terms of percentage reduction in yield between nonstress and stress conditions (Mederski and Jeffers 1973, Blum 1973). But soybean cultivars that were susceptible by this definition (Mederski and Jeffers 1973) still had better yields than resistant cultivars under drought stress because of their high yield potential.

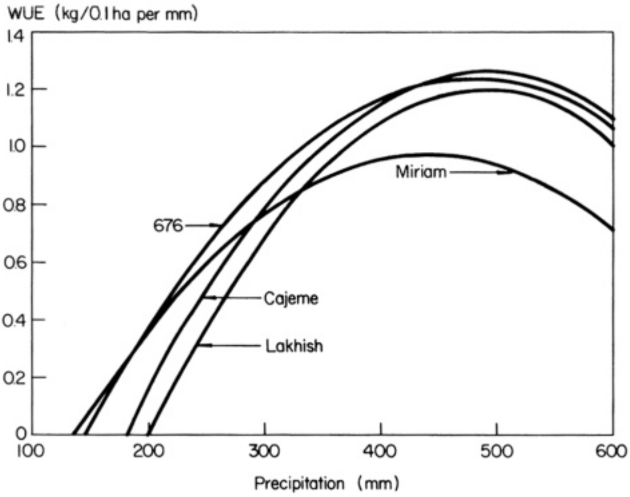
The problem of dissociating the effect of drought resistance from that of potential yield on the yield performance of a genotype under stress was approached by Fischer and Maurer (1978) through a calculated index of susceptibility(s):

$$Y_d = Y_p \ (1 - SD)$$

where $Y_d$ is stress yield, $Y_p$ is potential yield under nonstress conditions, and $D$ is drought intensity. $D$ is calculated as 1 - ($X_d - X_p$) where $X_d$ and $X_p$ are the average yields over all cultivars tested under stress and nonstress environments.

Although $S$ appears to account for yield-potential variations among cultivars, it must carry an effect of the potential yield level. In a subsequent study (Fischer and Wood 1979), $S$ across a set of wheat cultivars under stress was unrelated to plant-water relations but was related to various nonstress plant attributes.

The commonly used stability analysis (Finlay and Wilkinson 1963, Eberhart and Russell 1966) can be useful in defining drought resistance in terms of yield, provided that the major component of variation in the environmental index as used in the analysis can be attributed to the water regime (Nor and Cady 1979, Blum 1980b). The approach has been used by Laing and Fischer (1977) to test the relative adaptation of CIMMYT wheats to rainfed conditions.



**1.** Regression between water-use efficiency (WUE) in yield and total seasonal precipitation in 4 wheat cultivars. Regression functions are presented in Table 1.

**Table 1. Regression between annual (seasonal) precipitation (rainfall + irrigation) in millimeters and water-use efficiency (kg/0.1 ha per mm), integrated water-use efficiency of given precipitation ranges, and the resultant classification of 7 common wheat cultivars.**

| Cultivar | Regression | Coefficient of determination | Simpson's[a] integral over | | Classification | |
|---|---|---|---|---|---|---|
| | | | 350 to 550 mm | 100 to 350 mm | Yield potential | Drought resistance |
| Cajeme-71 | $y = -1.89 + 0.0129 \times - 0.0000131 \times^{2}$ | 0.86 | 224 | 60 | High | Susceptible |
| BTL | $y = -1.92 + 0.0126 \times - 0.0000131 \times^{2}$ | 0.81 | 186 | 48 | Low | Susceptible |
| Lakhish | $y = -2.35 + 0.0147 \times - 0.0000151 \times^{2}$ | 0.82 | 210 | 39 | Medium | Susceptible |
| H-895 | $y = -1.81 + 0.0130 \times - 0.0000134 \times^{2}$ | 0.86 | 234 | 77 | High | Medium |
| Barkaee | $y = -1.95 + 0.0140 \times - 0.0000148 \times^{2}$ | 0.79 | 233 | 87 | High | Medium |
| 676 | $y = -1.37 + 0.0110 \times - 0.0000115 \times^{2}$ | 0.80 | 217 | 101 | Medium | Resistant |
| Miriam | $y = -1.10 + 0.0095 \times - 0.0000108 \times^{2}$ | 0.79 | 206 | 102 | Low | Resistant |

[a] Integration from data points.

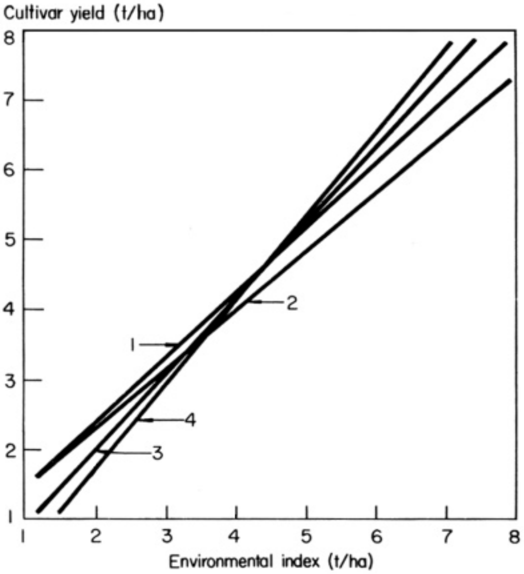
For example, a set of wheat cultivars were yield tested over 31 locations in Israel. Water-use efficiency (kilograms grain/0.1 ha per mm precipitation) was regressed against total precipitation (Fig. 1, Table 1) for each cultivar. Two cultivars, Miriam and 676, performed relatively better than other cultivars at low moisture regimes. Miriam had a lower yield potential than 676 in nonstress conditions. These two cultivars were classified as relatively drought resistant, while a distinct difference was maintained in their potential yield levels. All other cultivars were ranked accordingly for drought response and potential yield level (Table 1).

The same data sets were used in a stability analysis (Fig. 2, Table 2). Because yield was significantly associated with water regime across environments, the analysis can be used for drought response. Miriam and 676 again showed a relative advantage in low yielding drought environments. The regression slope (*b*) again indicated the relative superiority of 676 over Miriam in potential yield level. All cultivars were classified according to their relative drought resistance (intercept *a*) and potential yield (slope *b*) (Table 2). The classification was consistent with one obtained through water-use efficiency-precipitation relationships (Table 1).

The common stability analysis refers only to the slope *b* as an estimate of stability. Because the source of variation in the environmental index usually is unidentified, breeders prefer a stable variety, as characterized by $b = 1.00$. If the source of variation in the environmental index is attributed to the water regime, drought-resistant cultivars are identified through the intercept (*a*) and their potential yields evaluated through their relative slopes (*b*).

## Physiological

Total drought resistance is impossible to physiologically define. Drought resistance is process specific and its definition is linked to plant processes at any plant organization level.



**2.** Linear regression between cultivar yield over 31 tests and environmental index (calculated as mean test yield). 1 = 676, 2 = Miriam, 3 = Lakhish, 4 = Cajeme. Regression functions are in Table 2.

**Table 2. Stability analysis, predicted yield levels (by the regression equation), and resultant classification of 7 common wheat cultivars.**

| Cultivar | Regression between location mean yields and cultivar yield | Coefficient of determination | Grain yield (kg/ha) | | Classification | |
|---|---|---|---|---|---|---|
| | | | Potential[a] | Stress[b] | Yield potential | Drought resistance |
| Cajeme- 71 | $y = -702 + 1.207\times$ | 0.95 | 8950 | 1710 | High | Susceptible |
| BTL | $y = 76 + 0.894\times$ | 0.97 | 7230 | 1860 | Low | Susceptible |
| Lakhish | $y = -86 + 1.077\times$ | 0.94 | 8540 | 2070 | High | Medium |
| H-895 | $y = 80 + 1.048\times$ | 0.95 | 8460 | 2180 | High | Medium |
| Barkaee | $y = 423 + 1.009\times$ | 0.90 | 8500 | 2440 | High | Resistant |
| 676 | $y = 405 + 0.958\times$ | 0.94 | 8070 | 2320 | Medium | Resistant |
| Miriam | $y = 576 + 0.856\times$ | 0.95 | 7420 | 2290 | Low | Resistant |

[a] Cultivar yield at the potential level (× = 8000).
[b] Cultivar yield at a stress level (× = 2000).

Levitt (1972) presented a comprehensive classification of drought resistance components, but a concise, simple classification is more useful for initiating breeding work.

Two major physiological components of drought resistance are:

- Dehydration avoidance, which represents the plant's ability to maintain a high level of water status or turgor under conditions of increasing soil moisture deficit.
- Dehydration tolerance, which represents the plant's relative ability to sustain the least injury to life functions at decreasing levels of tissue water status or turgor.

Drought escape is sometimes recognized as an important plant factor affecting crop performance under stress (May and Milthorpe 1962, Blum 1979). It relates to early-maturing genotypes that escape the effect of drought through a synchronization between important plant developmental phases and a given profile of drought. However, Blum (1979) shows that early maturity, as it is associated with reduced leaf area, is an effective factor in dehydration avoidance.

## GENETIC VARIATION IN DEHYDRATION AVOIDANCE

Variations in leaf water potential among cultivars or strains under moisture stress were found in wheat (Kaul 1967, Fischer and Sanchez 1979, Quarrie and Jones 1979, Blum 1980a), sorghum (Blum 1974a, Stout and Simpson 1978, Ackerson et al 1980), soybean (Boyer 1980), and rice (O'Toole and Moya 1978, O'Toole and Cruz 1979). Variations in leaf relative water content were found among cultivars of wheat (Dedio 1975) and sorghum (Blum 1974b). The range of variation among cultivars differs from one study to another but always increases with drought stress intensity. A difference in leaf water potential of up to 10-13 bars between extreme genotypes was found in rice (O'Toole and Moya 1978) and wheat (Blum 1980a), while only 1.5-2 bars were sufficient to significantly differentiate among wheat strains.

The integration or averaging of leaf water potential over the whole stress cycle is a better estimate of cultivar response than a single measurement obtained at peak stress (Blum 1974a, O'Toole and Moya 1978, Blum 1980a), although cultivars usually maintain their relative ranking as leafwater potential decreases with stress intensity.

Reports on genetic variation in dehydration avoidance show striking differences among well-adapted, elite, and standard cultivars. Even advanced-generation wheat breeding materials that were never exposed to stress in early selection stages differed markedly in dehydration avoidance (Blum 1980a). Genetic evaluation in dehydration avoidance is apparently common in crop breeding gene pools. A priori use of exotic plant materials (Atsmon 1979) is not required.

The pressure chamber, the standard field method for measuring leaf water potential, is too slow to use in screening work. Faster indirect methods can be used as aids in selection.

Blum et al (1678) developed a method for sorghum in which a low-altitude aerial, color infrared photograph was made of a stressed breeding nursery. The color saturation of individual genotype canopies in the photograph (instrument measured or visually scored) was related to leaf water potentials.

Remotely sensed leaf canopy temperatures, measured with an infrared thermometer in water-stressed wheat nurseries, differentiated genotypes in relation to dehydration avoidance (Blum 1980a).

O'Toole and Cruz (1979) found that a system of scoring the rate of leaf rolling in drought-stressed rice was sufficiently reliable to be used as an estimate of dehydration avoidance.

Instead of measuring water status to estimate dehydration avoidance, Hanson (1980) proposed monitoring the accumulation of an inert metabolite (such as betaine) as an integrated function of tissue water deficits. Such a method would be valuable if the relations between metabolite and leaf water potential are consistent across the range of genetic materials, constituting a reliable estimate of tissue dehydration across genotypes.

## Factors controlling dehydration avoidance

Attributes of plant morphology and phenology may affect dehydration avoidance. Leaf area affects total evapotranspiration up to the stage of full ground coverage. Reduction in leaf growth when water stress develops is a major mechanism by which plants reduce water requirements (Perrier et al 1961, Turk and Hall 1980).

Narrow leaves are considered a stress-adaptive trait by some wheat breeders (Blum 1980b). Narrow leaves decrease the total leaf area per plant. A detailed modeling by Gates (1968) also shows that narrow leaves, because of aerodynamic implications, are less likely to be water stressed. The dehydration avoidance of super okra leaf cotton type is partly ascribed to the smaller leaf area per plant (Karami et al 1980). Possible associated effects of reduced leaf area on interception of solar radiation and crop photosynthesis are of little consequence under plant drought stress because expected plant productivity is below the potential level.

Leaf area also is reduced during water stress through senescence of older leaves. The associated effect on plant productivity is controversial (Begg 1980) and no conclusion can be drawn with regard to selection for senescence or nonsenescence reactions. Senescence of older leaves should not be confused with firing of younger leaves during drought, a trait selected against in maize breeding under conditions of drought (Castleberry 1980).

Leaf orientation may affect leaf water status, as is shown by the legume *Stylosanthes humilis* H. B. K. (Begg 1980). Under severe stress conditions, leaves of this legume are parallel to the incident radiation, which decreases the energy load on the leaf. Upright leaf configuration in soybean (Stevenson and Shaw 1971) caused lower leaf temperature and lower leaf diffusive resistance under stress in comparison to normal leaf configuration. Among cereals, distinct genetic variations in leaf angle exist. Narrow upright leaves should be selected as a drought-adaptive trait instead of wide lax leaves.

Plant height genes are manipulated in cereal crop breeding programs. Height genes in wheat (Pepe and Welsh 1979, Holbrook and Welsh 1980), barley (Irvine et al 1980), and sorghum (Bower and Clegg 1972) do not appear to markedly affect water use and plant performance under stress. Fischer and Wood (1979) indicated an association between the Norin-10 dwarfing gene and wheat susceptibility to water stress. Experience in Israel showed excellent performance of some dwarf wheats (Tables 1 and 2) under stress. Apparently a possible deleterious effect of a dwarfing gene per se can be offset by genetic background.

Higher leaf water potential can be maintained by stomatal closure. There are genetic variations in the relationship between stomatal conductance and leaf water potential (Blum 1974a, Henzell et al 1975, Fischer and Sanchez 1979, O'Toole and Cruz 1980a). Midday leaf diffusive resistance in cotton was associated with additive and dominant genetic variance, with high resistance completely dominant (Roark and Quisenberry 1977). Maintenance of dehydration avoidance through stomatal closure implies a negative effect on plant production through reduced carbon dioxide exchange. However, studies such as those on sorghum (Blum 1974a) and wheat (Blum 1980a) indicate that a large proportion of dehydration-avoiding genotypes do not close stomata, possibly because of osmotic adjustment of stomata under stress (Ludlow 1980). It is suspected that high yielding genetic germplasm unconsciously were selected for maintenance of high stomatal conductance under variable environmental conditions (Khan and Tsunoda 1970, Shimshi and Ephrat 1975, Brinkman and Frey 1978), while natural selection in native vegetation prefers complete stomatal closure as a survival mechanism (Ludlow 1980). Dehydration avoidance in improved man-made plant populations apparently is mediated primarily by nonstomatal plant attributes.

The effectiveness of stomatal control over transpiration efficiency (the ratio between transpiration and $CO_2$ exchange) would increase if nonstomatal transpiration pathways were eliminated. An important nonstomatal water vapor pathway is the leaf cuticle. Cuticular permeability, or cuticular transpiration, is affected by the amount, composition, and physical configuration of epicuticular wax deposits (Milthorpe 1959, Blum 1975a, Schonherr 1976, Hull 1978). Genetic variation in epicuticular wax content or cuticular transpiration is found in maize (Dube et al 1975), oats (Bengtson et al 1978), rice (O'Toole et al 1979), and sorghum (Blum 1975a, b). Heavy deposits of epicuticular wax also affect the spectral characteristics of leaves (Blum 1975b) to the extent that net radiation (the energy load on the leaf) is reduced. It should be noted that Fischer and Wood (1979) found drought susceptibility in wheat associated with low waxiness. Relatively rapid colorimetric (Ebercon et al 1977) or chromatographic (O'Toole et al 1979) methods for measuring epicuticular wax content are available for screening whenever the trait is significantly important.

Root size, morphology, depth, length density, and function are important in maintaining high leaf water potential against evapotranspiration demand. Of all root attributes, root length density (centimeters root per cubic centimeter soil volume) is probably the major operative factor (Newman 1972).

Two contrasting drought stress profiles with respect to the desirable root model may be recognized. One stress profile is characterized by limited seasonal soil moisture, typical of conditions of stored soil moisture. Under these conditions, control over the seasonal distribution of soil moisture use is critical. Excessive use of soil moisture early in the growing season may result in severe moisture deficits in the reproductive growth stages, Reasonable seasonal distribution of soil moisture use is achieved by a reduction in leaf area and root density in the juvenile stage (Blum 1974a, Blum and Naveh 1976) or by increased axial root resistance to water transport (Passioura 1972).

The other drought-stress profile is characterized by unpredictable, intermittent seasonal wetting-and-drying cycles, coupled with the deep percolation typical of many light-textured soils in the tropics. Under these conditions, deep and high density root systems may have an advantage.

The development of a model of the desirable root system for a given environment is a prerequisite for direct selection of root attributes, as has been demonstrated by Hurd (1963, 1968).

Evidence for genetic variation in root growth parameters is ample (Reynier et al 1979, Hurd 1968, Derera et al 1969, Bruce et al 1969, Blum et al 1977, Jordan et al 1979, O'Brien 1979). The problem is identifying the relevant root attributes within the available range of variation. For example, screening based on seminal root growth in juvenile sorghum plants has no significance for the total root system development as affected by crown root initiation and growth rates (Blum et al 1977a,b).

Most plant breeders are not equipped to pursue direct selection for root characteristics. Use of a transparent-tube culture, as was adopted by MacKay (1973), appears to be a useful approach. A good review of root-observation methods was published recently (Bohm 1979).

## Osmotic adjustment

Maintenance of plant tissue turgor is dependent on the relationship between total water potential and osmotic adjustment (matric potential neglected):

$$P = \psi_1 + \psi_s$$

where $P$ is turgor pressure, $\psi_1$ is water potential and $\psi_S$ is osmotic potential (Turner and Jones 1980). The lower the osmotic potential at a given water potential, the higher the turgor pressure (depending also on the elastic modulus of cell walls). Osmotic potential is developed upon dehydration because of solute accumulation in the cells, with cell size having an important effect (Cutler 1977, Zimmerman 1978). Osmotic adjustment occurs in most crop species, including rice. The osmotic solutes vary in composition with species. They consist of direct photosynthetic products, organic acids, amino acids, and ions such as potassium.

Osmotic adjustment allows further reduction of leaf water potential (in the range of several bars) against the evapotranspirational demand before zero turgor (wilting) is reached. The extent of osmotic adjustment with prolonged stress or repeated stress cycles is limited (Cutler et al 1980a).

Genetic variation in osmotic adjustment was found in sorghum (Stout and Simpson 1978, Ackerson et al 1980) and wheat (Morgan 1977, Fischer and Sanchez 1979). No differences were found in osmotic adjustment between four rice genotypes (Cutler et al 1980) and two sorghum genotypes (Jones and Turner 1978).

Osmotic adjustment is time dependent. Progression of water stress has to be sufficiently slow to allow solutes to accumulate. Its value as a drought-resistance mechanism is expected to be limited under the rapid desiccation typical in crops growing on shallow sandy soils.

The measurement of osmotic potential (or turgor) by either psychrometry (Brown and Van Haveren 1972) or pressure-volume relationships (Wenkert 1980) is too elaborate for selection work. Faster methods are not yet available.

## DEHYDRATION TOLERANCE

Dehydration tolerance may occur in any plant life process affected by water deficit. Correlated tolerance responses among various processes within a genotype are not obligatory (Blum 1978).

To dissociate the effect of tolerance from that of dehydration avoidance over an array of genetic materials, tolerance attributes need to be evaluated on the basis of a given tissue water potential in all genotypes.

Measurement of dehydration tolerance in terms of plant growth gives a good estimate of the integrated response of the system. It may be performed by linearly measuring organ growth such as leaves (Cutler et al 1980b), total plant dry weight (Younis et al 1963, Blum et al 1980), or total cessation of growth and tissue mortality (Williams et al 1967, Nour et al 1978, O'Toole et al 1978, Sullivan and Ross 1979).

The cell membranes constitute a central site of activity for cellular metabolic processes. Thus, their tolerance for dehydration stress is important (Bewley 1979). Sullivan (1972) developed a fairly rapid method of assessing the rate of injury to cell membranes of sorghum by dehydration through the measurement in vitro of electrolyte leakage from water-stressed leaf disks. The method is applicable to various crop species (Blum and Ebercon 1981), including soybean and rice (Blum, unpubl.).

Free proline amino acid accumulation occurs in leaves of many plant species subjected to various environmental stresses, including water stress (Stewart and Hanson 1980). The possibility that proline accumulation constitutes a stress-adaptive trait is controversial.

Hanson (1980) concluded that proline accumulation in barley indicates drought susceptibility rather than drought tolerance. He worked with two barley cultivars and their progeny that differed in dehydration avoidance. Because proline accumulation is related to leaf water potential, the nondehydration-avoiding (susceptible) genotypes accumulated more proline when grown under stress in the field. Higher proline accumulation due to lower leaf water potential also was found in a nondehydration-avoiding cotton cultivar (Ferreira et al 1979) and, therefore, was associated with drought susceptibility. However, when the physiological role of proline as a dehydration tolerance attribute is determined, dehydration avoidance should be accounted for by assaying proline accumulation at a given water potential in all genotypes. Singh (1973) found that when this requisite was met, proline accumulation in 14 barley cultivars was related to leaf survival rate during stress and recovery of growth upon dehydration. The rates of proline accumulation during stress in various sorghum genotypes, when compared at the same leaf water potential (Blum and Ebercon 1976), were related to growth and respiration upon recovery. Results similar to those of Singh (1973) in barley were found in wheat (Blum, unpubl.).

Proline assay at a given leaf water potential across cultivars is not a simple task. One approach is to analyze for proline in leaf disks after floating on a solution of polyethylene glycol (6000) (PEG) as the dehydration medium. When the method was used on wheat and barley (40% PEG for 48 h), the treatment was found to be nonlethal (as evidenced by full turgor recovery when disks were transferred to water) and disks of all genotypes had similar water potentials by the end of the treatment. Proline accumulation in water-stressed wheat and barley leaf disks was not associated with dead leaf tissues, as was concluded by Hanson (1980).

The possible role of proline as a dehydration tolerance factor has to be explored. Proline may serve as an energy pool to be used upon recovery (Blum and Ebercon 1976, Bogges et al 1978) or as an osmotic agent (Gould and Measures 1977, Brown and Hellebust 1978). Recently published data (Withers and King 1979) indicate that proline is an effective cryoprotectant against freeze-induced dehydration of cells, possibly through its effect on membrane stabilization (Heber et al 1971).

Translocation of photosynthates within the plant is more tolerant of water stress relative to growth and photosynthesis (Boyer 1976). It is therefore reasonable to take advantage of translocation as a yield-supporting process under stress. Growth of cereal grain is supported by both transient photosynthesis in the flag leaf and the inflorescence and by translocation of assimilates stored mainly in the stems (Evans 1975). When stress develops, the relative importance of translocation in supplying carbohydrates to the grain increases (Evans 1975, Reynier and Jacquot 1978, Hunt 1979, Austin 1980). Varieties differ in the amount of stored stem carbohydrates and in the rate of their translocation into the grain under stress. A good correlation was found across eight small grain cultivars between grain yield under late-season stress and the rate of reduction in stem dry weight during grain growth (Rawson et al 1977). Up to 31% of rice grain yield under stress was accounted for by translocation of stem reserves. A variety that yielded well under stress had an advantage in this respect (Reynier and Jacquot 1978).

Work in Israel is attempting to reveal the differential ability of wheat genotypes to sustain translocation-based grain growth under stress by destroying the photosynthetic source at the grain filling stage. This is done by spraying field plots 12 days after anthesis with a chemical contact desiccant (magnesium chlorate) that kills leaf blades, awns, and glumes. Injury to 1,000-grain weight by this treatment ranged from 0 to 43% across 38 genotypes. Injury by late-season water stress was correlated with injury by chemical desiccation.

The possibility of using chemical desiccation for revealing genetic variation in translocation-based grain growth is being explored.

## DROUGHT RESISTANCE AND YIELD: THE MISSING LINK

Although information on genetic variability in the components of drought resistance has accumulated, the logistical incorporation of this information into breeding work is limited. Apart from the problems in screening methods, a major setback is our almost complete ignorance of the relationships between physiological drought resistance traits and plant productivity under stress. For a given crop species and a drought profile, we encounter difficulties in deciding on the important drought-resistance mechanism to select in terms of the final result, which is plant production.

For example, assuming proline accumulation as an adaptive trait, there is no way of evaluating the extent to which a high-proline genotype with a good yield potential will be buffered against stress or whether this advantage will be masked by the genotype's susceptibility in other components of drought response. It is apparent that no single drought-resistance factor can indicate an advantage in plant productivity under stress (Blum 1978, Sammons et al 1979).

One solution is to apply multiple selection criteria for drought resistance to advanced-stage high-yielding populations (Blum 1980b). This approach is based on two assumptions: 1) that genetic variation for drought resistance exists within the population, and 2) that high yield potential is not negatively associated with the selection criteria involved.

Alternatively, the importance of singular drought-adaptive traits should be established and quantified for given agriculture ecosystems. At our present stage of knowledge, such research appears to be critical for further development of plant breeding.

## REFERENCES CITED

Ackerson, R. C., D. R. Krieg, and F. J. M. Sung. 1980. Leaf conductance and osmoregulation of field grown sorghum. Crop Sci. 20:10-14.

Atsmon, D. 1979. Drought resistance in barley, wheat and related wild species: developmental physiological and metabolic parameters as possible criteria for breeding. Proc. Israel-Italian Joint Meeting on Genetics and Breeding of Crop Plants. Genet. Agrar. 4:189-203.

Austin, R. B., C. L. Morgan, M. A. Ford, and R. D. Blackwell. 1980. Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. Ann. Bot. 45:309-319.

Begg, J. E. 1980. Morphological adaptation of leaves to water stress. Pages 33-42 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stresses. Wiley Interscience, New York.

Bengtson, C., S. Laarson, and C. Liljenberg. 1978. Effects of water stress in cuticular transpiration rate and amount and composition of epicuticular wax in seedlings of six oat varieties. Physiol. Plant. 44:319-324.

Bewley, J. D. 1979. Physiological aspects of desiccation tolerance. Ann. Rev. Plant Physiol. 30:195-238.

Blum, A. 1973. Components analysis of yield responses to drought of sorghum hybrids. Exp. Agric. 9:159-167.

Blum, A. 1974a. Genotypic responses in sorghum to drought stress. I. Response to soil moisture stress. Crop Sci. 14:361-364.

Blum, A. 1974b. Genotypic responses in sorghum to drought stress. II. Leaf tissue water relations. Crop Sci. 14:691-693.

Blum, A. 1975a. Effect of the *b*m gene on epicuticular wax content and the water relations of *Sorghum bicolor* L. (Moench.). Israel J. Bot. 24:50. (Abst.)

Blum, A. 1975b. Effect of the *b*m gene on epicuticular wax deposition and the spherical characteristics of sorghum leaves. SABRAO J. 7:45-52.

Blum, A. 1978. Genetic improvement of drought resistance in crop plants: a case for sorghum. Pages 430-445 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Blum, A. 1979. Principles and methodology of selecting for drought resistance in sorghum. Proc. Israeli-Italian Joint Meeting on Genetics and Breeding of Crop Plants. Genet. Agrar. 4:205-215.

Blum, A. 1980a. Drought avoidance in wheat and its rapid estimation by remote infrared thermal leaf canopy measurements. Proc. 3rd Int. Wheat Conf., May 22-June 3, Madrid, Spain.

Blum, A. 1980b. Breeding programs for improving crop resistance to water stress. *In* P. J. Kramer and C. D. Raper, Jr., eds. Crop reactions to water and temperature stress in humid, temperate climates.

Blum, A., and M. Naveh. 1976. Improved water-use efficiency in dryland grain sorghum by promoted plant competition. Agron. J. 68:111-116.

Blum, A., and A. Ebercon. 1976. Genotypic responses in sorghum to drought stress. III. Free proline accumulation and drought resistance. Crop Sci. 16:428-431.

Blum, A., G. F. Arkin, and W. R. Jordan. 1977a. Sorghum root morphogenesis and growth. I. Effect of maturity genes. Crop Sci. 17:149-153.

Blum, A., W. R. Jordan, and G. F. Arkin. 1977b. Sorghum root morphogenesis. II. Manifestation of heterosis. Crop Sci. 17:153-157.

Blum, A., K. F. Schertz, R. W. Toler, R. I. Welch, D. T. Rosenow, J. W. Johnson, and L. E. Clark. 1978. Selection for drought avoidance in sorghum using infrared photography. Agron. J. 70:474-477.

Blum, A., B. Sinmena, and O. Ziv. 1980. An evaluation of seed and seedling drought tolerance screening test in wheat. Euphytica 29:727-736.

Blum, A., and A. Ebercon. 1981. Desiccation and heat tolerance tests in wheat. Crop Sci. 21. (in press)

Bogges, S. F., D. E. Koeppe, and C. R. Stewart. 1978. Oxidation of proline by plant mitochondria. Plant Physiol. 62:22-25.

Bohm, W. 1979. Methods of studying root systems. Page 320 *in* Ecological studies, Vol. 33. Springer Verlag, Berlin.

Bower, J. T., and M. D. Clegg. 1972. Examination of root growth of RS610 isogenic hybrids by a soil coring technique. Pages 58-67 *in* The physiology of yield and management of sorghum in relation to genetic improvement. The Rockefeller Foundation, Ann. Rep. 6. Univ. of Nebraska, ARS, USDA.

Boyer, J. S. 1976. Photosynthesis at low water potentials. Phils. Trans. R. Soc. London, Ser. B, 273:501-512.

Boyer, J. S. 1980. Water and the genetic improvement of soybean yields in the Midwest. *In* P. J. Kramer and C. D. Raper, Jr., eds. Crop reactions to water and temperature stress in humid, temperate climates.

Brinkman, M. A., and R. J. Frey. 1978. Flag leaf physiological analysis of oat isolines that differ in grain yield from their recurrent parents. Crop Sci. 18:69-73.

Brown, L. M., and J. A. Hellebust. 1978. Sorbitol and proline as intracellular osmotic solutes in the green algae *Stichococcus bacillaris.* Can. J. Bot. 56:676-679.

Brown, R. W., and B. P. Van Haveren. 1972. Psychrometry in water relations research. Utah Agricultural Experiment Station, Utah State University.

Bruce, R. R., J. O. Sanford, C. O. Grogan, and D. L. Myhre. 1969. Soil water supply and depletion pattern differentiate among *Zea mays* L. single- and double-cross hybrids. Agron. J. 61:416-422.

Castleberry, R. M. 1980. Breeding programs for stress tolerance in corn. *In* P. J. Kramer and D. C. Raper, Jr., eds. Crop reactions to water and temperature stress in humid, temperate climates.

Cutler, J. M., D. W. Rains, and R. S. Loomis. 1977. The importance of cell size in the water relations of plants. Physiol. Plant 40:255-260.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1980a. Dynamics of osmotic adjustment in rice. Crop Sci. 20:310-314.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1980b. Influence of water deficits and osmotic adjustment on leaf elongation in rice. Crop Sci. 20:314-318.

Daday, H., F. E. Biner, A. Grassia, and J. W. Peak. 1973. The effect of environment on heritability and predicted selection response in *Medicago sativa.* Heredity 31:293-308.

Dedio, W. 1975. Water relations of wheat leaves as screening tests for drought resistance. Can. J. Plant Sci. 55:369-378.

Derera, N. F., D. R. Marshall, and L. N. Balaam. 1969. Genetic variability in root development in relation to drought tolerance in spring wheats. Exp. Agric. 5:327-337.

Dube, P. A., K. R. Stevenson, G. W. Thurtell, and R. B. Hunter. 1975. Effects of water stress on leaf respiration, transpiration rates in the dark and cuticular resistance to water vapor diffusion of two corn in breds. Can. J. Plant Sci. 55:565-572.

Ebercon, A., A. Blum, and W. R. Jordan. 1977. A rapid colorimetric method for epicuticular wax content of sorghum leaves. Crop Sci. 17:179-180.

Eberhart, S. A., and W. A. Russell. 1966. Stability parameters for comparing varieties. Crop Sci. 6:36-40.

Evans, L. T. 1975. Crop physiology: some case histories, Cambridge University Press, London. 374 p.

Ferreira, L. G. R., J. G. De Souza, and J. T. Prisco. 1979. Effects of water deficit on proline accumulation and growth of two cotton genotypes of different drought resistance. Z. Pflanzenphysiol. 93:189-199.

Finlay, K. W., and G. N. Wilkinson. 1963. The analysis of adaptation in plant breeding programme. Aust. J. Agric. Res. 14:742-754.

Fischer, R. A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:897-912.

Fischer, R. A., and M. Sanchez. 1979. Drought resistance in spring wheat cultivars. II. Effects on plant water relations. Aust. J. Agric. Res. 30:801-814.

Fischer, R. A., and J. T. Wood. 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. Aust. J. Agric. Res. 30:1001-1020.

Frey, K. J. 1964. Adaptation reaction of oat strains selected under stress and non-stress environmental conditions. Crop Sci. 4:55-58.

Gates, D. M. 1968. Transpiration and leaf temperature. Ann. Rev. Plant Physiol. 19:211-238.

Gould, G. W., and J. C. Measures. 1977. Water relations in single cells. Phils. Trans. R., Soc. London, Ser. B, 278:151-166.

Hanson, A. D. 1980. Interpreting the metabolic responses of' plants to water stress. HortScience 15:623-629.

Heber, U. D., L. Tyankova, and K. A. Santarius. 1971. Stabilization and inactivation of biological membrane during freezing in the presence of amino acids. Biochem. Biophys. Acta 241:578-592.

Henzell, R. G., K. J. McCree, C. H. M. Van Bavel, and K. F. Schertz. 1975. Method for screening sorghum genotypes for stomata sensitivity to water deficit. Crop Sci. 15:512-518.

Holbrook, F. S., and J. R. Welsh. 1980. Soil water use by semidwarf and tall winter wheat cultivars under dryland field conditions. Crop Sci. 20:244-246.

Hull, H. M., L. N. Wright, and C. A. Bleckman. 1978. Epicuticular wax ultrastructure among lines of *Eragrostis lehmanniana* Nees developed for seedling drought resistance tolerance. Crop Sci. 18:699-704.

Hunt, L. A. 1979. Stem weight changes during grain filling in wheat diverse sources. Pages 923-929 *in* Proc. 5th International Wheat Genetics Symposium.

Hurd, E. A. 1963. Root study of three wheat varieties and their resistance to drought and damage by soil cracking. Can. J. Plant Sci. 44:240-248.

Hurd, E. A. 1968. Growth of roots of seven varieties of spring wheat at high and low moisture levels. Agron. J. 60:201-205.

Irvine, R. B., B. L. Harvey, and B. G. Rossnagel. 1980. Rooting capabilities as it relates to soil moisture extraction and osmotic potential of semidwarf and normal standard genotypes of six-row barley. Can. J. Plant Sci. 60:241-248.

Johnson, G. R., and K. J. Frey. 1967. Heritabilities of quantitative attributes of oat (Avena sp.) at varying levels of environmental stresses. Crop Sci 7:43-46.

Jones, M. M., and N. C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Jordan, W. R., F. R. Miller, and D. E. Morris. 1979. Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci. 19:468-472.

Kaul, R. 1967. A survey of water suction forces in some prairie wheat varieties. Can. J. Plant Sci. 47:323-326.

Karami, E., D. R. Krieg, and J. E. Quisenberry. 1980. Water relations and carbon 14 assimilation of cotton with different leaf morphology. Crop Sci. 20:421-426.

Khan, M. A., and S. Tsunoda. 1970. Differences in leaf photosynthesis and leaf transpiration rates among six commercial wheat varieties of West Pakistan. Jpn. J. Breed. 20:344-350.

Laing, D. R., and R. A. Fischer. 1977. Adaptation of semidwarf wheat cultivars to rainfed conditions. Euphytica 26:129-139.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York. 697 p.

Ludlow, M. M. 1980. Adaptive significance of stomatal responses to water stress. Pages 123-138 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

MacKay, J. 1973. The wheat root. Pages 827-842 *in* Proc. 4th International Wheat Genetics Symposium.

May, L. H., and F. L. Milthorpe. 1962. Drought resistance of crop plants. Field Crops Abstr. 15:171-179.

Mederski, H. J., and D. L. Jeffers. 1973. Yield responses of soybean varieties grown at two soil moisture stress levels. Agron. J. 65:410-412.

Milthorpe, F. L. 1959. Transpiration from crop plants. Field Crop Abstr. 12:1-9.

Morgan, J. M. 1977. Differences in osmoregulation between wheat genotypes. Nature 270:234-235.

Newman, E. I. 1972. Root and soil water relations. Pages 363-440 *in* E. W. Carson, ed. The plant root and its environment. University Press of Virginia, Charlottesville.

Nor, K. M., and F. B. Cady. 1979. Methodology for identifying wide adaptability in crops. Agron. J. 71:556-559.

Nour abd ellatif, M., D. E. Weibel, and G. W. Todd. 1978. Effects of repeated drought periods on the survival of sorghum seedlings. Agron. J. 70:509-510.

O'Brien, L. 1979. Genetic variability of root growth in wheat *Triticum aestivum* L. Aust. J. Agric. Res. 30:587-595.

O'Toole, J. C., R. S. Aquino, and K. Alluri. 1978. Seedling stage drought response in rice. Agron. J 70:1101-1103.

O'Toole, J. C., and T. B. Moya. 1978. Genotypic variation in maintenance of leaf water potential in rice. Crop Sci. 18:873-876.

O'Toole, J. C., and R. T. Cruz. 1979. Response of leaf water potential, stomatal resistance and leaf rolling to water stress. Plant Physiol. 65:428-432.

O'Toole, J. C., R. T. Cruz, and J. N. Seiber. 1979. Epicuticular wax and cuticular resistance in rice. Physiol. Plant 47:239-244.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Pepe, J. F., and J. R. Welsh. 1979. Soil water depletion patterns under dryland field conditions of closely related height lines of winter wheat. Crop Sci. 19:677-680.

Perrier, E. R., C. M. McKell, and J. M. Davidson. 1961. Plant-soil-water relations of two subspecies of orchardgrass. Soil Sci. 92:413-420.

Quarrie, S. A., and H. G. Jones. 1979. Genotypic variations in leaf water potential, stomatal conductance and abscisic acid concentration in spring wheat subjected to artificial drought stress. Ann. Bot. 44:323-332.

Rawson, H. M., A. K. Bagga, and P. M. Bremner. 1977. Aspects of adaptation by wheat and barley to soil moisture deficits. Aust. J. Plant Physiol. 4:389-401.

Reynier, F. N., J. M. Kalms, and J. Ridders. 1975. Etude due comportement de deux types de varietes de riz selon leur alimentation hydrique. I. Etude des facteurs permettant d'esquirer la secheresse Republique de Cote d'Ivoire, Ministre de la Recherche Scientifique, IRAT. 15 p.

Reynier, F. N., and M. Jacquot. 1978. Demarke pour l'obtention de la resistance varietale à la secheresse: cas du riz pluvial. L'Agron. Trop. 33:314-317.

Roark, B., and J. E. Quisenberry. 1977. Environmental and genetic components of stomatal behavior in two genotypes of upland cotton. Plant Physiol. 59:354-356.

Sammons, D. J., D. B. Peters, and T. Hymowitz. 1979. Screening soybeans for drought resistance. II. Drought box procedure. Crop Sci. 19:719-722.

Schonherr, J. 1976. Water permeability of isolated cuticular membranes: the effect of cuticular waxes on diffusion of water. Planta 131:159-164.

Shimshi, D., and J. Ephrat. 1975. Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis and yield. Agron. J. 67:326-331.

Singh, T. N., L. G. Paleg, and D. Aspinall. 1973. Stress metabolism. III. Variations in response to water deficit in the barley plant. Aust. J. Biol. Sci. 26:65-76.

Stevenson, K. R., and R. H. Shaw. 1971. Effects of leaf orientation on leaf resistance to water vapor diffusion in soybean (*Glycine max* L. Merr) leaves. Agron. J. 63:327-329.

Stewart, C. R., and A. D. Hanson. 1980. Proline accumulation as a metabolic response to water stress. Pages 173-190 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Stout, D. G., and G. M. Simpson. 1978. Drought resistance of *Sorghum bicolor*. I. Drought avoidance mechanisms related to leaf water status. Can. J. Plant Sci. 58:213-224.

Sullivan, C. Y. 1972. Mechanisms of heat and drought resistance in grain sorghum and methods of measurement. Pages 247-264 *in* N. G. Rao and L. R. House, eds. Sorghum in the seventies. Oxford and IBH Publ. Co., New Delhi, Bombay, Calcutta.

Sullivan, C. Y., and W. M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. Pages 263-281 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Turk, K. J., and A. E. Hall. 1980. Drought adaptation of cowpeas. III. Influence of drought on plant growth and relations with seed yield. Agron. J. 72:428-433.

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustment. A review and evaluation. Pages 87-104 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Wenkert, W. 1980. Measurement of tissue osmotic pressure. Plant Physiol. 65:614-617.

Williams, T. V., R. S. Snell, and J. F. Ellis. 1967. Methods of measuring drought tolerance in corn. Crop Sci. 7:179-182.

Withers, L. A., and P. L. King. 1979. Proline: a novel cryoprotectant for the freeze preservation of cultured cells of *Zea mays* L. Plant Physiol. 64:675-678.

Younis, M. A., F. D. Stickler, and E. L. Sorensen. 1963. Reactions of seven alfalfa varieties under simulated moisture stresses in the seedling stage. Agron. J. 55:177-181.

Zimmerman, U. 1978. Physics of turgor and osmoregulation. Ann. Rev. Plant Physiol. 29:121-181.

# COMPONENTS OF DROUGHT RESISTANCE

# THE ROLE OF ROOT SYSTEM CHARACTERISTICS IN THE DROUGHT RESISTANCE OF CROP PLANTS

J. B. PASSIOURA

The transport of water by roots from soil to shoot is discussed, with emphasis on morphological characters that may influence drought resistance through their effects on a) the amount of water transpired by a crop, b) the efficiency with which that water is used to produce dry matter, and c) the proportion of that dry matter that ends up in the grain.

Two characters stand out:

- the ability of a crop to produce a large rooting density at depth if deep subsoil water exists.
- a longitudinal resistance to flow which may influence the rate at which water collected in the subsoil is transported to the shoots.

Depending on the environment, it may be worthwhile to decrease the resistance, if there is evidence that roots are leaving available water in the soil at maturity, or to increase the resistance, if there is evidence that roots are leaving an inadequate supply of water in the soil at flowering.

Until a few years ago, it was generally assumed that an essential feature of a drought-resistant plant was a "deep, wide-spreading, much-branched root system, such as that of sorghum" (Kramer 1969). Such an assumption is no doubt

---

CSIRO Division of Plant Industry, P.O. Box 1600, Canberra City, ACT 2601, Australia.

true for plants in a natural ecosystem which compete with each other for a limited supply of water. But for a crop in an extensive area of similar or even identical genotypes, the criteria become more subtle. Donald (1968, 1981) persuasively argued that one would expect to get the best performance as a crop from plants that are weak competitors as individuals. It is important to consider the root system of the community of plants, not the root system of individual plants. For example, if a crop extracts virtually all the available water from its soil before maturity (which commonly happens in many drought-prone environments), it is no longer axiomatic that the drought resistance of that crop would be improved if it had a more extensive and vigorous root system. The reverse might in fact be true.

Drought resistance is a nebulous term. I will use it only in a relative sense and will consider what attributes of a root system are likely to improve crop yields when yield is limited by water. When thinking of the yield of a grain crop in relation to water supply, I have found it convenient to view yield as the product of three components: the *amount* of water used by the crop, the efficiency with which that water is used in producing dry matter (the amount of dry matter produced per unit of water transpired), and the harvest index (the proportion of dry matter that ends up in the grain) (Passioura 1977). These components are largely independent of each other, so improving any one should improve yield. Attributes of roots may influence these components. The few explicit attempts that have been made to change the root system to improve drought resistance are based on factors influencing the movement of water from the soil through the roots to the shoot.

## TRANSPORT OF WATER THROUGH SOIL AND ROOT TO THE SHOOT

Some salient points of several recent reviews (Greacen et al 1976, Tinker 1976, Passioura 1981) relate to the role of roots in improving drought resistance.

It is convenient to think of the path of water from soil to shoot as consisting, somewhat arbitrarily, of five sections: pararhizal, from outside the rooting zone to within it; perirhizal, through the soil within the rooting zone; across the interface between root and soil; radial in the root, through the cortex and stele to the xylem; and axial, along the xylem. Flow along the path is driven by gradients in matric suction except when semipermeable membranes are encountered, where gradients in osmotic pressure also influence flow rate.

The flow of water in the soil obeys Darcy's Law:

$$\text{(in one-dimensional form) } F = K\,(\mathrm{d}h/\mathrm{d}x)$$

where $F$ is flow rate (m/s),
$K$ is hydraulic conductivity (m/s),
$h$ is soil water suction expressed in terms of a head of water (m), and
$x$ is distance (m).

$K$ is a rapidly increasing function of q, the soil water content, and may decrease by as much as 10 orders of magnitude as a soil dries from saturation to a matric suction, t, of 15 bars. It is usually more convenient when considering the movement of water to roots to describe $F$ in terms of gradients of water content rather than of $h$. So we have:

$$F = -D(\mathrm{d}\theta/\mathrm{d}x)$$

where $D$ ($\mathrm{m}^2\,\mathrm{s}^{-1}$) is the diffusivity of soil water.

$D$ also increases with increasing $\theta$, hence with decreasing suction, but its relationship with suction is approximately independent of soil type and the variation is not so great as the variation in $K$. To within a factor of about two, we usually can be confident that $D$ = $10^{-9}$ m/s (1 $\mathrm{cm}^2$/day) at a suction of 15 bars, $10^{-8}$ m/s (10 $\mathrm{cm}^2$/day) at a suction of 1 bar, and $10^{-7}$ m/s (100 $\mathrm{cm}^2$/day) at a suction of 0.1 bar. This consistency in $D$ helps in understanding the factors affecting the rate of water uptake by roots.

## Pararhizal flow

The boundary of the rooting zone generally is ill-defined unless there is a horizon or another layer in the soil profile (for example, a tough plow pan) that prevents the further penetration of roots. Where there is no such layer, the boundary can be defined by an arbitrarily low value of the rooting density (the length of root per unit volume of soil) of, say, 0.21 $\mathrm{cm/cm}^3$. In general, pararhizal flow would be expected to be of little importance during drought because of the low values of $K$ that prevail when t exceeds about 1 bar (typically < $10^{-4}$ cm/day). Even when suction is as low as 0.1 bar, $K$ is typically < $10^{-2}$ cm/day, so that a suction gradient of 0.01 bar/cm (10 cm water head/cm) would be needed to give a flow rate of 1 mm/day. At a suction of 0.1 bar, even sparse roots would have little difficulty in rapidly extracting water from the soil. It is the extension of the rooting zone into previously untapped volumes of soil that is of great importance if the available water in that soil is to be taken up.

## Perirhizal flow

The radial flow of water to a root can be described by the diffusion equation and by some appropriate assumptions about the geometry of the roots and about the boundary conditions at the root surfaces and in the soil at the mid-point between adjacent roots. A solution to the equation based on the best of the reasonably simple assumptions is (Passioura 1980):

$$\int_{\theta_a}^{\theta_b} D(\theta)\,\mathrm{d}\theta \simeq 0.5\,Qb^2\,(0.5\text{-}\ln b/a) = \mathrm{QG}/2\pi\mathrm{L} \tag{1}$$

where $Q(=\mathrm{d}\theta/\mathrm{d}t)$ is the rate of change of $\theta$,

- $L$ is the effective rooting density (length of water-absorbing root/unit volume of soil),
- $a$ is the radius of the root,
- $b$ is $(\pi L)^{-0.5}$, the radius of a cylinder of soil to which we can assume the root has sole access, and
- $G$ is the geometric factor (0.5-ln $b/a$) which would typically be ~– 2.

If we assume $D$ to be constant and $G$ = 2, the equation simplifies further to:

$$\Delta\theta \simeq \mathrm{Q}/\pi LD = \mathrm{I}/\pi D \tag{2}$$

where $\Delta\theta$ is the difference in $\theta$ between the bulk soil and that at the surface of the root and $I$ (= $Q/L$) is the rate of uptake per unit length of root.

This equation, together with a curve relating suction to water content, enables us to get a rapid appreciation of the influence of the main variables on the uptake of water by roots. Thus, if $D$ = 10 $cm^2$/day (corresponding to a suction of 1 bar), $L$ = 1 $cm/cm^3$, and $Q$ = 0.05 $cm^3/cm^3$ per day (corresponding to a transpiration rate of 10 mm/day spread uniformly through a 20-cm-thick layer of soil), then $\Delta\theta \simeq$ 0.0015, which is negligibly small. But if $D$ were 3 $cm^2$/day and $L$ were 0.2 $cm/cm^3$, then for the same $Q$, $\Delta\theta \simeq$ 0.025. Depending on the steepness of the q/suction curve, this could represent a large drop in suction between the bulk soil and the surface of the root, with deleterious consequences for the water potential of the plant. However, in general, any values of $L$ greater than 0.5 should enable the roots to extract water from the soil with reasonable ease, unless the soil is nearly devoid of available water. Then $D$ would be low (< 3 $cm^2$/day) and suction high.

## The interface between root and soil

Despite this conclusion, several researchers have found that plants have difficulty extracting water from even quite moist soil. The reason may be that the proportion of roots contributing to the uptake of water is small (Caldwell 1976) or that there is a major interfacial resistance between root and soil (Herkelrath et al 1977, Faiz and Weatherley 1978). As yet there are no reliable estimates of the proportion of the root length of roots growing in soil that contributes to water uptake, but for young wheat plants at fairly high suction it is probably about one-third (Passioura 1980). If this proportion is typical of crop plants, then it is necessary to redefine the boundary of the rooting zone to that marked by an observed rooting density of about 0.5 $cm/cm^3$.

There has been speculation for many years about the possibility of a vapor gap forming between root and soil if root tissues shrink during water stress. Such a gap could be a major impediment to water flow. Interest in the gap was stimulated when Huck et al (1970) showed that cotton roots growing in soil could shrink and swell diurnally by about 40%. However, I doubt that such shrinkage is likely to be important in normal circumstances in the field. If, as is commonly believed, the major hydraulic resistance in the root is at the endodermis, then it follows that the cortex of the root will typically have a water potential close to that of the adjacent soil. Therefore, it will be strongly buffered against diurnal changes in water potential in the rest of the plant, unless it has already lost contact with the soil. The root that Huck et al observed appeared to be growing in a large void in the soil. Its cortex was probably not buffered against diurnal changes in water potential and would be expected to shrink. I have been unable to find any evidence for a large interfacial resistance between root and soil in young wheat plants (Passioura 1980).

## Radial flow in the root

Radial flow in the root is thought to cause much of the drop in the potential of water as it flows from soil to leaf. There seems to be no obvious reason why this radial resistance should be a particular problem in times of drought unless the drought drastically decreases the root length per unit area of ground surface. It is possible that variation in the resistance could account for the startling behavior reported by Eavis and Taylor (1979). They showed that, with soybean growing in soil under water stress, water uptake depended on the water content of the soil, not on rooting density. Changes in radial resistance also might explain the equally startling behavior reported by Blizzard and Boyer (1980). They showed that hydraulic resistance of soybean plants increased dramatically as the soil in which they were growing dried, causing a much greater water stress in the leaves than one would expect from conditions in the soil. If the radial resistance is a problem during drought, then there may be sufficient genetic variation available to improve it. But any selection would have to be implicit without easy ways to measure radial resistance.

### Axial flow in the roots

Axial flow in the roots of dicots is not likely to limit the uptake of water. Their facility for secondary growth normally ensures that they have abundant xylem vessels. Only the presence of vascular disease or a large resistance at nodes or at the junctions between roots is likely to cause a problem.

In cereals, which have no secondary growth, axial resistances can be important (Passioura 1974, Greacen et al 1976). Spring cereal plants commonly have to rely on their seminal root system (that arising from the seeds) to extract water from the subsoil. Only three main seminal roots per plant typically penetrate deeply into the subsoil. Each of these roots typically has only one large xylem vessel of about 70 µm diameter. The upper parts of these roots can be a major bottleneck to the flow of water from subsoil to shoot. Depending on the water supply, this bottleneck may either improve or lower the drought resistance of the crop.

## THE INFLUENCE OF THE ROOT SYSTEM ON DROUGHT RESISTANCE

The preceding discussion has concerned factors influencing the collection of water by roots. The drought resistance of a crop, however, is expressed in terms of the yield of a crop that has been affected by drought. The following discussion concerning the connection between the two is based on the simple model of yield in relation to water use outlined in the introduction.

### Amount of water collected

From what we know of the movement of water through soil, roots having an effective density greater than 0.5 cm/cm$^3$ should be able to extract water rapidly from soil of $\tau < 1$ bar without inducing a major drop in $\tau$ in the soil (equation 2). By the time $\tau$ has risen to 3 bars, flow through the soil may be starting to limit the transpiration rate if $L$ is as low as 0.5. But even with such a low $L$, the roots should be able to extract water to a suction of 15 bars within about 20 days, which is not long in the life of a crop.

Nevertheless, there are many reports of roots failing to extract large amounts of apparently available water from the soil at the bottom of the rooting zone even though the plants were suffering from drought (Schultz 1971, Blum 1974, Hurd 1974, Walter and Barley 1974, Jordan and Miller 1980). The explanation presumably lies within the roots. Either the effective rooting density is much less than the observed or the axial resistance in the roots is large. Axial resistance is likely in spring cereals, which seem to be particularly prone to leave available water at depth.

In a deeply wet soil profile, the amount of water available to a crop depends on the depth to which the roots can produce a reasonable rooting density ($L$ > 0.5 cm/cm$^3$ if one-third of the root length is active) and perhaps on the axial resistance to flow in the main roots.

If rooting depth is the problem, it is probably for both genetic and environmental reasons. Most root systems will penetrate rapidly under optimal conditions. Their ability to grow into inhospitable subsoils is usually the problem. Many subsoils are dense and can have high shear strengths. They may be low in such nutrients as Ca and B, which are essential to root growth and which have to be available on the spot because of their poor transport in the phloem. Or they may contain toxic concentrations of aluminum or manganese. These factors, discussed in several chapters in Carlson (1974) and Russell (1977), are often aggravated if the temperature of the subsoil is low. In climates with low mean annual temperatures, subsoil temperatures are low because at depths greater than about 1 m, the temperature of the soil deviates little from the mean annual temperature. In a breeding program, selecting for rooting depth obviously would be out of the question. However, selecting for parents with deep roots is feasible. Hurd (1974) appears to have done this in his wheat breeding program for the Canadian prairies.

Two other root characters could be associated with rooting depth, but the connection is very tenuous. The first applies to graminaceous crops having several seminal roots, such as wheat. O'Brien (1979) found a large genetic variation in the angle of growth of the seminal axes, which he measured by determining the spread of axes at a depth of 10 cm in the soil. Presumably, the greater the spread, the less likely it is that the roots will penetrate deeply.

The second root character is a bizarre one devised by Chloupek (1977, 1980). He selects plants by means of a capacitance meter. There is a low but definite positive correlation between the size of the root system and its capacitance, which is determined by placing one electrode of a capacitance meter on the base of a plant and the other in the soil a few centimeters from the base. This technique says nothing about the distribution of the roots.

Axial resistance may be a problem in spring cereals if the upper part of the seminal root system becomes a bottleneck to the flow of water from the subsoil to the shoot. It might be possible to improve axial resistance by breeding for larger xylem vessels in the main seminal roots. Since the resistance depends inversely on the fourth power of the diameter of the main vessel in each root (Greacen et al 1976), a small increase in diameter could cause a large drop in resistance. The heritability of the diameter in wheat is large enough to mount a successful breeding program. Measurement of the diameter, while not quick by ordinary breeding standards, takes less than 2 minutes (Richards and Passioura 1981a,b).

I have been unable to find any data on the morphology of the seminal root system of dryland rice, but conceivably it could be similar to that of wheat. Because the seminal roots are so much finer than the late nodals, and usually much fewer, they usually escape notice when one pulls a plant out of the ground and examines its root system. Until about the time of Krassovsky (1926), it was generally assumed that the seminal root system in both wheat and barley was ephemeral. Its important role in extracting water from the subsoil was unnoticed. Conceivably, the seminal root system fulfills a similar role in dryland rice, although it presumably is destroyed by transplanting.

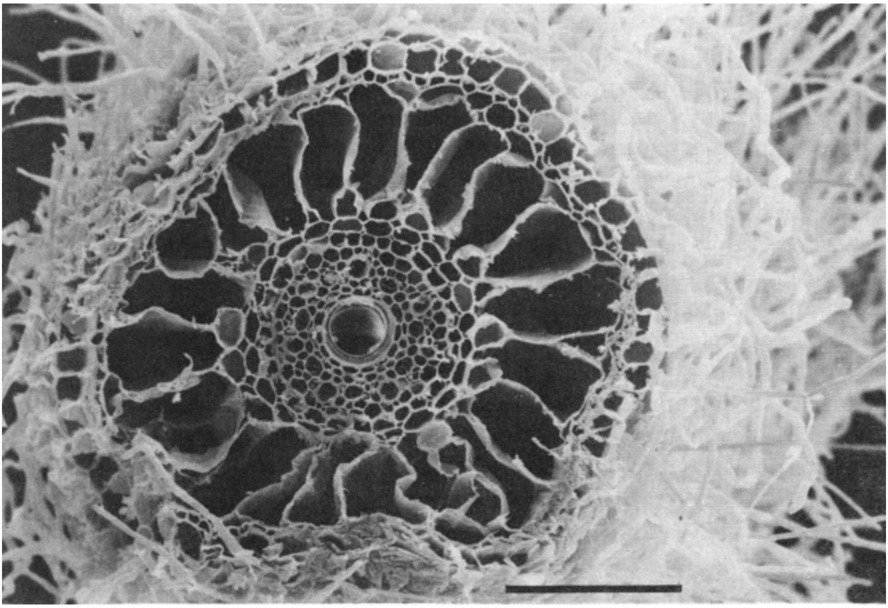
But the inability of many rice crops to extract adequate water from the subsoil may be due to low vertical conductances in their root systems. In experiments with root boxes, Puckridge and O'Toole (1981) noted that even drought-resistant rice plants appeared to have only one main root axis each at depths below 40 cm. If this frequency occurs in the field, each root would have to carry water at an average rate of 1 mg/second if it were to satisfy the transpiration rate with water collected below 40 cm (assuming a plant density of $200/m^2$ and a transpiration rate at midday of 20 mm/day). The gradients of pressure along such roots would be very large, particularly since rice roots appear to have very narrow xylem vessels. Table 1 shows the diameters of the main xylem vessels in the roots of young rice plants and the calculated values ofpressure gradients along the roots, assuming Poiseuille flow at a rate of 1 mg/second per plant spread across all root axes (Fig. 1). The gradients are very large. Later-formed root axes may contain much larger vessels with much greater conductances.

I have so far considered the withdrawal of water from the bottom of the rooting zone. In many drought-prone environments, particularly when rain falls in small showers during the life of a crop, the loss of potentially available water by direct evaporation from the soil surface may be a problem. Fischer and Turner (1978) estimated that such losses could account for up to 50% of the rainfall. The extent of the loss will depend on many things, not least the erectness of the leaves of the crop. Erect leaves channel rain to the stem of each plant, concentrating it so that it penetrates more deeply into the soil where it is not so prone to direct evaporation. The extraordinarily high rooting density that some crops achieve in the topsoil may not be the extravagance it at first appears, if those roots can rapidly recover

**Table 1. Dimensions of xylem vessels and calculated axial pressure gradients (Poiseuille) in root axes of young rice plants.**[a]

| Cultivar | Largest xylem vessel mean diameter (µm) |  | Axialpressure gradient required for 1 mg/s flow rate per plant (bar/cm) |
|---|---|---|---|
|  | Largest root | All roots |  |
| Calrose | 45 | 35 | 0.6 |
| Starbonnet | 45 | 35 | 0.7 |
| IR24 | 45 | 35 | 0.6 |
| OS4 | 50 | 45 | 0.25 |
| Rikuto Norin 21 | 45 | 40 | 0.6 |
| Khao Lo | 60 | 50 | 0.25 |

[a] Total number of axes per plant at 2 weeks ranged from 3 to 6. Xylem in each root was dominated by one large central vessel (Fig. 1). Older plants had many roots containing several large vessels somewhat smaller than the large vessels in the early roots. Combined conductance was no greater.



**1.** Transverse section of a young rice plant root axis (cultivar IR24). Note the largest central xylem vessel. Bar denotes 100 µm. (Scanning electron micrograph prepared by Mike Moncut and Josie Tait)

from drought to be able to take up recent rain. The responses of roots to alternate wetting and drying are not well known, but from my own observations and those of Portas and Taylor (1976), it seems that roots become dormant and presumably highly suberized when the soil surrounding them dries. When the soil is watered, the roots start growing again. Presumably only the new root length is effective in taking up water. If this is so, then the recovery of the root system in a dry topsoil may depend on the number of viable root tips it contains. Such a character as this would probably be even more difficult to use in a breeding program than would rooting depth. In tropical environments, where rainfalls typically are heavy, losses of water by direct evaporation from the soil probably are minor.

## Efficiency of water use

If the amount of available water is limiting, then the efficiency with which the crop produces biomass (the ratio of biomass to water used) is surprisingly uniform, after taking into account the average vapor pressure deficit in the air and including the roots in the biomass estimate. The only clear-cut difference across a large range of genotypes is an approximately twofold difference between $C_3$ and $C_4$ plants (Fischer and Turner 1978). However, estimates of water-use efficiency are usually based on the amount of shoot produced per unit water used, so variation in the root:shoot ratio should influence this. In general, if water is limiting growth, the ideal size of the root system is that at which the extra water collected by investing more assimilate in roots results in no change in the assimilate available to invest in the shoot. There is no point in a plant investing a parcel of assimilate in its roots if the extra water obtained does not even allow the shoot to replace the assimilate spent.

Jordan and Miller (1980) have calculated for sorghum that increasing *L* by 1 cm/cm$^3$ over a depth of 125 cm would require 800 kg/ha more dry matter in the roots (the roots weigh about 60 μg/cm). Estimates from the data of Merrill and Rawlins (1979) for sorghum (50 μg/cm) and of Gregory et a1 (1978) for wheat (40 μg/cm) are similar. Assuming a transpiration ratio of 300, the investment of an additional 800 kg/ha in roots would be worthwhile if the roots could thereby extract an additional 20 mm of water from the soil. Given that about 50 mm of water appears to be left behind in the soil when a crop has reached maturity in the environment as Jordan and Miller (1980) discussed, emphasis on increasing *L* appears to be justified.

However, two other factors may have to be considered in determining the cost-benefit ratio. First, soil-grown roots appear to respire (or at least consume assimilate) much more rapidly per unit dry weight than does the shoot (Sauerbeck and Johnen 1976) so that the simple use of the transpiration ratio in this calculation may greatly underestimate the water lost in producing a given amount of root. Second, any water left by a crop at depth in the soil need not necessarily have accumulated during the life of the crop and any preceding fallow. The water may in fact represent several years accumulation. A deep-rooted crop could mine it only once. It is the annual amount of local recharge of ground water that provides an upper limit to any sustained advantage deep-rooted plants have over shallow-rooted ones. This may be much less than the amount of water apparently left behind by the crop.

The large concentrations of roots that some crops produce in the topsoil (Barley 1970) seem extravagant and may be a relic of times when wild ancestors of crop plants competed with other plants for a limited supply of water. In a crop of uniform genotype, competition between plants for water loses its meaning. One might speculate that domestication has reduced the root-to-shoot ratio or changed the distribution of roots with depth to favor deeper rooting. No data appear to be available. But where rooting densities in the topsoil appear to be many times larger than what is needed to extract all the water at a reasonable rate, there could be scope for reducing the root:shoot without prejudicing the supply of water to the shoot, unless high rooting density is important in lessening evaporative losses, in supplying nutrients, or in enabling the crop to compete with weeds.

## The pattern of water use

The yield of a crop, particularly a cereal crop, ultimately depends on the number of grains set per unit area and on the plant's ability to fill those grains. The pattern of water use can affect both of these profoundly.

In general, a series of short droughts that result in the roots providing an approximately steady, but growth-limiting, supply of water to the shoot will have no deleterious effect on the harvest index (Passioura 1977). The size of the shoot accommodates to the water supply and severe stress is avoided. Setting and filling of grain are in proportion to shoot size. It is a sudden change in water status that has very deleterious effects on grain set, particularly if it occurs shortly before or at flowering (Fischer 1973, Morgan 1980). It is important that roots show a compromise between extracting water rapidly to ensure that all available water is made use of and extracting water slowly to avoid the risk of a sudden severe deterioration in the water status of the shoot. I suspect that the roots of drought-resistant cultivars show such a compromise.

My emphasis so far has been on the physics of the flow of water through soil and root. But roots are more than wicks. They send cytokinins to the shoot (Itai and Benzioni 1976). It is quite possible that the root tips, which are thought to contain the sites of cytokinin synthesis, may be able to sense the water potential of the soil and adjust the production of cytokinins accordingly. Unlike the vascular system of the root, which has a good hydraulic connection with the shoot, root tips must have a water potential strongly buffered by that of the adjacent soil. Such a mechanism could explain the observation that transpiration rates of soybean are influenced by $\theta$ but not by $L$ (Eavis and Taylor 1979). Variation in the production of cytokinin could influence plant behavior in relation to water supply, either prodigally or conservatively. Either type of behavior might be appropriate, depending on the type of drought expected — prodigal if it is unlikely that any drought would be severe enough for the plants to exhaust the water in the soil before the next rain, conservative if a prolonged drought is likely.

One form of facultatively conservative behavior appears to occur in spring cereals. In these cereals, the seminal root system is largely responsible for extracting water from the subsoil. The nodal root system typically is restricted to the top 30-40 cm of the soil profile (Passioura 1974). When the topsoil is dry, which happens during a sustained drought, plants have to rely on only about three xylem vessels each to transport water from the wet subsoil through the dry subsoil to the transpiring leaves. These vessels constitute a bottleneck which may force the plants to use subsoil water slowly. But if the topsoil is wet, the nodal root system proliferates and amply supplies the leaves with water.

One not uncommon but extreme form of drought is that in which a crop experiences a terminal drought after sowing. The crop is sown at the end of a wet season when the soil contains much water but completes its growth during a dry season. In these circumstances, grain yield depends on the amount of available water left in the soil at around the time of flowering (Nix and Fitzpatrick 1969, Passioura 1972). It is important that the roots do not extract the soil water so quickly that an inadequate amount is left to use during grain filling. Conservative plants are likely to yield better than prodigal ones. There is evidence that wheat plants growing in a terminal drought may not be conservative enough. Richards and I have embarked on a breeding program aimed at increasing the hydraulic resistance of the upper part of the seminal root system by selecting for small xylem vessels (Richards, this volume).

## CONCLUSION

This discussion has concentrated on morphological characters of roots that might influence one or more components of yield: the amount of water collected by the roots, the efficiency with which the water is collected (how the investment of assimilate in the roots may influence the amount of biomass produced per unit water transpired), and the harvest index, which is largely determined by the pattern of water use during the life of the crop. I have concentrated on morphological characters primarily because, in principle, they are much easier to handle than physiological ones if one is concerned with trying to manipulate characters to improve drought resistance.

Two characters stand out in importance. The first is root density, which may largely determine the extent to which roots can extract water from the adjacent soil. Where the soil is deeply wet, it is important to have a large rooting density ($>0.5$ cm/cm$^3$) at depth if the water there is to be extracted. Such a character is laborious to measure and is of no use in a breeding program except in the initial selection of parents.

The second important character, at least in spring cereals, is the longitudinal resistance to flow in the main roots which may influence the rate at which water in the subsoil can be transported by the roots through a dry topsoil to the shoot. This character is simply related to the sue of the main xylem vessel in the seminal axes of the plants. This can be measured quickly enough to be of use in a breeding program. Depending on the environment, it may be worthwhile to decrease the resistance if the crops are leaving much available water in the soil at maturity or to increase it if the roots are leaving an inadequate supply of stored water in the soil at flowering so that the crop has a poor harvest index.

## REFERENCES CITED

Barley, K. P. 1970. The configuration of the system in relation to nutrient uptake. Adv. Agron. 22:159-201.

Blizzard, W. E., and J. S. Boyer. 1980. Comparative resistance of the soil and the plant to water transport. Plant Physiol. 66:809-814.

Blum, A. 1974. Genotypic responses in sorghum to drought stress. I. Response to soil moisture stress. Crop Sci. 14:361-364.

Caldwell, M. M. 1976. Root extensionand water absorption. Pages 63-85 *in* O. L. Lange, L. Kappen, and E. D. Schulze, eds. Water and plant life: problems and modern approaches. Springer-Verlag, Berlin.

Carlson, E. W. 1974. The plant root and its environment. University of Virginia Press, Charlottesville.

Chloupek, O. 1977. Evaluation of the size of a plant's root system using its electrical capacitance. Plant Soil 48:525-532.

Chloupek, O. 1980. Wurze1systemgrösse unde Productivität der Luzerne. Z. Acker Pflanzenbau 149:107-116.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Donald, C. M. 1981. Competitive plants, communal plants, and yield in wheat crops. Pages 223-247 *in* L. T. Evans and W. J. Peacock, eds. Wheat science – today and tomorrow. Cambridge University Press, Cambridge.

Eavis, B. W., and H. M. Taylor. 1979. Transpiration of soybeans as related to leaf area, root length, and soil water content. Agron. J. 71:441-445.

Faiz, S. M. A., and P. E. Weatherley. 1978. Further investigations into the location and magnitude of the hydraulic resistances in the soil:plant system. New Phytol. 81:19-28.

Fischer, R. A. 1973. The effect of water stress at various stages of development on yield processes in wheat. UNESCO: Plant response to climatic factors. Proc. Uppsala Symp. 1970:233-241.

Fischer, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semi-arid zones. Annu. Rev. Plant Physiol. 29:277-317.

Greacen, E. L., P. Ponsana, and K. P. Barley. 1976. Resistance to water flow in the roots of cereals. Pages 86-100 *in* O. L. Lange, L. Kappen, and E. D. Schulze, eds. Water and plant life: problems and modern approaches. Springer–Verlag, Berlin.

Gregory, J. P., M. McGowan, P. V. Biscoe, and B. Hunter. 1978. Water relations of winter wheat. I. Growth of the root system. J. Agric. Sci. Camb. 91:91-102.

Herkelrath, W. N., E. E. Miller, and W. R. Gardner. 1977. Water uptake by plants. I. The divided root experiments. Soil Sci. Soc. Am. J. 41:1003–1038.

Huck, M. G., B. Klepper, and H. M. Taylor. 1970. Diurnal variations in root diameter. Plant Physiol. 45:529-530.

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. Agric. Meteorol. 14:39–55.

Itai, C., and A. Benzioni. 1976. Water stress and hormonal response. Pages 225–242 *in* O. L. Lange, L. Kappen, and E. D. Schulze, eds. Water and plant life: problems and modem approaches. Springer–Verlag, Berlin.

Jordan, W. R., and F. R. Miller. 1980. Genetic variability in sorghum root systems: implications for drought tolerance. Pages 383-399 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley, New York.

Kramer, P. J. 1969. Plant and soil water relationships: a modern synthesis. McGraw-Hill, New York.

Krassovsky, I. 1926. Physiological activity of the seminal and nodal roots of crop plants. Soil Sci. 21:307-325.

Merrill, S. D., and S. L. Rawlins. 1979. Distribution and growth of sorghum roots in response to irrigation frequency. Agron. J. 71:736-745.

Morgan, J. M. 1980. Possible role of abscisic acid in reducing seed set in water-stressed wheat plants. Nature (Lond.) 285:655-657.

Nix, H. A., and E. A. Fitzpatrick. 1969. An index of crop water stress related to wheat and grain sorghum yield. Agric. Meteorol. 6:321-337.

O'Brien, L. 1979. Genetic variability of root growth in wheat (*Triticum aestivum* L.). Aust. J. Agric. Res. 30:587-595.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Passioura, J. B. 1974. The effect of root geometry on the water relations of temperate cereals (wheat, barley, oats). Pages 357-363 *in* J. Kolek, ed. Structure and function of primary root tissue. Veda, Bratislava.

Passioura, J. B. 1977. Grain yield, harvest index, and water use of wheat. J. Aust. Inst. Sci. 43:117-120.

Passioura, J. B. 1980. Transport of water from soil to shoot in wheat seedlings. J. Exp. Bot. 31:333–345.

Passioura, J. B. 1981. Water collection by roots. Pages 39-53 *in* L. Paleg and D. Aspinall, eds. The physiology and biochemistry of drought resistance in plants. Academic Press, Sydney.

Portas, C. A. M., and H. M. Taylor. 1976. Growth and survival of young plant roots in dry soil. Soil Sci. 121:170-175.

Puckridge, D. W., and J. C. O'Toole. 1981. Dry matter and grain production of rice, using a line source sprinkler in drought studies. Field Crops Res. 3:303-319.

Richards, R. A. 1982. Breeding and selecting for drought resistance in wheat. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Richards, R. A., and J. B. Passioura. 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. Crop Sci. 21.

Richards, R. A., and J. B. Passioura. 1981b. Seminal root morphology and water use of wheat. II. Genetic variation. Crop Sci. 21.

Russell, R. S. 1977. Plant root systems: their function and interaction with the soil. McGraw-Hill, London.

Sauerbeck, D., and B. Johnen. 1976. Der Umsatz von Pflamenaurzeln in Laufe der Vegetationsperiode und dessen Beitrag zur "Bodenatmung." Z. Pflanzenerauehr Bodenkd 3:315-328.

Schultz, J. E. 1971. Soil water changes under fallow-crop treatments in relation to soil type, rainfall and yield of wheat. Aust. J. Exp. Agric. Anim. Husb. 11:216-242.

Tinker, P. B. 1976. Transport of water to plant roots in soil. Phil. Trans. R. Soc. London, Ser. B, 273:445-461.

Walter, C. J., and K. P. Barley. 1974. The depletion of soil water by wheat at low, intermediate and high rates of seeding. Proc. 10th Int. Congr. Soil Sci. Moscow 1:150-158.

# SOIL PHYSICAL PROPERTIES THAT AFFECT RICE ROOT SYSTEMS UNDER DROUGHT

B. P. GHILDYAL AND V. S. TOMAR

Drought is defined as the condition in which soil water is insufficient to ensure maximum plant growth. Water intake characteristics and water storage capacity of the root zone soil profile of some typicaldrought-prone soils are described. The intake characteristics of a soil are affected by depth, texture, presence of impeding layer, and hydraulic conductivity of the profile. The available storage capacity of a soil is governed by texture, layering sequence, depth of profile, and water retention and release characteristics.

The root systems of rice cultivars differ. Wetland adapted cultivars have more roots in the surface layers near the center of the plant, dryland adapted cultivars have deep and more lateral roots. Under drought stress, maximum root length is higher than total root volume at all stages of growth. Rice root porosity, number of roots, and root dry weight are low under stress. Size and rigidity of pores influence the growth and penetration of roots. Root growth is best in silty clay loam and is adversely affected by higher penetration resistance.

This indicates that the hydrophysical properties of soil that affect infiltration, root zone profile available water storage capacity, and rooting characteristics are important in drought studies. An understanding of the interactions among these physical properties and rooting characteristics is necessary for breeding and selecting for drought resistance.

---

Department of Soil Science, G.B. Pant University of Agriculture and Technology, Pantnagar (Nainital), U.P., India.

Drought can be defined as the condition in which the available soil water is insufficient to ensure maximum plant growth. Hydrological drought is the absence of precipitation and agricultural drought is soil water deficiency, which can be related to hydrological drought but is not identical.

Rainfall deficits may lead to the soil water deficits that cause crop failure. Equally important factors are the rate at which soil water is extracted by a crop, or evapotranspiration, and the available water storage capacity in the root zone during the absence of precipitation. The extent and frequency of drought in a season will thus depend upon the amount of daily precipitation entering the soil (intake rate and capacity), the maximum water storage capacity of the soil profile in the root zone, and the daily evapotranspiration (rate of depletion of soil water reservoir).

## SOIL PHYSICAL PROPERTIES AND DROUGHT

A typical drought-prone soil is a shallow coarse-textured loam and sandy loam overlaying coarse sands or gravels or unconsolidated debris with limited available water storage capacity.

### Intake characteristics

The process by which water enters soil is known as infiltration. Precipitation or other surface water is divided between overland flow and downward subsurface flow. The subsurface water is retained in the soil profile for crop use during a dry spell.

Water entry into the soil is caused by matric and gravitational forces. The flux which the soil profile can absorb through its surface when it maintains contact with water at atmospheric pressure is called infiltrability. As long as the rate of water supply to the surface is lower than soil infiltrability, water infiltrates as fast as it is supplied. The supply rate determines the infiltration rate. Once the supply rate exceeds soil infiltrability, the process is controlled by soil profile characteristics.

Soil infiltrability and its variation with time depend upon initial moisture content and suction, texture, structure, and profile characteristics (homogeneous or heterogeneous). In general, soil infiltrability is high in the early stages of infiltration, particularly where the soil initially is relatively dry, tends to decrease monotonically and eventually approaches asymptotically a constant rate called the steady-state infiltrability.

Profile characteristics of typical rice soils of drought-prone areas in India are described in Table 1 (Anonymous 1979, Dr. R. P. Gupta pers. comm.). Soils such as the Lingampalli series, Hyderabad (A. P.), are shallow and coarse textured with high infiltration rates and hydraulic conductivity. The Pichanur series, Coimbatore (T. N.), although relatively deep, have a high mechanical impedance layer that results in lower hydraulic conductivity of the subsoil and lower final infiltration rate of the profile. Some of the red sandy clay loam soils of Hyderabad are shallow and have a high bulk density and low intake rate. Their pores become very rigid on drying. This hardness restricts root penetration. The permeability of air to

**Table 1. Physical characteristics of drought-prone soils of India (Anonymous 1979)**

| Depth (cm) | Coarse sand (%) | Fine sand (%) | Silt (%) | Clay (%) | Texture[a] | Bulk density (g/cm$^2$) | Infiltration rate (cm/h) | | Hydraulic conductivity (cm/h) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Initial | Final | |
| *Shallow soils: Lingampalli series, Rangareddy District (A.P.)* | | | | | | | | | |
| 0-10 | – | * 81.2 | 4.8 | 14.0 | SL | 1.55 | 18.6 | 4.0 | 8.0 |
| 10-65 | – | 61.6 | 6.8 | 6.4 | SCL | 1.65 | – | – | 3.6 |
| 65 + | – | 73.2 | 6.4 | 20.4 | SCL | 1.70 | – | – | 3.4 |
| *High mechanical impedance soils: Pichanur series, Coimbatore (T.N.)* | | | | | | | | | |
| 0-12 | 33.6 | 32.6 | 9.3 | 23.1 | LS | 1.65 | 16.2 | 0.5 | 10.4 |
| 12-32 | 18.8 | 18.6 | 12.2 | 43.5 | C | 1.65 | – | – | 0.9 |
| 32-108 | 38.8 | 16.6 | 21.8 | 21.8 | GSCL | 1.72 | – | – | 4.6 |
| 108-125 | Sandy clay loam mixed with parent material | | | | | 1.81 | – | – | 8.7 |
| *Hardening soils: red sandy clay loam, Hyderabad (A.P.)* | | | | | | | | | |
| 0-10 | 8.9 | 53.5 | 12.5 | 23.5 | SCL | 1.5 | 10.5 | 2.8 | – |
| 10-32.5 | 8.9 | 38.3 | 14.8 | 35.7 | SC | 1.7 | | | |
| 32.5-65 | Loose calcareous gravelly and murrum layer admixed with soil | | | | | | | | |
| 65 + | Disintegrated schistose with pockets of amorphous lime paralithic contact | | | | | | | | |
| *Highly water retentive, slowly permeable soil: black clay, Kuthuliya Farm, Rewa (M.P.)* | | | | | | | | | |
| 0-15 | – | 25.0 | 30.0 | 45.0 | C | 1.36 | – | 0.20 | 1.34 |
| 15-20 | – | 27.5 | 27.5 | 45.0 | C | 1.48 | – | – | 2.04 |
| 30-45 | – | 25.0 | 30.0 | 45.0 | C | 1.49 | – | – | 4.76 |
| 45-60 | – | 35.0 | 40.0 | 25.0 | L | 1.52 | – | – | 12.84 |
| 60-75 | – | 32.5 | 40.0 | 27.5 | CL | 1.55 | – | – | 0.34 |
| 75-90 | – | 35.0 | 42.5 | 22.5 | CL | 1.52 | – | – | 0.34 |
| *Highly permeable soils: desert series, Sikar, Jobner (Rajasthan)* | | | | | | | | | |
| 0-23 | – | 91.9 | 1.2 | 7.7 | S | 1.44 | – | 17.0 | 7.32 |
| 23-40 | – | 90.0 | 3.0 | 9.1 | S | 1.46 | – | – | 9.50 |
| 40-75 | – | 90.8 | 2.9 | 6.4 | S | 1.46 | – | – | 12.67 |
| 75-126 | – | 91.7 | 1.6 | 5.8 | S | 1.48 | – | – | 14.71 |
| 126-190 | – | 92.8 | 1.9 | 6.3 | S | 1.52 | – | – | 15.24 |

[a] SL = sandy loam, SCL = sandy clay loam, LS = loamy sand, C = clay, GSCL = gravelly sandy clay loam, L = loam, CL = clay loam, S = sand.

the roots through such soils is largely retarded. Some soils that are heavy textured with high retentive capacities, such as the black clay soil of Kuthuliyafarm, Rewa (M. P.), have a low intake rate and low hydraulic conductivity. They are drought prone if rain is received in only a few storms. The amount of water that infiltrates is very low and runoff increases. On the other hand, desert soils, such as the series of Sikar, Jobner (Rajasthan), are deep, very light textured, and have a very high infiltration rate and hydraulic conductivity. Soil drought in these excessively permeable soils is caused by their low water retention capacity.

## Water storage capacity of the root-zone soil profile

A plant is rooted in the soil-water reservoir and its foliage, subjected to external atmosphere, is required to transpire unceasingly. To grow successfully, a plant must achieve water economy through a balance between the water demand and the available supply. Because the evaporative demand of the atmosphere is almost continuous and rainfall occurs only occasionally and often irregularly, the plant must rely upon the soil-water reservoir to survive during dry spells.

The concept of soil water availability has rarely been defined in physical terms. According to Veihmeyer and Hendrickson (1927, 1949, 1955), soil water is available equally throughout a definable range of soil moisture from field capacity (the upper limit) to permanent wilting (the lower limit). Both are constant for a given soil. However, Richards and Wadleigh (1952) produced evidence indicating that soil-water availability decreases with decreasing soil wetness. They indicated that a plant may suffer water stress and reduction in growth well before the wilting point is reached. In a glasshouse study, Tomar and Ghildyal (1973) observed that when soil $y_m$ decreased below –2.0 bars for plants grown in unsaturated soils, leaf water potential and transpiration rate started decreasing. Normally, the allowable depletion factor has been used. Transpiration of crop plants began to decrease when 25% of the total extractable water remained in the root zone (Ritchie 1973). This threshold value of water content was the lower limit for potential evaporation (Ritchie et al 1972).

The amount and rate of water uptake depends on the ability of roots to absorb water from the soil as well as the ability of the soil to supply and transmit water to the roots at a rate sufficient to meet transpiration requirements. These, in turn, depend on the physical properties of soil (hydraulic conductivity, diffusivity, matric suction, and moisture content relationships), plant characteristics (rooting density, root depth distribution, rate of root extension, and the physiological ability of roots to increase suction to extract water from relatively dry soils at the rate needed to avoid wilting), and meteorological conditions affecting transpiration requirements.

The water storage capacity of a soil profile is mainly governed by texture, layering sequence, and depth. Water retention characteristics and some chemical properties of drought prone soils are described in Table 2 (Anonymous 1979).

Clay soils retain more water longer than sandy soils. The black clay soils of Kuthuliya farm, Rewa (M. P.), India, are representative of soils with high water retention capacities. These soils retain 0.243 $cm^3/cm^3$ between –1/3 and –15 bars soil $y_m$. The desert soil series Sikar, Jobner (Rajasthan), retains a very low amount

Table 2. Moisture retention and chemical properties of drought-prone soils of India (Anonymous 1979).

| Depth (cm) | EC 1:2 (mmho/cm) | pH 1:2 | Organic carbon (%) | Moisture content ($cm^3/cm^3$) | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Saturation | 1/10 bar | 1/3 bar | 15 bars | 1/3-15 bars |
| *Shallow soil: Lingampalli series, Rangareddy Dist. (A.P.)* | | | | | | | | |
| 0-10 | 0.12 | 6.5 | 0.20 | – | – | 0.225 | 0.096 | 0.129 |
| 10-65 | 0.20 | 6.3 | 0.35 | – | – | 0.307 | 0.124 | 0.183 |
| 65 + | 0.10 | 6.4 | 0.10 | – | – | 0.262 | 0.139 | 0.123 |
| *High mechanical impedance soils: Pichanur series, Coimbatore (T.N.)* | | | | | | | | |
| 0-12 | 0-20 | 7.6 | 0.60 | 0.525 | 0.422 | 0.267 | 0.112 | 0.155 |
| 12-32 | 0-20 | 7.2 | 0.35 | 0.757 | 0.670 | 0.525 | 0.277 | 0.248 |
| 32-108 | 0-20 | 7.2 | – | 0.638 | 0.440 | 0.317 | 0.181 | 0.136 |
| 108-125 | 0-20 | 7.2 | – | – | – | – | – | – |
| *Hardening soils: red sandy clay loam, Hyderabad (A.P.)* | | | | | | | | |
| 0-10 | 0.13 | 8.2 | Low | 0.624 | – | 0.281 | 0.134 | 0.147 |
| 10-32.5 | 0.13 | 8.2 | V. Low | 0.780 | – | 0.377 | 0.184 | 0.193 |
| 32.5 | – | – | – | – | – | – | – | – |
| 65 + | – | – | – | – | – | – | – | – |
| *Highly water retentive, slowly permeable soils: black clay, Kuthuliya Farm, Rewa (M.P.)* | | | | | | | | |
| 0-15 | 0.9 | 7.4 | 0.31 | 0.677 | 0.605 | 0.500 | 0.295 | 0.205 |
| 15-30 | 0.8 | 7.5 | 0.24 | – | – | – | – | – |
| 30-45 | 0.8 | 7.6 | 0.16 | 0.732 | 0.685 | 0.568 | 0.323 | 0.245 |
| 45-60 | 0.8 | 7.7 | 0.17 | – | – | – | – | – |
| 60-75 | 1.0 | 7.7 | 0.24 | 0.804 | 0.752 | 0.617 | 0.339 | 0.278 |
| 75-90 | 0.9 | 7.7 | 0.11 | – | – | – | – | – |
| *Highly permeable soils: desert series, Sikar, Jobner (Rajasthan)* | | | | | | | | |
| | | | | | | | | 1/10-15 bars ($cm^3/cm^3$) |
| 0-23 | 0.60 | 7.8 | 0.24 | 0.294 | 0.161 | 0.073 | 0.025 | 0.136 |
| 23-40 | 0.69 | 7.7 | 0.25 | 0.340 | 0.171 | 0.101 | 0.053 | 0.118 |
| 40-75 | 0.61 | 8.3 | 0.21 | 0.327 | 0.180 | 0.096 | 0.038 | 0.142 |
| 75-126 | 0.57 | 7.6 | 0.25 | 0.340 | 0.185 | 0.096 | 0.041 | 0.144 |
| 126-190 | 0.48 | 7.7 | 0.22 | 0.333 | 0.175 | 0.100 | 0.033 | 0.142 |

of water, 0.14 cm$^3$/cm$^3$, between –1/10 and –15 bars soil $y_m$ in the soil profile. Kuthuliya farm black clay soils, however, have high retentive capacities but are drought prone because of slow permeability (Table 1). The Lingampalli series of Rangareddy district and the red sandy clay loam of Hyderabad (A. P.) are shallow and light textured. Their water storage capacity is also low.

We have considered –1/3 bar soil $y_m$ as the upper limit of available water, except in the desert soil series (–1/10 bar soil $y_m$), and –15 bars soil $y_m$ as the lower limit of available water. These limits, while not sound in physical terms, are reproducible and practicable.

Besides the total water storage capacity of the soil profile, the presence of impeding layers that affect redistribution of moisture and root growth is important from the point of view of water availability. The Pichanur series of Coimbatore (T. N.), with an impeding layer in its profile that inhibits the redistribution of water, has low available water (Tables 1 and 2). In soils such as sandy clay loam at Hyderabad, pores become rigid on drying and the soil becomes hard, affecting water storage capacity.

## SOIL PHYSICAL PROPERTIES AND RICE ROOT SYSTEMS

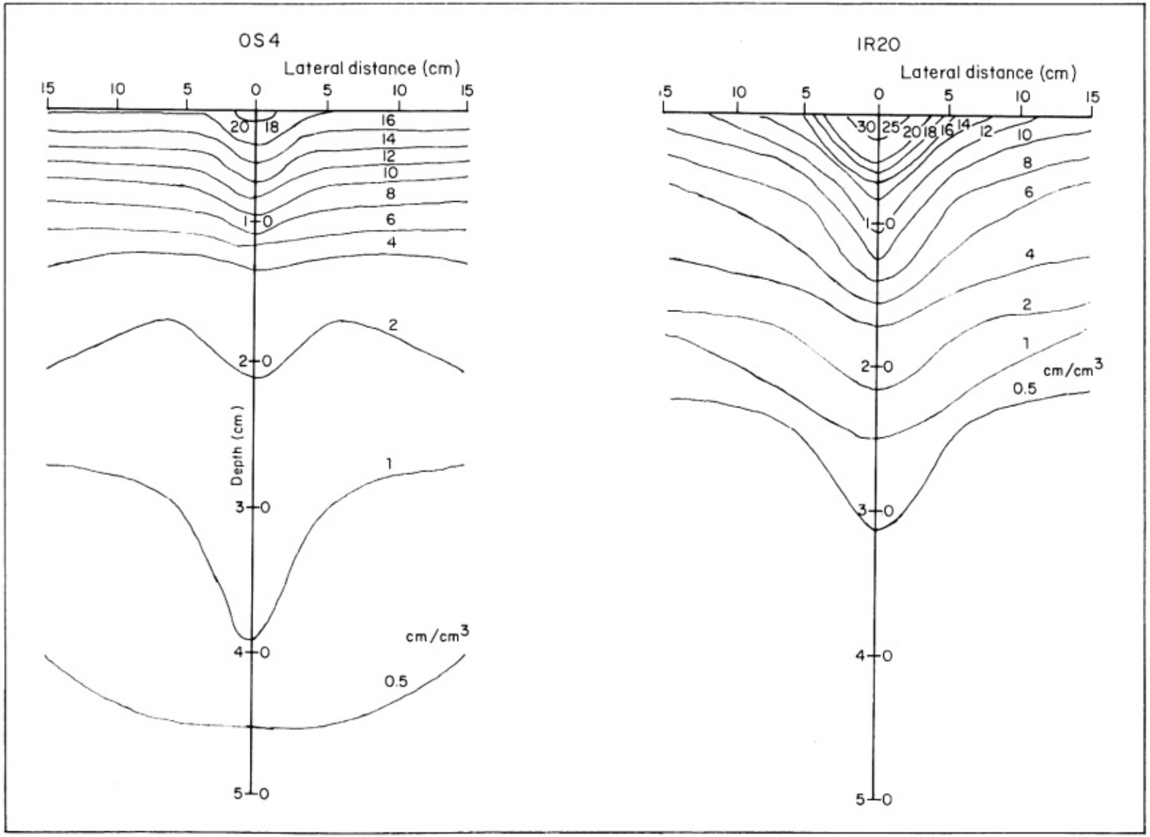
The rate at which soil water is extracted or depleted depends upon rooting characteristics. To meet the evaporative demand, a plant relies on absorption by roots and the water storage and transmission characteristics of the soil. For mature plants, with root systems occupying a more or less fixed volume of soil, changes in uptake with depth and time are believed to be caused by differences in the rooting density and root activity and by changes in hydraulic characteristics over space and time (Ogata et al 1960, Van Bavel et al 1968, Arya et al 1975).

In his study of the nature of the interaction between plant rooting characteristics and soil hydraulic properties, Gardner (1964) concluded that the water uptake pattern is most sensitive to soil properties and relatively insensitive to total water uptake and total extent of the root system. Theoretically, rooting density distribution may correlate with the uptake pattern under conditions in which soil resistance to flow dominates. Results of some laboratory experiments, however, suggest a weak dependence when water is more readily available (Reicosky et al 1972).

On the basis of current understanding ofthe soil-plant-atmosphere system and rooting characteristics, Hsiao et al (1980) proposed a procedure to estimate extractable soil water. They considered an upper limit for retention of moisture corresponding to 0.1 bar suction for all soils. But for the lower limit of moisture content, they considered rooting the main variable affecting soil suction at different depths in the soil profile. The shallower the rooting, the more positive was the lower limit for soil water potential at a given depth.

### Varietal differences in rice root systems

Variations occur in the rooting characteristics of wetland- and dryland-adapted rice cultivars. Hasegawa et al (1979) reported the vertical and lateral distribution of roots of OS4 (dryland) and IR20 (wetland) cultivars. Root samples were taken 0, 5, and 15 cm away from hills. Ten cores were taken at each sampling site. Figure 1



**1.** Iso-density diagrams of OS4 and IR20, 41-43 days after seeding. IRRI, 1977 wet season (Hasegawa et al 1979).

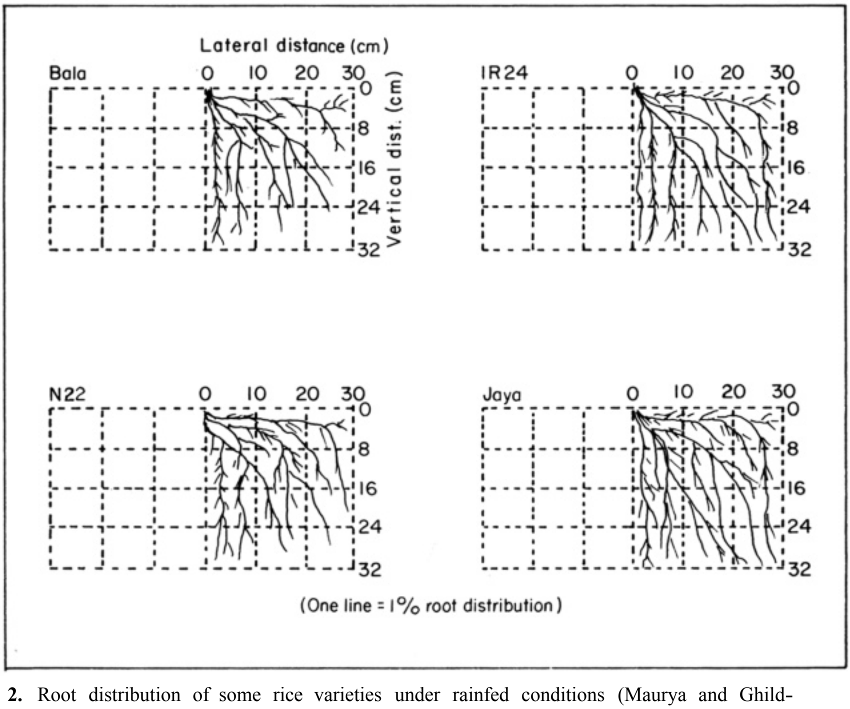
shows the lateral and vertical distribution of roots by means of iso-density curves, which show points of the same root density both vertically and laterally.

Wetland variety IR20 had more roots distributed within the soil surface layers than dryland variety OS4. OS4 had higher root densities in deeper layers. Furthermore, OS4 had more thick roots and developed deeper root systems than did IR20. Over 90% of all roots were distributed within the top 20 cm for wetland varieties and within 40 cm for dryland varieties. The effective root length (defined as the depth at which root density is higher than 0.5 cm/cm$^3$ of soil) of dryland varieties was 60 cm, about twice the depth shown by wetland rice varieties. Irrigated OS4 grown in the dry season established a denser root system than rainfed OS4 grown in the wet season. This difference in density helps to show the importance of soil moisture condition to root development.

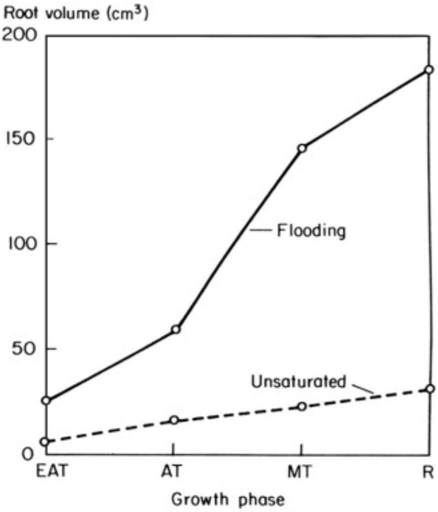
Maurya and Ghildyal (1975) observed that the percentage of root distribution at a depth of 24-32 cm and at a lateral distance of 20-30 cm was higher in rainfed (2.3-4.1%) than in flooded conditions (0.9-3.6%). Roots under high moisture stress tend to go deeper. In rainfed conditions, 23.9% of Bala roots were in a 20-40 cm lateral soil zone up to 32 cm in depth, compared with only 16.2% of IR24 roots (Fig. 2). N22 and Bala had better laterally developed root systems in rainfed conditions.

### Influence of soil moisture stress on rice root growth

The effect of soil moisture stress (0-1/3 bar suction cycle) is compared with the



2. Root distribution of some rice varieties under rainfed conditions (Maurya and Ghildyal 1975).



**3.** Volume of rice root at different growth stages. EAT = early active tillering, AT = active tillering, MT = maximum tillering, R = reproductive (Kar et al 1974).

effect of continuous flooding on maximum root length and volume of TN1 roots in Figure 3 (Kar et al 1974). The maximum root length was higher at all stages of growth in moisture-stress conditions, while root volume was less. The degeneration of roots, a unique phenomenon in submerged conditions, increased as the plant grew. By the flowering stage, 78% of the roots had degenerated during the early active tillering phase under flooding or during the entire growth period under saturation.

Rice root porosity is lower, roots are less dense, and dry weight is lower in unsaturated soil conditions than in flooded soil (Pradhan et al 1973), mainly because of a high oxygen diffusion rate (Table 3). Although plant growth is poor in unsaturated soils, the maximum root length is high.

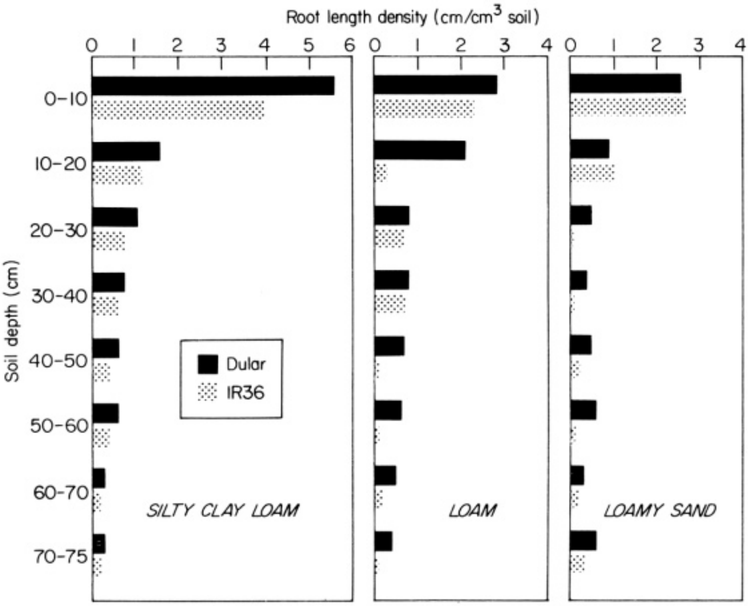
## Particle size distribution and rice root growth

The size and rigidity of pores in a porous medium influence the growth and penetration of roots. Tomar and O'Toole (1979) grew IR36 and Dular in deep containers (75 cm deep soil, 200-liter capacity) in silty clay loam, loam, and loamy sand. Root length and density of both cultivars decreased with depth (Fig. 4). In loam and loamy sand, however, Dular had relatively higher density than IR36 at lower depths. The rooting density of IR36 was quite low, below 20 cm in loamy sand and below 40 cm in loam in comparison to Dular. Because of its high rooting density, Dular extracted water from deeper layers in all three soils. IR36 had a rooting density as high as that of Dular in silty clay loam.

Kar et al (1979) in a laboratory study using steel cylinders 15 cm in diameter and 30 cm long found that roots grew best in silty clay loam (Table 4). The decreasing order of soils with reference to rice root growth was: silty clay loam >sandy loam >

**Table 3. influence of different soil moisture conditions on oxygen diffusion rate in soil, root porosity, and growth of rice at maximum tillering phase (Pradhan et al 1973).**

| Soil moisture treatment | Oxygen diffusion rate ($10^{-8}$g/cm$^2$ per min) | Root porosity (%) | Plant height (cm) | Tillers (no.) | Dry shoot (g) | Root length (cm) | Roots (no.) | Dry root weight (g) |
|---|---|---|---|---|---|---|---|---|
| Flooding 6 ± 1 cm | 3.98 | 25.48 | 61.75 | 49.25 | 18.75 | 31.32 | 532.5 | 8.25 |
| Flooding 3 ± 1 cm | 5.41 | 24.01 | 59.00 | 57.25 | 21.75 | 33.95 | 551.5 | 9.50 |
| Saturation | | | | | | | | |
| 0-millibar | 8.62 | 19.25 | 57.50 | 55.50 | 19.75 | 37.45 | 494.0 | 7.25 |
| 20-millibar | 28.45 | 12.49 | 57.00 | 45.25 | 17.50 | 40.95 | 476.0 | 7.00 |
| 60-millibar | 45.18 | 8.66 | 54.12 | 36.25 | 13.12 | 45.20 | 427.0 | 5.50 |
| 350-millibar | 68.41 | 5.43 | 52.75 | 31.25 | 9.75 | 51.30 | 409.0 | 4.62 |
| 500-millibar | 82.91 | 3.85 | 51.25 | 25.75 | 8.75 | 55.12 | 370.5 | 3.50 |
| 1000-millibar | 90.29 | 3.50 | 47.25 | 22.25 | 6.75 | 51.50 | 325.0 | 3.12 |
| S.E.M. ± | 6.04 | 0.11 | 0.50 | 1.68 | 0.91 | 0.65 | 10.65 | 0.50 |
| LSD at 5% | 12.95 | 0.55 | 1.48 | 4.92 | 2.67 | 2.51 | 32.24 | 1.49 |
| LSD at 1% | 17.96 | 0.74 | 2.02 | 6.69 | 3.64 | 3.12 | 44.54 | 2.03 |



**4.** Root length density patterns of IR36 and Dular in different layers of 3 soils.

silt > sand > loam > clay loam > clay > silty clay. A high percentage of silt or sand coupled with a moderate clay content (20-35%) provided a favorable physical environment for root growth and penetration.

## Soil strength and soil temperature interactions

The effect of soil strength on shoot and root growth of emerging rice seedlings in a lateritic sandy clay loam soil shows a close relationship between penetration resistance and shoot and root length (Kumar et al 1970). At higher penetration resistance, emergence was adversely affected (Table 5). Although plumule did not emerge, radicle elongation was not appreciably influenced in high-strength soils. Root penetration continued to a considerable depth, showing that the roots are capable of exerting higher pressure than the shoot.

However, root growth appears to be a function of soil strength and is adversely affected by higher penetration resistance. When penetration resistance increased from 1.03 J/cm$^3$ to 6.12 J/cm$^3$, the maximum root length decreased from 10.8 cm to 1.7 cm.

Soil temperature and mechanical impedance and their interaction influence root growth. Root growth increased as the submerged-soil temperature was raised (Mar et al 1976). Beyond a 37°-25° C temperature range and above a bulk density of 1.6 g/cm$^3$, root growth decreased drastically (Table 6). Rice roots degenerated in submerged conditions, especially under higher temperature regimes. But the degeneration at higher temperature regimes was low at lower bulk densities.

**Table 4. Influence of particle size distribution on rice root growth (Kar et al 1979).**

| Soil | Penetration depth (cm) | Roots at base (no.) | Roots near tip (no.) | Volume ($cm^3$) | Dry weight (g) | Shoot-root ratio |
|---|---|---|---|---|---|---|
| Clay | 13.9 | 176.2 | 41.0 | 3.50 | 0.54 | 4.96 |
| Silty clay | 12.9 | 160.2 | 38.2 | 3.22 | 0.52 | 4.44 |
| Clay loam | 15.5 | 164.5 | 41.7 | 3.65 | 0.55 | 4.28 |
| Silt | 18.0 | 247.2 | 53.0 | 5.22 | 0.83 | 3.76 |
| Silty clay loam | 20.1 | 239.7 | 61.2 | 5.92 | 0.89 | 3.96 |
| Loam | 16.2 | 211.2 | 47.0 | 4.22 | 0.67 | 3.97 |
| Sandy loam | 23.2 | 239.3 | 58.2 | 5.50 | 0.85 | 3.95 |
| Sand | 18.4 | 261.0 | 70.0 | 5.00 | 0.79 | 3.71 |
| S.E.M. ± | 0.21 | 3.97 | 2.53 | 0.11 | 0.02 | 0.07 |
| LSD at 5% | 0.91 | 11.69 | 7.46 | 0.34 | 0.05 | 0.20 |
| LSD at 1% | 1.24 | 15.91 | 10.15 | 0.46 | 0.07 | 0.27 |

**Table 5. Influence of soil strength on emergence and seedling growth (Kumar et ai 1970).**

| Penetration resistance (J/cm$^3$) | Bulk density (g/cm$^3$) | Emergence (%) | Side roots (no.) | Shoot length (cm) | Maximum root length (cm) |
|---|---|---|---|---|---|
| 1.029 | 1.5 | 95.0 | 3.30 | 10.70 | 10.80 |
| 1.686 | 1.6 | 80.0 | 3.45 | 9.35 | 6.65 |
| 2.622 | 1.7 | 75.0 | 2.40 | 10.45 | 7.90 |
| 4.750 | 1.8 | 25.0 | 1.15 | 3.55 | 5.70 |
| 5.125 | 1.9 | 5.0 | 0.50 | 1.75 | 4.95 |
| 6.121 | 2.0 | 0.0 | 0.00 | 0.00 | 1.70 |

**Table 6. Effect of interaction between submerged soil temperature regime and bulk density of a lateritic sandy loam soil on root growth of rice (Kar et al 1976).**

| Bulk density (g/cm$^3$) | Soil temperature regime (ºC) | | | | LSD | |
|---|---|---|---|---|---|---|
| | 27-15 | 32-20 | 37-25 | 42-30 | 5% | 1 % |
| | | *Root dry weight* (g) | | | | |
| 1.5 | 1.46 | 3.18 | 3.44 | 1.22 | | |
| 1.6 | 1.53 | 3.05 | 3.62 | 1.25 | 0.25 | 0.33 |
| 1.7 | 1.60 | 2.38 | 2.46 | 1.41 | | |
| 1.8 | 1.63 | 1.80 | 1.92 | 1.49 | | |
| | | *Roots at base (no.)* | | | | |
| 1.5 | 274.6 | 466.6 | 485.6 | 232.3 | | |
| 1.6 | 289.0 | 454.0 | 528.6 | 243.3 | 8.64 | 11.62 |
| 1.7 | 330.6 | 375.3 | 419.6 | 271.0 | | |
| 1.8 | 346.3 | 360.6 | 355.6 | 312.0 | | |
| | | *Degenerated roots at base (no.)* | | | | |
| 1.5 | 29.3 | 181.0 | 290.3 | 164.3 | | |
| 1.6 | 20.0 | 104.6 | 205.6 | 151.0 | 6.81 | 9.16 |
| 1.7 | 7.0 | 71.6 | 92.0 | 96.6 | | |
| 1.8 | 11.6 | 67.6 | 74.6 | 109.6 | | |

## CONCLUSION

Efficient management of water resources in diverse drought-prone areas is an important environmental modification for improving yields. The hydrophysical properties of soil that affect infiltration, root-zone available water storage capacity, and rooting characteristics are important in drought studies. Soil physical properties such as intake rate, texture, soil strength (compaction), and hydraulic characteristics (retention and transmission) need to be determined in all studies. Interaction among these physical properties and rooting characteristics (rooting depth, rooting density, and root porosity) should be considered in understanding the effects of drought and in breeding and selecting cultivars for drought resistance.

## REFERENCES CITED

Anonymous. 1979. Physical properties of soils of India, I.C.A.R. Coordinated Research Project on Improvement of Soil Physical Conditions, Division of Agricultural Physics, IARI, New Delhi.

Arya, L. M., G. R. Blake, and D. A. Farrell. 1975. A field study of soil water depletion patterns in presence of growing soybean roots: II. Effect of plant growth on soil water pressure and water loss patterns. Soil Sci. Soc. Am. J. 39:430-436.

Gardner, W. R. 1964. Relation of root distribution to water uptake and availability. Agron. J. 56:41-45.

Hasegawa, S., F. T. Parao, and S. Yoshida. 1979. Root development and water uptake under field condition. IRRI Saturday Seminar, 24 February 1979. (mimeo.)

Hsiao, T. C., J. C. O'Toole, and V. S. Tomar. 1980. Water stress as a constraint to crop production in the tropics. Pages 339-369 *in* Priorities for alleviating soil-related constraints to food production in the tropics. International Rice Research Institute, Los Baños, Philippines.

Kar, S., S. B. Varade, and B. P. Ghildyal. 1979. Pore size distribution and root growth relations of rice in artificially synthesized soils. Soil Sci. 128:364-368.

Kar, S., S. B. Varade, T. K. Subramanyam, and B. P. Ghildyal. 1974. Nature and growth pattern of rice root system under submerged and unsaturated conditions. Il Riso 23(2):173-179.

Kar, S., S. B. Varade, T. K. Subramanyam, and B. P. Ghildyal. 1976. Soil physical conditions affecting rice root growth: bulk density and submerged soil temperature regime effects. Agron. J. 68:23-26.

Kumar, V., K. T. Mahajan, and S. B. Varade. 1970. Effect of soil strength on germination, emergence and growth of paddy seedlings. The Harvester.

Maurya, P. R., and B. P. Ghildyal. 1975. Root distribution pattern of rice varieties evaluated under upland and flooded field conditions. I1 Riso 24 (3):239-244.

Ogata, G., L. A. Richards, and W. R. Gardner. 1960. Transpiration of alfalfa determined from water content changes. Soil Sci. 80:179-182.

Pradhan, S. K., S. B. Varade, and S. Kar. 1973. Influence of soil water conditions on growth and root porosity of rice. Plant and Soil 38:501-507.

Reicosky, D. C., R. J. Millington, A. Klute, and D. B. Peters. 1972. Patterns of water uptake and root distribution of soybeans in the presence of a water table. Agron. J. 64:292-297.

Richards, L. A., and C. H. Wadleigh. 1952. Soil water and plant growth. Page 13 *in* Soil physical conditions and plant growth. Amer. Soc. Agron. Monogr. 2.

Ritchie, J. T. 1973. Influence of soil water status and meteorological conditions on evaporation from a corn canopy. Agron. J. 65:893-897.

Ritchie, J. T., R. Burnett, and R. C. Henderson. 1972. Dryland evaporative flux in a subhumid climate: III. Soil water influence. Agron. J. 64:168-173.

Tomar, V. S., and B. P. Ghildyal. 1973. Internal leaf water status and transport of water in rice plants. Agron. J. 65:861-865.

Tomar, V. S., and J. C. O'Toole. 1979. Lower limit of available water and rice response to soil moisture during drought stress. IRRI Saturday Seminar, 17 November 1979. (mimeo.)

Van Bavel, C. H. M., G. B. Stirk, and K. J. Brust. 1968. Hydraulic properties of a clay loam soil and the field measurement of water uptake by roots: II. The water balance of the root zone. Soil Sci. Soc. Am. J. 31:317-321.

Veihmeyer, F. J., and A. H. Hendrickson. 1927. Soil moisture conditions in relation to plant growth. Plant Physiol. 2:71-78.

Veihmeyer, F. J., and A. H. Hendrickson. 1949. Methods of measuring field capacity and wilting percentage of soils. Soil Sci., 68:75-94.

Veihmeyer, F. J., and A. H. Hendrickson. 1955. Does transpiration decrease as the soil moisture decreases? Trans. Amer. Geo. Phys. Union 36:425-448.

# THE RICE ROOT SYSTEM: ITS DEVELOPMENT AND FUNCTION

**S. YOSHIDA AND S. HASEGAWA**

The rice root system is basically composed of nodal roots. A tiller and roots emerge simultaneously from the same node. When the nth leaf emerges, a tiller and roots emerge from the (n-3)th node. Rice varieties differ laterally and vertically in their rooting habits. Differences in the root density of deep- and shallow-rooted varieties are found in the soil layers deeper than 30 cm below the soil surface. This provides an empirical basis for using deep root-to-shoot ratio to characterize the deep rooting habit in rice. The deep root-to-shoot ratios of rice varieties are correlated with drought resistance under field conditions.

Comparison of root systems in rice and sorghum indicates no relation between plant height and rooting depth. Tillering habit is associated with rooting habit. A plant with few and early tillers tends to have a deep root system.

In an environment where drought is a common cause of crop failure, not only water stress per se limits yield; low levels of nitrogen fertilizer also impose a limit. Under such conditions, the target yield should be set at a moderate level of 3-4 t/ha. Low tillering capacity is not a restraint to achieving such moderate yields.

When water is supplied uniformly to all soil profiles, rice roots extract water preferentially from the shallow layers. As soil water potential in the surface decreases, water retained in the deeper layers makes a larger contribution to evapotranspiration. When most soil water in the shallow layers has been extracted, the plant

---

Department of Plant Physiology, The International Rice Research Institute, Los Baños, Philippines, and National Rice Research Institute of Agricultural Engineering, Tsukuba, Japan.

> is unable to extract sufficient water to satisfy evapotranspiration demands, even though the soil water potential in deep layers is still high.
>
> Thus, although the surface soil can be depleted of water to – 15 bars and the crop suffers severe water stress, a considerable amount of soil water remains unused in the deep layers. A deep root system has greater ability to absorb soil water and soil nitrogen or fertilizer nitrogen from the deep soil layers than a shallow root system. Under drought, a deep root system helps the plant avoid water stress by absorbing water stored in the deep soil layers. When rainfall is adequate and nitrogen is required for better growth, deep roots help the plant absorb soil or fertilizer nitrogen from the deep soil layers.

Rice varieties differ markedly in both shoot and root morphology. A deep root system is considered an important component of drought resistance because it relates to the plant's ability to exploit water retained in the deep soil layers.

An elegant technique for length measurement, devised by Newman (1966), modified by Marsh (1971), and combined with a core-sampling technique (Burch et al 1978), has provided an efficient means to study root systems quantitatively. The root box of simple design (Parao et al 1976) also has provided an easy way to examine a relatively large number of genotypes for rooting depth. Data presented here have been obtained mostly by these two techniques.

This paper discusses a) the rice root system, b) plant type and root growth, c) water uptake, and d) absorption of soil and fertilizer nitrogen.

## THE RICE ROOT SYSTEM

Rice develops a radicle (seminal root), mesocotyl roots, and nodal (adventitious) roots. After germination, one radicle emerges and elongates to a maximum length of about 15 cm. It functions until the seventh leaf stage. Mesocotyl roots emerge from the axis between the node of the coleoptile and the base of the radicle. Mesocotyl roots develop only under deep seeding or when the seed is treated with certain chemicals (Hoshikawa 1975).

The rice root system is composed basically of nodal roots. Rice differs in this regard from wheat, which develops and maintains several seminal roots until maturity.

A simple rule operates in rice tillering and rooting. A tiller and its roots come from the same node at the same time. When the nth leaf emerges, a tiller and roots start emerging from the (n-3)th node. Each node usually develops 5-25 roots (Fujii 1974). When the development of root, leaf, and tiller is examined, it is more convenient to regard an internode rather than a node as a unit (Kawata et a1 1963). A leaf and thin roots emerge from the internode's upper region and tiller and thick roots develop from the internode's lower region.

Root growth, in terms of weight, number, and gross morphology appears to reach its maximum around flowering. Branching, however, continues to produce new active portions of the root system until maturity. Those active portions may have important functions during the grain filling period (Kawata and Soezima 1974). Presence of newly branched roots also may indicate adequacy of the soil environment for root growth. Under lowland conditions, rice is known to develop 6-order branched roots until maturity. In root-box grown rice, we have observed 5th order branched roots at flowering. Root diameter becomes successively smaller (ranging from about 1,000 to 40 µm) as the order of branching increases.

Formation of root hairs is affected by the root environment. Aerobic conditions in dryland soils favor root hair formation; reductive conditions in flooded soils impair it (Kawata and Ishihara 1959, 1961). Rice root hairs are 5-10 µm in diameter and 50-200 µm long.

Thick or thin roots are an easily recognizable root characteristic, although it is not easy to estimate quantitative proportions of thick or thin roots to the whole root mass. The roots of some traditional drought-resistant dryland varieties, such as OS4 and Palawan, are mostly long and thick. Those of semidwarfs, such as IR8 and IR20, generally are thin and fibrous (Chang and Vergara 1975). Often it is claimed that a high proportion of thick roots in a root system is associated with deep penetration.

In our examination of 13 varieties grown in root boxes under dryland conditions, thick roots are defined as those that can be easily separated from fibrous roots by hand. The diameters of these thick roots ranged from 0.7 to 1.5 mm. Thick roots of some dryland varieties are thicker than those of wetland varieties. The percentages of total weight of thick roots to the whole root mass range from 44% for IR8 to 69% for Bluebonnet (Table 1). This variation is rather small compared with variation in root-to-shoot ratios. As a result, thick root weight per gram of shoot is correlated with the root-to-shoot ratio. With higher root-to-shoot ratios, more thick roots are found per gram of shoot. Because traditional dryland

**Table 1. The ratios of roots to shoots, percentages of thick roots in total root weight, and ratios of thick roots to shoots of dryland and wetland rice varieties (IRRI 1975).**

| Variety | Root:shoot (mg/g) | Thick roots (% of root total wt) | Thick roots:shoot: (mg/g) |
|---|---|---|---|
| Rikuto Norin 21 | 117 | 63 | 74 |
| OS4 | 113 | 61 | 69 |
| Palawan | 112 | 54 | 60 |
| M1-48 | 104 | 62 | 64 |
| Miltex | 88 | 60 | 53 |
| IR5 | 83 | 57 | 47 |
| IR8 | 82 | 44 | 36 |
| PI 215936 | 81 | 67 | 54 |
| Bluebonnet | 75 | 69 | 52 |
| Peta | 71 | 51 | 36 |
| H4 | 61 | 54 | 33 |
| IR20 | 49 | 64 | 31 |

**Table 2. Effects of variety, depth, and growth stage on length-to-weight ratio of roots of four rice varieties (IRRI 1978).**

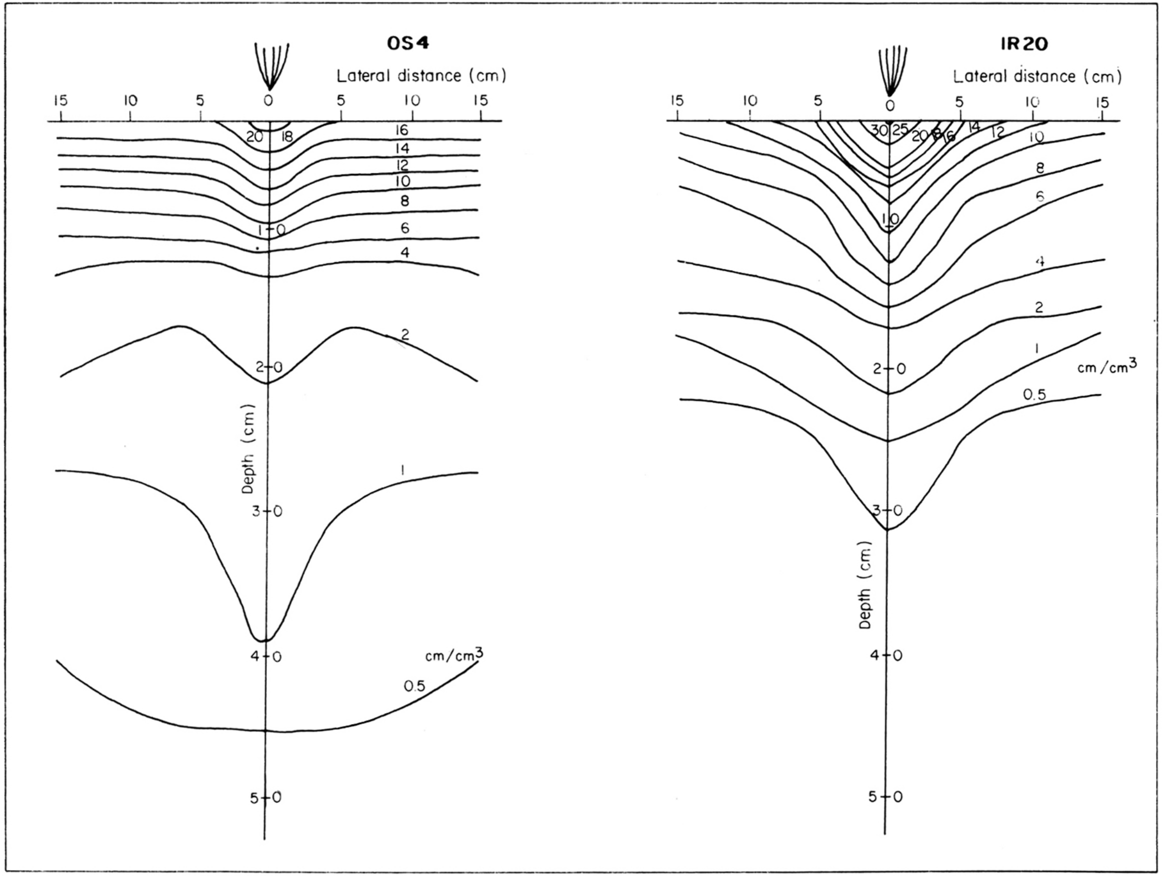
| Variety | Specific root length (m/g) | | | |
|---|---|---|---|---|
| | 4 wk | | Heading | |
| | Total roots | Roots below 30 cm | Total roots | Roots below 30 cm |
| Jappeni Tungkungo | 334 | 651 | 440 | 705 |
| IR20 | 238 | 530 | 433 | 973 |
| N22 | 310 | 497 | 319 | 549 |
| OS4 | 204 | 355 | 163 | 285 |
| Mean | 272 | 508 | 339 | 628 |

rice varieties usually have higher root-to-shoot ratios, they tend to have more thick roots per gram of shoot. The percentages of thick roots are not necessarily higher in dryland than in wetland varieties.

Average diameter of the entire root system can be estimated by total root length and root weight. Specific root length or length-to-weight ratio is defined as length in meters per gram of dry root. The specific root length varies with variety, depth, and growth stage (Table 2). Greater specific root lengths imply smaller diameters. At heading, drought-resistant OS4 and N22 have much smaller specific root lengths than drought-susceptible IR20 and Jappeni Tungkungo. Roots are much thinner in the deep soil layer than in the shallow layer. Average specific root length of 4 varieties at two growth stages is about 300 m/g. Assuming that average dry matter of roots is 10%, a specific root length of 300 m/g corresponds to a diameter of 0.2 mm (IRRI 1978).

Rice varieties differ markedly in their rooting habits, both laterally and vertically. Iso-root density curves indicate that roots of IR20 are concentrated around the center of the plant. Those of OS4 are spread laterally (Fig. 1). In the upper soil layers, 0-30 cm, there is not much difference in root density between the two varieties. Below 30 cm the vertical distribution of roots of the 2 varieties differs significantly. Further information on the rice root system was obtained for seven varieties grown in the field (Table 3). Traditional dryland varieties have much deeper root distributions than wetland varieties. Differences in the root density of deep- and shallow-rooted varieties are found in the soil layers deeper than 30 cm below the surface. The root-box technique and core-sampling method in the field agree on the varietal difference in vertical root distribution unless there is a high degree of mechanical impedance in the field soil.

Rice often is described as a shallow-rooted crop. The susceptibility of rice to drought also is attributed to its shallow rooting habit. But is rice really shallow-rooted compared with other crop species? Figure 2 shows vertical root distribution of four dryland crops and two rice varieties. The two rice varieties have much larger root lengths per unit land area than the dryland crops. IR36, a wetland variety, has much shallower roots than five other crops. Root densities of OS4 (a



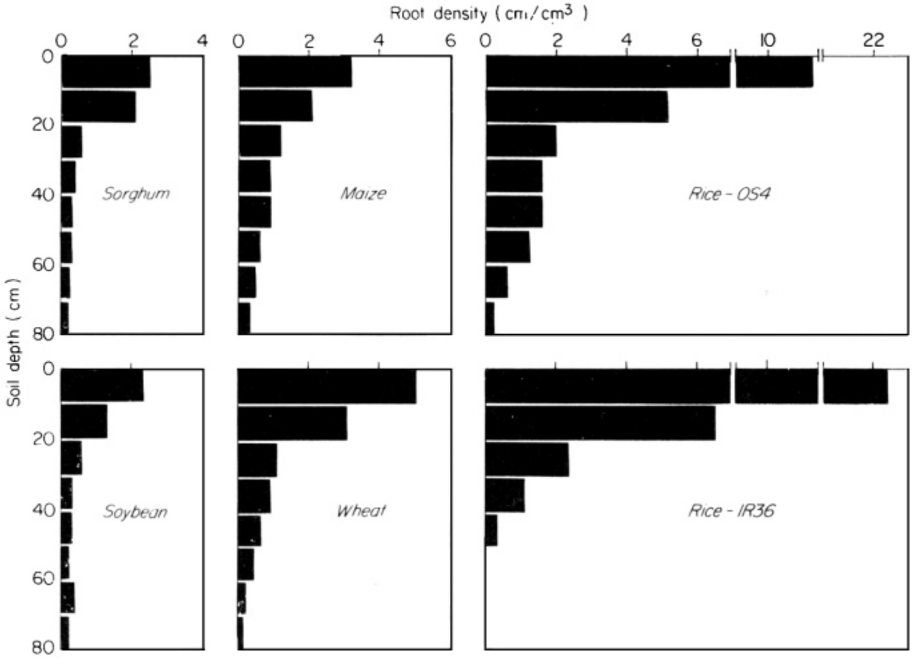
**1.** Iso-root density diagrams of OS4 and and IR20 at 41-43 days after sowing (IRRI 1978).

**Table 3. Vertical distribution of root density of 7 rice varieties grown in a dryland field (IRRI 1978).**

| Designation | Root density ($\text{cm}^{-2}$) at depth of | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 0-10 cm | 10-20 cm | 20-30 cm | 30-40 cm | 40-50 cm | 50-60 cm | 60-70 cm | 70-80 cm |
| IR20 | 14.4 | 2.8 | 0.9 | 0.4 | 0.1 | - | - | - |
| IR2035-117-3 | 22.7 | 5.8 | 0.8 | 0.1 | 0.1 | - | - | - |
| IR442-2-58 | 16.8 | 7.1 | 1.2 | 0.3 | 0.1 | 0.1 | 0.1 | 0.1 |
| OS4 | 12.6 | 1.4 | 0.8 | 0.9 | 0.8 | 0.5 | 0.5 | 0.5 |
| Moroberekan | 11.8 | 2.3 | 0.9 | 0.8 | 0.6 | 0.8 | 0.4 | 0.2 |
| Salumpikit | 16.2 | 5.5 | 1.9 | 1.4 | 0.8 | 0.6 | 0.3 | 0.1 |
| 20 A | 19.8 | 2.6 | 0.9 | 0.8 | 0.9 | 0.9 | 0.6 | 0.4 |

dryland rice variety) in the deep soil layers are as high as or even higher than those of sorghum, maize, and soybean. One remarkable characteristic of the rice root system is high root density in the surface soil. IR36's root density is greater than 20 cm/cm$^3$ near the soil surface. Such a high root density is attributed to rice's tillering and nodal rooting habits.

Rooting depth appears to be influenced by water regimes. The rooting depth of a variety is deepest when it is grown under dryland conditions and the shallowest under submerged conditions without percolation. Rooting depth becomes intermediate when adequate percolation is provided under submerged conditions (IRRI 1977). This suggests that an aerobic soil environment favors deep root



**2.** Vertical root distribution of 4 upland crops and 2 rice varieties.

growth. A wetland rice tends to be shallow-rooted because typical wetland varieties are genetically shallow-rooted and the anaerobic environment impairs root depth. The presence of hardpan near the soil surface also may restrict deep-growing roots.

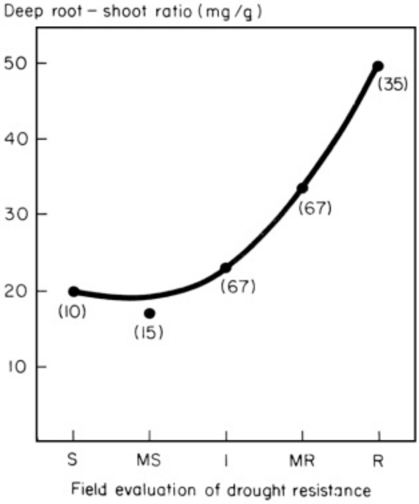
Deep root-to-shoot ratio is one way to characterize depth growth of a rice root system. Meguro (1961) first used the reciprocal of deep root-to-shoot ratio. The deep root-to-shoot ratio is based on the concept that the ability of a variety to absorb water from the deep soil layers is one important characteristic determining a variety's resistance to drought because soil drying starts with the surface soil during drought. Moisture available for the crop is retained in the deep soil layers. Shoot weight may represent the magnitude of a crop's demand for transpiration.

Thus, the deep root-to-shoot ratio is considered an index to express a supply-demand relationship in a crop's water economy during drought. Deep root-to-shoot ratio is the weight in milligrams of a root fraction below 30 cm from the soil surface per 1 gram of shoot. Deep root-to-shoot ratios range from less than 10 to 90 mg/g. Most varieties have deep root-to-shoot ratios of 10-50 mg/g.

The difference between shallow-rooted and deep-rooted varieties lies in root penetration of the soil layers deeper than 30 cm from the surface. This provides an empirical basis for use of the deep root-to-shoot ratio to characterize deep rooting habit. The deep root-to-shoot ratios of rice varieties are well correlated with drought resistance under field conditions (Fig. 3).

## PLANT TYPE AND ROOT GROWTH

Since root characteristics are invisible, it would be highly desirable if relationships between plant type and root growth characteristics were known. Such information would facilitate better understanding of yield performance of rice varieties under different water regimes and would be useful for plant breeders whose primary



**3.** Relationship between deep-root-to-shoot ratio and field evaluation of drought resistance, as scored at IRRI. The numbers in parentheses indicate number of genotypes examined. S = susceptible, MS = moderately susceptible, MR = moderately resistant, R = resistant.

**Table 4. Correlation coefficients for 1,081 entries screened for deep root systems (IRRI 1980).**

| | Plant height | Tiller number | Deep root score |
|---|---|---|---|
| Days to flowering | 0.133** | 0.152** | 0.075* |
| Plant height | | –0.462** | -0.435** |
| Tiller number | | | 0.385** |

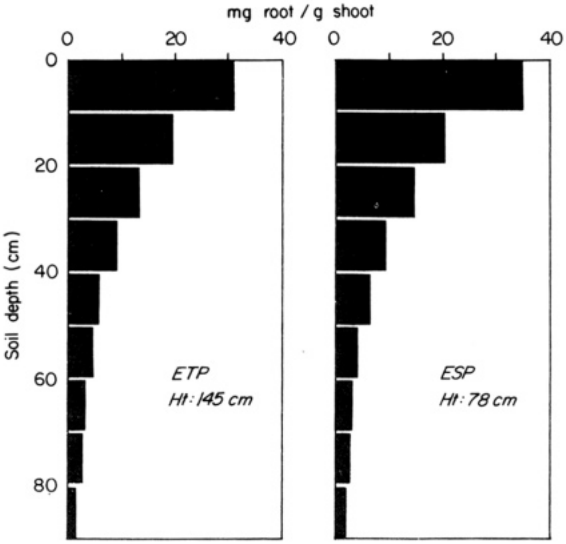
*Significant at 5% level
**Significant at 1% level

concern is to select varieties for varied environments.

Traditional dryland rice varieties generally are described as tall, low-tillering, deep-rooted, and early maturing (Chang and Vergara 1975). However, these varietal traits may not necessarily be related to drought resistance. Tall stature, for example, makes rice more competitive with weeds (Moody 1977).

To study the relationship between plant type and root growth 1,081 varieties and lines were grown in root boxes. Simple correlation coefficients were computed between deep root score and agronomic characteristics (Table 4). The deep root score (1-5) is the simplified and standardized measure of deep root-to-shoot ratio, using OS4 as a deep-rooted check (score 2) and IR20 as a shallow-rooted check (score 5).

Growth duration (days to flowering) is not correlated with the deep root score. In fact, many dryland rice varieties are early maturing and deep rooted. In wheat, however, a longer growth duration is related to a deeper root system (Asana and Sinha 1970). The deep root score is negatively correlated with plant height. Tall varieties tend to have deep root systems. The deep root score is positively corre-

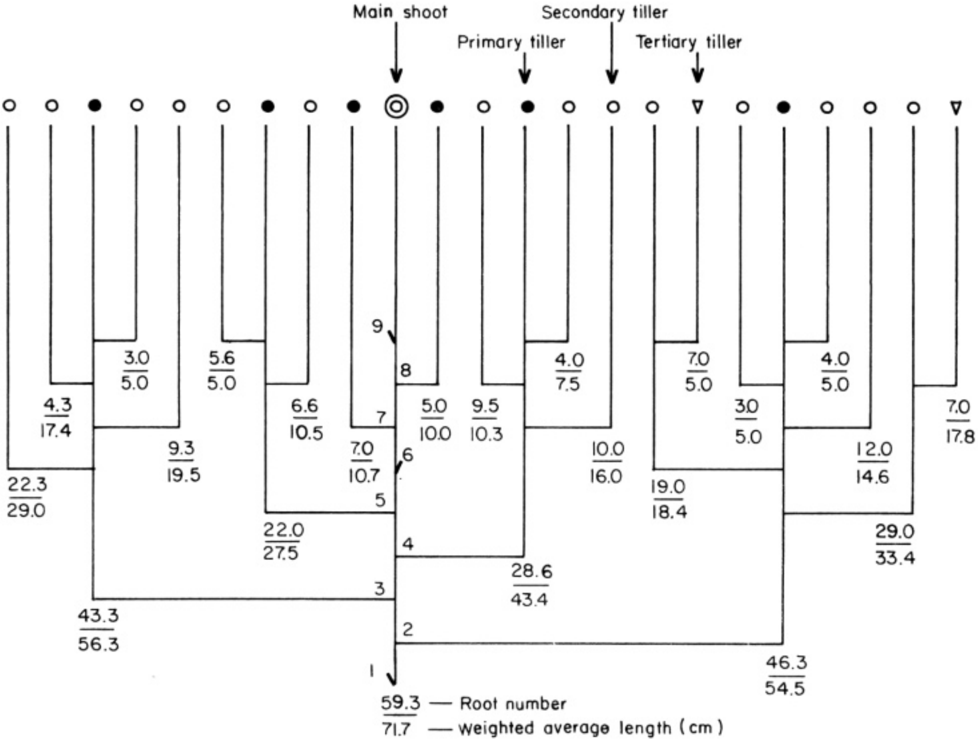


**4.** Vertical root distribution of early tall (ETP) and early short Peta (ESP) at flowering (IRRI 1975).

lated with tiller number, implying that low tillering varieties tend to have deep root systems. There is a negative correlation between plant height and tiller number. These results confirm the common observation that dryland rice varieties are usually tall, low tillering, and deep rooted. The question remains whether tall plant stature or low-tillering habit is genetically or physiologically linked with deep root system.

To answer that question, vertical root distributions of two isogenic lines and three sorghum varieties were examined. The two isogenic lines of rice differ markedly in their plant height but are almost identical in their rooting habit (Fig. 4). In the three sorghum varieties tested, the shortest variety, Mini Milo Br. 54, had the deepest and most proliferated root system (IRRI 1975). Those experiments indicate that there is no apparent relationship between plant height and rooting depth in rice and sorghum. Consequently, it should be possible to screen rice varieties for short stature with a deep root system.

Since the nth leaf and a tiller and roots from the axil of the n-3th node emerge synchronously, chronological age of tillers can be identified. In Figure 5, tillers arranged on the same horizontal line are considered to be the same age. A clear trend shows that early tillers have more and longer roots than late tillers, regardless of tiller order and the position of the node from which they emerge. Roots of the main shoot are the longest and largest in number. Among the primary tillers, tillers



**5.** Relationship between tillering pattern and root characteristics of rice (variety Lalnakanda 41).

**Table 5. Number of roots found on tillers of different orders at flowering (mean of 3 replications) (IRRI 1978).**

| Tiller order | Shoots (no.) | Total roots[a] (no.) | Roots in each tiller (no.) | Maximum length (cm) | Weighted average length (cm) |
|---|---|---|---|---|---|
| | | *IR20* | | | |
| Main shoot | 1 | 64.0 ( 7.6) | 64.0 | 105.0 | 22.9 |
| Primary tiller | 9 | 302.3 (35.9) | 33.6 | 95.0 | 9.7 |
| Secondary tiller | 20 | 355.4 (42.3) | 17.8 | 75.0 | 6.7 |
| Tertiary tiller | 9 | 119.0 (14.1) | 13.2 | 25.0 | 5.5 |
| Total | 39 | 840.7 | 128.6 | | |
| | | *OS4* | | | |
| Main shoot | 1 | 63.6 (15.9) | 63.6 | 135.0 | 47.5 |
| Primary tiller | 6 | 129.7 (32.4) | 21.6 | 125.0 | 22.1 |
| Secondary tiller | 10 | 148.3 (37.1) | 14.8 | 125.0 | 14.3 |
| Tertiary tiller | 6 | 58.5 (14.6) | 9.7 | 75.0 | 12.3 |
| Total | 23 | 400.1 | 109.7 | | |
| | | *Lalnakanda 41* | | | |
| Main shoot | 1 | 59.3 (16.1) | 59.3 | 135.0 | 71.7 |
| Primary tiller | 6 | 152.2 (41.5) | 25.4 | 115.0 | 33.7 |
| Secondary tiller | 14 | 141.6 (38.6) | 10.1 | 115.0 | 14.0 |
| Tertiary tiller | 2 | 14.0 ( 3.8) | 7.0 | 55.0 | 11.4 |
| Total | 23 | 367.1 | 101.8 | | |
| | | *CRI43-2-2* | | | |
| Main shoot | 1 | 65.3 (22.8) | 65.3 | 105.0 | 49.1 |
| Primary tiller | 5 | 120.2 (42.0) | 24.0 | 105.0 | 31.1 |
| Secondary tiller | 13 | 95.4 (33.4) | 7.3 | 95.0 | 11.4 |
| Tertiary tiller | 1 | 5.0 ( 1.7) | 5.0 | 5.0 | 5.0 |
| Total | 20 | 285.9 | 101.6 | | |

[a] Figures in parentheses are percent of whole plant.

2 and 3 have more and longer roots than tiller 4, which in turn has more and longer roots than tiller 5. Such a trend in root number per shoot agrees with Iwatsuki's (1932) findings on wetland rices.

The relationship between tillers and roots also can be examined by tiller order (Table 5). Within the same variety, the primary tillers are larger in both numbers of roots per tiller and weighted average root length than the secondary tillers, which in turn are larger than the tertiary tillers. Drought-resistant Lalnakanda 41 has the deepest root system and drought-susceptible IR20 has the shallowest root system. Maximum root length of the main shoot ranges from 105 cm for IR20 and CR143-2-2 to 135 cm for OS4 and Lalnakanda 41; the weighted average length ranges from 23 cm for IR20 to 72 cm for Lalnakanda 41. Varietal differences were much greater in weighted average length than in maximum root length. Such marked differences in weighted average length may be accounted for in part by differences in assimilate supply to root growth.

First, competition for assimilate supply would occur between a growing tiller and roots of the mother shoot when active tillering proceeds. As a consequence, assimilate supply to roots of the mother shoot would be reduced, resulting in restricted root growth.

Second, even after the tiller has become self-sustaining, an increased number of tillers per plant would increase mutual shading within the plant. Shading reduces root growth more than shoot growth (IRRI 1976). A similar effect of low light intensity on root growth has been reported for bean plants (*Phaseolus vulgaris*) (Brouwer and De Wit 1968).

For these reasons, a highly-tillered plant tends to have a short root system. The partition of assimilate between shoot and root accounts for the difference between IR20 and three other deep-rooted varieties. However, it fails to account for the differences among the three. Obviously, some other factors affect the weighted average length of roots.

This discussion indicates that a rice root system is composed of many nodal roots. A plant with few and early tillers tends to have a deep root system. Low tillering capacity appears to be one desirable characteristic when a rice plant has to depend on soil moisture retained in the deep soil layers during frequent droughts.

On the other hand, the low tillering capacity of traditional dryland varieties is considered to limit their yield potentials under the most favorable cultural conditions. This is based on the analysis that the inherent low yielding capacity of traditional dryland varieties is due to limited panicle numbers per unit area (Chang et a1 1972). Such analysis led Chang and Vergara (1975) to conclude that the low tillering capacity of most dryland varieties is the main restraint to high yields.

The adequacy of this conclusion must be examined in terms of the target yield, water regimes under which rice is grown, and stability versus high yield.

In an environment where drought is a usual cause of crop failure, the farmer's primary concern would be to stabilize yield rather than to achieve high yields. Because of high risk, the farmer would be reluctant to put much input, such as fertilizers, into rice farming. Rising costs of fertilizers would increase that reluctance. Under such conditions, not only does water stress *per se* limit the yield; low levels of nitrogen fertilizer also impose a limit on rice yield. Therefore, the target yield should be set at a moderate level, 3-4 t/ha.

Because the efficiency of applied fertilizer to rice production is about 15-25 kg rice/kg applied N, a considerable amount of fertilizer nitrogen is required to produce 3 t/ha. The amount is dependent on the level of soil fertility (Yoshida and Oka 1982). When a soil without fertilizer can produce 2 t/ha, 50 kg N/ha will produce 2.75-3.25 t/ha. Most dryland soils are much less fertile than this model and require more than 50 kg N/ha to produce 3 t/ha.

Now the question is whether low tillering capacity is still a restraint to such a moderate yield. Chang and Vergara (1975) stated that average yields of traditional dryland varieties such as Palawan, M1-48, and OS4 are limited to about 3 t/ha. They also stated that, under the most favorable climatic and soil conditions in the Philippines, about 4 t/ha seems to be the upper limit for most traditional dryland varieties. These statements indicate that low tillering capacity is not a restraint to achieving 3-4 t/ha.

Yielding ability of traditional tall dryland varieties may be increased by modifying plant height to moderately tall or short stature. Traditional tall and low tillering varieties usually bear large panicles. It may be possible to look for varieties that bear even larger panicles on the main shoot and a few primary or secondary tillers. Furthermore, when panicle number per unit area is limiting, yield can be increased by increasing seeding density.

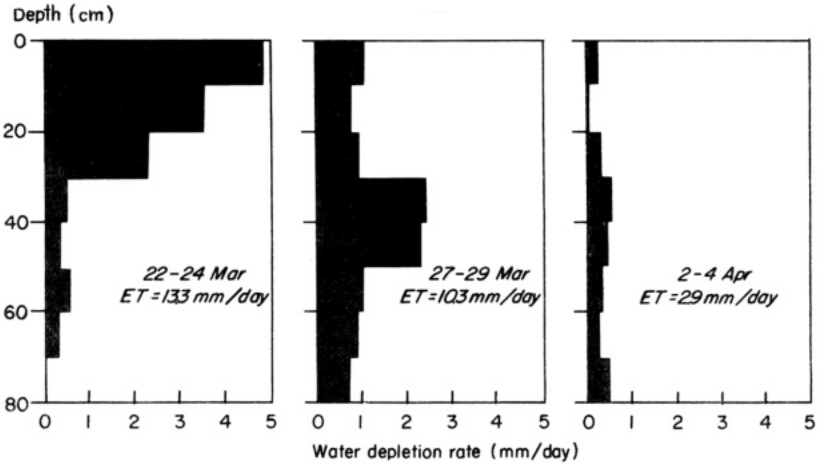
When rainfall is abundant and evenly distributed throughout the crop season, such as in the Peruvian jungle, good wetland varieties perform well (Kawano et al 1972). Under such conditions, water stress is not the problem. The major problems are disease resistance and soil acidity. It is obvious that the choice of a desirable plant type is environment-specific.

Apart from tillering capacity, some other traits merit attention. Specific leaf weight is one. Increasing photosynthetic rate per unit leaf area is one way to increase water use efficiency, because the amount of transpiration is primarily related to leaf area. Larger specific leaf weights are correlated with higher leaf photosynthetic rates (Murata 1961, Ohno 1976) or higher net assimilation rates (Ohno 1976). A wide range of differences are found in specific leaf weights of rice varieties (Ohno 1976).

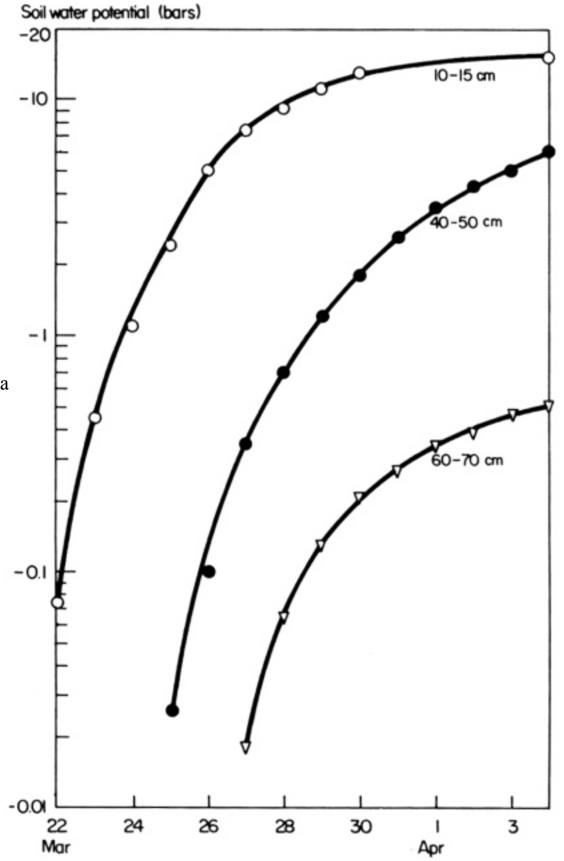
Droopy leaves are considered desirable for wheat grown in nonirrigated areas. The droopy-leaved canopy may retain dew better and longer than the erect-leaved canopy (Asana and Sinha 1970). In rice, tall varieties normally have long, droopy leaves. The leaf arrangement of a rice canopy is largely determined by plant height.

## WATER UPTAKE BY A RICE ROOT SYSTEM

When water is supplied uniformly to all soil profiles, rice roots extract water preferentially from the shallow layers (Fig. 6, left). As the soil water potential in the surface decreases, water retained in the deeper layers makes a larger contribution to evapotranspiration (Fig. 6, middle). When most soil water in the shallow layers has been extracted, the plant is unable to extract sufficient water to satisfy evapotranspiration demand, even though the soil water potential in the deepest



**6.** Water extraction patterns of OS4 crop after irrigation in March 1978 (Hasegawa and Yoshida, 1981a). ET = evapotranspiration.



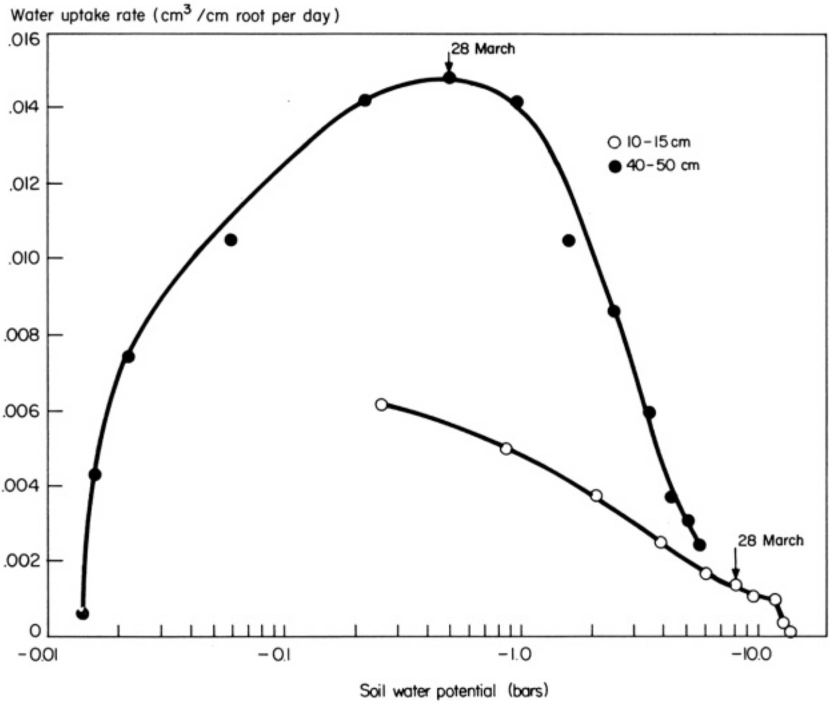
**7.** Soil water potentials with time at 3 depths (Hasegawa and Yoshida 1981a).

layer is still high (Fig. 7). Presumably, root density in the deep soil layers is too low to meet the crop's requirement.

One major reason why shallow layers are depleted first is high root densities. Also, there is evidence to indicate the presence of axial resistance in rice root systems.

Water uptake rate by rice root systems is not a simple function of soil water potential or soil moisture content (Fig. 8). Water uptake rate of rice roots in the 10–15 cm soil layer decreases with a decrease in soil water potential. However, in the 40–50 cm soil layer, water uptake rate increases with a decrease in soil water potential down to –0.5 bar, then starts decreasing with a further decrease in soil water potential.

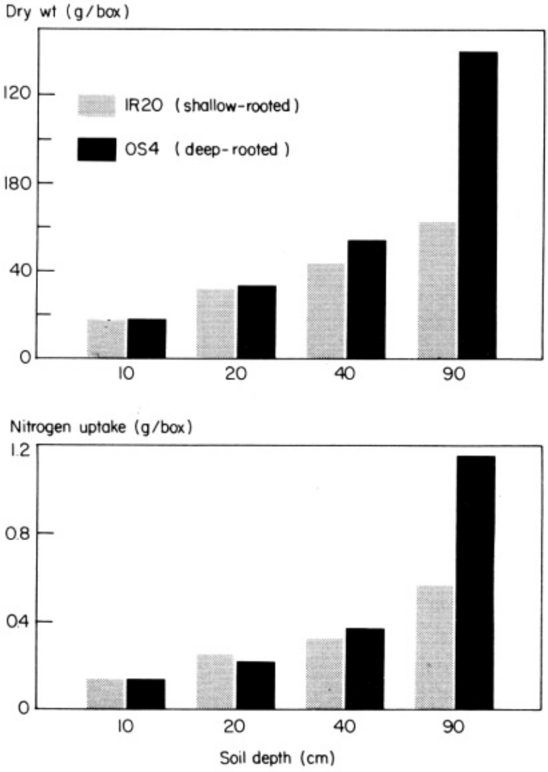
These results can be explained if axial resistance is assumed to be significant. The existence of resistances to water movement from soils to plants has been the subject of intensive studies (Gardner et al 1962, Newman 1969, Lawlor 1972, Reicosky and Ritchie 1976). Kramer (1969) reported considerable resistance to movement of water through roots because of an immediate increase in water



**8.** Rates of water uptake as a function of soil water potential for 2 soil layers. Individual points were obtained on different days during soil-drying cycle (Hasegawa and Yoshida 1982).

absorption if the roots of a rapidly transpiring plant are cut off. If axial resistance is very low compared with soil-plant resistance (resistance between soil and root xylem), water potential within the roots should be about the same regardless of depth. Water uptake rate should be maximum on the day just after an irrigation and should decrease uniformly throughout the layers with decreasing soil water potential. On the other hand, if axial resistance is significantly large, plants will extract water from shallow layers during the early period after an irrigation and from deeper layers as soil-plant resistance in shallow layers becomes predominant over axial resistance.

Rice roots at different depths extract water to different soil water potentials. In Figure 7, the potential evapotranspiration period continued until 28 March, after which the rice crop suffered water stress. Evapotranspiration of the crop on 3 April was about one-fourth of the potential evapotranspiration. Soil water potential at 10-15 cm decreased rapidly after the irrigation, but soil water potential at 60-70 cm did not increase markedly until several days after the irrigation and was still relatively high even when the crop suffered severe water stress. At the end of the potential evapotranspiration period, soil water potential was –10 bars at 10-15 cm and –0.7 at 40-50 cm. In the 10-15 cm layer, soil water potential declined to –15



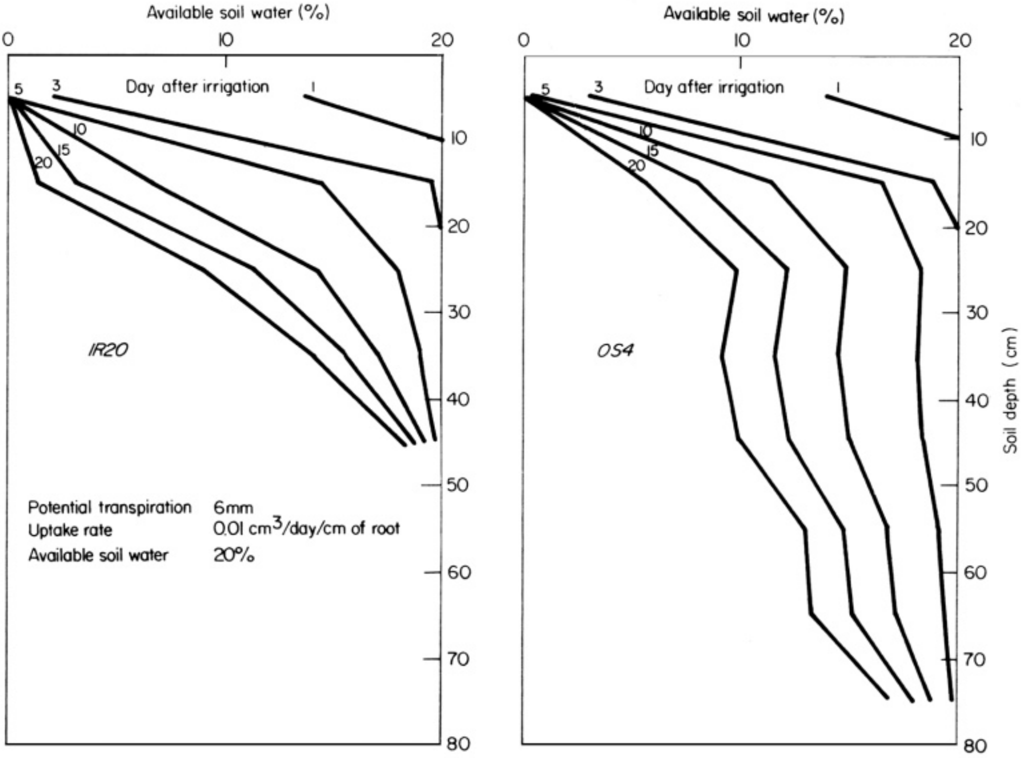
**9.** Growth and nitrogen uptake of 2 rice varieties grown on unfertilized Maahas clay (IRRI 1976).

bars as the crop continued to absorb water. Although the surface soil can be depleted of water to –15 bars and the crop can suffer severe water stress, a considerable amount of soil water remains unused in the deep soil layers.

The difference in soil water use between a deep-rooted and a shallow-rooted variety is illustrated by a simple water uptake model (Hasegawa 1982). The model assumes that a) rate of water uptake is proportional to contact area between root surface and soil water, and b) significant axial resistance exists in the rice root system. Deep-rooted variety OS4 can extract water retained in the deep soil layers better than a shallow-rooted variety IR20 (Fig. 9). These extraction patterns are similar to the ones measured in the root boxes (IRRI 1977). The computed water consumption during the 20-day period after the last irrigation is 57 mm for IR20 and 82 mm for OS4. Because crop growth is proportional to the amount of water transpired, all other things being equal, the growth of OS4 during drought should be better than that of IR20.

## ABSORPTION OF NITROGEN BY RICE ROOT SYSTEMS

A deep root system is expected to absorb more nutrients from deep soil layers than a shallow root system. Under the adequately rainy conditions that favor dryland



**10.** Successive moisture content profiles in the field for shallow- and deep-rooted varieties as predicted by a model (Hasegawa and Yoshida 1982).

rice and in moderate to coarse-textured soils, applied nitrogen may move downwards so that it may not be utilized by a shallow-rooted crop. In addition, the subsoil can be the source of other essential nutrients for rice.

When available soil depth is limited to 10 and 20 cm, little or no difference is found in dry weight and nitrogen absorption between deep-rooted OS4 and shallow-rooted IR20 (Fig. 10). However, at 90 cm the dry weight and nitrogen uptake of OS4 is more than twice that of IR20.

It is clear that a deep root system has a greater ability to absorb soil nitrogen from the deep soil layers than a shallow root system. Similarly, a deep-rooted variety has a greater ability to recover fertilizer nitrogen placed in the deep soil layers. The shallow-rooted variety IR20 recovers 31% of the fertilizer nitrogen from the soil at 70 cm depth while the deep-rooted varieties Khao Lo and OS4 recover 46 and 58% (Table 6). These two experiments show that deeper rooting depths of rice varieties are related to greater ability of the plants to absorb soil or fertilizer nitrogen from the deep soil layers. Thus, under drought, a deep root system helps the plant avoid water stress by absorbing water stored in the deep soil layers. When rainfall is adequate and nitrogen is required for better growth, deep roots help the plant absorb soil or fertilizer nitrogen from the deep soil layers.

**Table 6. Recovery of tagged fertilizer nitrogen placed at different depths in root boxes under dryland conditions (IRRI 1976).**

| Variety[a] | Depth of placement (cm) | Dry wt (g) | N absorbed (g) | | | Contribution of fertilizer N-15 to plant N (%) | Recovery of fertilizer N-15 (%) |
|---|---|---|---|---|---|---|---|
| | | | N-15 from fertilizer | Soil-N | Total | | |
| IR20 | 10 | 77.6 | 0.61 | 1.30 | 1.91 | 32 | 61 |
| | 40 | 55.5 | 0.50 | 0.95 | 1.45 | 34 | 50 |
| | 70 | 55.9 | 0.31 | 0.98 | 1.29 | 24 | 31 |
| Khao Lo | 10 | 87.3 | 0.57 | 1.27 | 1.84 | 31 | 57 |
| | 40 | 74.2 | 0.56 | 1.07 | 1.63 | 34 | 56 |
| | 70 | 74.8 | 0.46 | 1.09 | 1.55 | 30 | 46 |
| OS4 | 10 | 103.4 | 0.76 | 1.67 | 2.43 | 31 | 76 |
| | 40 | 90.8 | 0.69 | 1.54 | 2.23 | 32 | 69 |
| | 70 | 95.0 | 0.58 | 1.72 | 2.30 | 25 | 58 |

[a] Deep root-to-shoot ratio: IR20 = 10, Khao Lo = 47, OS4 = 47.

These functions of a deep root system should be particularly beneficial for dryland culture with low inputs.

## REFERENCES CITED

Asana, R. D. and S. K. Sinha. 1970. Tailoring new crop varieties for dry area. Pages 55-63 *in* Institute of Agricultural Research International. A new technology for dryland farming. New Delhi, India.

Brouwer, R., and C. T. de Wit. 1968. A simulation model of plant growth with special attention to root growth and its consequences. Pages 224-242 *in* Proceedings 15th Easter School Agricultural Science, University of Nottingham, United Kingdom.

Burch, G. J., R. C. G. Smith, and W. K. Masen. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. II. Crop evaporation, soil water depletion, and root distribution. Aus. J. Plant Physiol. 5:169-177.

Chang, T. T., G. Loresto, and O. Tagumpay. 1972. Agronomic and growth characteristics of upland and lowland varieties. Pages 656-661 *in* International Rice Research Institute. Rice Breeding. Los Banos, Philippines.

Chang, T. T., and B. S. Vergara. 1975. Varietal diversity and morpho-agronomic characteristics of upland rice. Pages 72-90 *in* International Rice Research Institute. Major research in upland rice. Los Banos, Philippines.

Fujii, Y. 1974. The morphology and physiology of rice roots. ASPAC, Food Fert. Technol. Cent. Tech. Bull. 20. Taiwan, China.

Gardner, W. R., and C. F. Ehlig. 1962. Some observations on the movement of water to plant roots. Agron. J. 54:453-456.

Hasegawa, S. 1982. A simple model for water uptake by upland rice root system. Dojo no butsurisei [soil physical properties] (Tokyo). (in press)

Hasegawa, S., and S. Yoshida. 1982. Water uptake by an upland rice root system during a soil drying cycle. Soil Sci. Plant Nutr. (Tokyo).

Hoshikawa, K. 1975. Growth of the rice plant. Nosan-gyosan-Bunka-Kyokai, Tokyo, 317 p.

IRRI (International Rice Research Institute). 1975. Annual report for 1974. Los Banos, Philippines. 384 p.

IRRI (International Rice Research Institute). 1976. Annual report for 1975. Los Banos, Philippines, 479 p.

IRRI (International Rice Research Institute). 1977. Annual report for 1976. Los Banos, Philippines, 418 p.

IRRI (International Rice Research Institute). 1978. Annual report for 1977. Los Baños, Philippines, 548 p.

IRRI (International Rice Research Institute). 1979. Annual report for 1978. Los Baños, Philippines. 578 p.

IRRI (International Rice Research Institute). 1980. Annual report for 1979. Los Baños, Philippines. 538 p.

Iwatsuki, S. 1982. Studies on paddy rice roots. Agric. Hon. (Tokyo) 7:64-70.

Kawano, K., P. A. Sanchez, M. A. Nureña, and J. R. Velez. 1972. Upland rice in the Peruvian jungle. Pages 637-643 *in* International Rice Research Institute. Rice breeding. Los Baños, Philippines.

Kawata, S., and K. Ishihara. 1959. Studies on the root hairs in rice plant. Proc. Crop Sci. Soc. Jpn. 27:341-348.

Kawata, S,., and K. Ishihara 1961. The relationship between the water percolation in the paddy soils and root hair formation in the crown roots of rice plants. Proc. Crop Sci. Soc. Jpn. 29:335-349.

Kawata, S., and M. Soejima. 1974. On superficial root formation in rice plants. Proc. Crop Sci. Soc. Jpn. 43:354-374.

Kramer, P. J. 1969. Plant and soil water relationships: A modern synthesis. Chapter 4. TMH Edition, TATA McGraw-Hill Publishing Co. Ltd.

Lawlor, D. W. 1972. Growth and water use of *Lolium perenne.* I. Water transport. J. Appl. Ecol. 9:79-105.

Marsh, B.-B. 1971. Measurement of length in random arrangements of lines. J. Appl. Ecol. 8:265-267.

Meguro, T. 1961. Drought resistance of upland rice. Pages 121-159 *in* Y. Togari, N. Yamada, T. Hayashi, eds. Crop physiology, vol. 3, Water physiology. Asakura Publ. Co., Tokyo.

Moody, K. 1977. Weed control in rice. Mimeographed lecture prepared for the participants attending the Fifth BIOTROP Weed Science Training course, 14 November-23 December 1977, Rubber Research Institute of Malaysia, Kuala Lumpur, Malaysia.

Murata, Y. 1961. Studies on the photosynthesis of rice plants and its cultural significance. Natl. Inst. Agric. Sci. Bull. D9. Tokyo, Japan, 169 p.

Newman, E. I. 1966. A method of estimating the total length of root in a sample. J. App. Ecol. 3:139-145.

Newman, E. I. 1969. Resistance to water flow in soil and plant. I. Soil resistance in relation to amounts of root: theoretical estimate. J. App. Ecol. 6:l-12.

Ohno, Y. 1976. Varietal differences of photosynthetic efficiency and dry matter production in indica rice. Trop. Agric. Res. Cent. Tech. Bull. 9. Tsukuba, Japan. 72 p.

Parao, F. T., E. Paningbatan, Jr., and S. Yoshida. 1976. Drought resistance of rice varieties in relation to their root growth. Philipp. J. Crop Sci. 1:50-55.

Reicosky, D. C., and J. T. Ritchie. 1976. Relative importance of soil resistance and plant resistance in root water absorption. Soil Sci. Soc. Am. 40:293-297.

Yoshida, S., and I. N. Oka. 1982. Factors influencing rice yield, production potential, and stability. *In* International Rice Research Institute. Rice research strategies for the future. Los Baños, Philippines.

# THE ROLE OF SHOOT CHARACTERISTICS IN DROUGHT RESISTANCE OF CROP PLANTS

N. C. TURNER

Drought-resistance mechanisms of plants are divided into three categories — phenological, morphological, and physiological. Current knowledge of the presence of the mechanisms in crops is discussed. The mechanisms are evaluated for suitability in three different types of drought conditions and for ease in screening.

All land plants face a dilemma: the air surrounding the shoot and containing the carbon dioxide for carbon assimilation is usually dry. In tropical regions, air humidity frequently drops as low as –60 leaf water potential (MPa) in the middle of the day. In arid areas, the humidity can drop as low as –300 MPa. The surfaces of the mesophyll cells within the leaf on which the atmospheric carbon dioxide is absorbed are usually saturated, leading to an inevitable loss of water whenever carbon dioxide is absorbed.

Nature has bestowed on higher land plants a range of mechanisms for dealing with the dilemma of carbon gained equals water lost. The one frequently highlighted is the evolution in higher land plants of an impermeable cuticle with valves or stomata to regulate the flow of carbon dioxide and water between the dry atmosphere and the wet leaf interior. However, stomatal regulation of water loss is only one of a variety of mechanisms used by crops to maintain carbon production in the face of limited available water. In some situations, stomatal regulation may be less beneficial than alternate mechanisms.

---

Commonwealth Scientific and Industrial Research Organization, Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T. 2601, Australia.

## MECHANISMS OF DROUGHT RESISTANCE

The mechanisms of drought resistance can be divided conveniently into three categories: phenological, morphological, and physiological (Table 1). Elsewhere I classified the mechanisms of adaptation to drought according to their influence on drought escape and tolerance (Turner 1979).

### Phenological mechanisms

*Changes in phenological development.* Phenology refers to the timing of major developmental events in the life of a crop, such as germination, floral initiation, flowering, and seed maturity. Although the phenological development of crop plants for drought-prone areas ideally might be linked to water availability, the effects of water deficits on phenological development are usually small. Mild water deficits hastened flowering and maturity by a few days in wheat (Turner 1966, Angus and Moncur 1977) but not in sunflower (Takami et al 1981). A delay in ear emergence and anthesis is more common under more severe conditions of water stress (Angus and Moncur 1977).

Other environmental variables, such as temperature and (particularly) photoperiod, have a much more marked influence on phenological development. The slight increase in time to flowering and maturity reported in mildly water-stressed wheat may have arisen from the higher plant temperatures often observed when plants suffer water deficits.

Variation in response to photoperiod can be used to optimize the growth of a crop in periods with the most favorable water regime. Curtis (1968) showed that, regardless of sowing date, the date of flowering of locally adapted sorghums in Nigeria was subtly controlled by photoperiodic sensitivity so that it coincided with the average date of the end of the wet season over a range of locations. O'Toole and Chang (1979) have suggested that, by appropriate selection, photoperiodic control of flowering could be used in regions of bimodal rainfall distribution to ensure that flowering and grain filling in rice would occur during the peak monsoon season.

However, the most rapid progress in developing crops for drier environments has been achieved not by using photoperiod sensitivity to match the growth period with rainfall distribution, but by lessening a crop's sensitivity to photoperiod and by shortening the growing season. Such a strategy has been applied most successfully on annual crops in regions in which drought terminates the growing season. The link between earliness to flowering and yield under conditions of drought has been widely studied in wheat (Reitz and Salmon 1959, Fischer and Maurer 1978) and has been reported in sorghum (Blum 1979) and rice (Krishnamurthy et al 1971).

*Developmental plasticity.* Under conditions of adequate moisture supply, crops bred for early flowering and maturity frequently have lower yields than later crops. For this reason, I have suggested taking a lesson from many of the desert ephemerals by incorporating a wide degree of developmental plasticity in crops for drought-prone areas (Turner 1979). Since most crops produce many more branches than flower-bearing branches and many more flowers than seeds and since the number of branches that are infertile and the number of flowers that are

**Table 1. Effects of mechanisms of adaptation to drought on productivity and on reversibility on relief of stress: ease in screening.**

| Mechanisms | Productive processes reduced | Reversible on relief of stress | Ease in screening |
|---|---|---|---|
| *Phenological* | | | |
| Changes in phenological development | Yes (?) | Yes | Easy |
| Developmental plasticity | No | Yes | Easy |
| *Morphological* | | | |
| Changes in leaf area | Yes | Limited | Easy |
| Changes in radiation interception | Yes | Yes | Easy |
| Changes in cuticular resistance | No | No | Difficult |
| Changes in hydraulic resistance | No | No | Difficult |
| Changes in root density and depth | No (?) | No (?) | Difficult |
| *Physiological* | | | |
| Changes in stomatal resistance | Yes | Yes | Difficult |
| Maintenance of turgor | No (?) | Yes | Very difficult |
| Changes in dehydration tolerance | Yes (?) | No | Easy |
| Changes in allocation of assimilates | No | Yes | Very difficult |

sterile increase with stress, branching or tillering and variation in flower, floret, and panicle development provide some measure of developmental plasticity.

Tiller death averaged 11 tillers/m$^2$ per day after maximum tiller initiation in stressed wheat plants, compared to a death rate of 3 tillers/m$^2$ per day in well-watered wheat (Turner 1966, Begg and Turner 1976). Stress also reduced the mean number of fertile florets per ear from 33 to 22. Stress about 7 days prior to anthesis can cause an even greater reduction in seed set (Fischer 1980), possibly because of the stimulation of abscisic acid synthesis at low leaf water potentials and the loss of pollen viability when abscisic acid is translocated to the apex (Morgan 1980a). Although some soluble carbon and nutrients transfer from dying to living tillers, the assimilates tied up in the dead tillers are wasted. However, because shedding takes place in most species before seed growth begins, the reduction in seed numbers from stress is less wasteful.

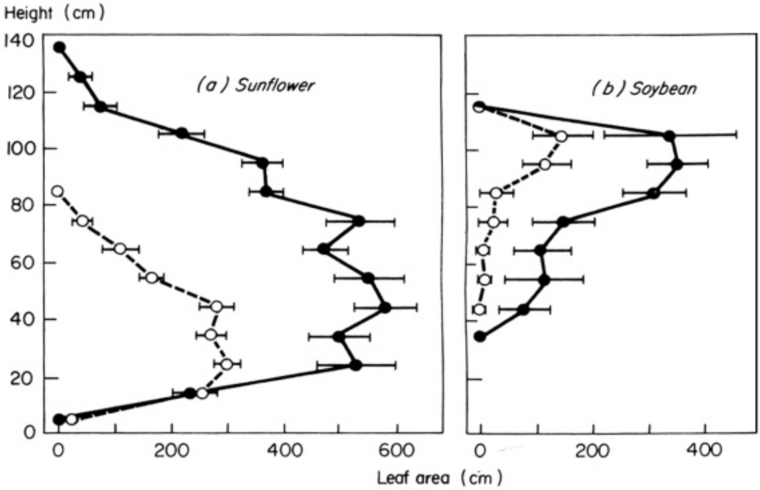
Nevertheless, both mechanisms of developmental plasticity appear wasteful of carbon in comparison to an indeterminate habit. The rapid development of a flower and seed after rain, followed by the development of further flowers and seeds if further water is available, provides efficient use of water for seed development, guarantees some reproductive turnover even in extremely dry years, and still provides the flexibility of a high yield in years of plentiful rain.

## Morphological mechanisms

*Changes in root density and depth.* Here the concern is with shoot characteristics of drought resistance. Therefore, only the first four morphological mechanisms (Table 1) will be considered. The effects of root density and depth are considered by Passioura (this volume).

*Changes in hydraulic resistance.* Passioura also considers the influence on drought resistance of changes in the hydraulic resistance of the root. When water is left in the profile, a decrease in root resistance may increase the reservoir of water available to the plant. With a limited volume of water in the soil, an increase in hydraulic resistance in the root saves water during vegetative growth for use during reproductive growth. Recent studies have suggested that hydraulic resistances can occur in the stem and leaf as well as in the roots (Begg and Turner 1970; Boyer 1971, 1974; Black 1979). If the magnitude of stem and leaf resistance exceeds that of root resistance, as has been shown in some studies, increasing the hydraulic resistance of the root will only slightly affect overall hydraulic resistance. However, as the location of the stem and leaf resistances have not been identified, it is not possible to say whether they can be changed to improve the drought resistance of a crop.

*Changes in leaf area.* The most obvious morphological change with the onset of drought is a reduction in leaf area, either through a reduction in leaf size or by the shedding or death of leaves. Several recent studies with sunflower have shown that water stress during vegetative development reduces leaf size by about two-thirds (Fig. 1a). Water stress reduced the leaf area index from 6 in irrigated plants to 2 in unirrigated plants. Ritchie (1974) demonstrated that, provided the soil surface is dry, once the leaf area index decreases below about 3, evapotranspiration decreases approximately linearly with leaf area to give zero evapotranspiration at zero leaf



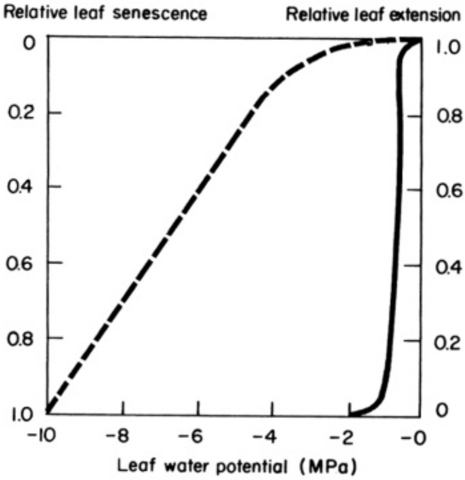
**1.** Vertical profiles of leaf area: (a) irrigated (•) and unirrigated (o) sunflower (cultivar Hysun 30) measured at flowering; details of experimental methods and stress history are given by Turner et al 1978b; and (b) unirrigated soybean (cultivar Ruse) measured 8 days apart – 97 (•) and 105 (o) days after sowing – during development of severe water deficits (from Constable and Hearn 1978; for details of stress conditions see also Burch et al 1978 and Turner et al 1978a). Bars give ± one standard error of the mean.

area.

In regions without frequent light showers, a reduction in leaf area index below 3 provides a powerful way of reducing water use by crops. The reduction in leaf area in sunflower is such that the rate of photosynthesis per unit leaf area is only rarely affected, even when the crop has to complete its entire life cycle on stored moisture (Rawson and Constable 1980, Rawson et al 1980).

In determinate crops, there is little opportunity for leaf size to be reduced once flowering has begun. Instead, a reduction in leaf area must be achieved by leaf senescence or shedding or both. Although leaf senescence has not been as widely studied as leaf expansion, it appears less sensitive to water deficits than leaf expansion (Fig. 2). Our studies with soybean suggest that leaf expansion is reduced when leaf water potential decreases below –1.0 to –1.2 MPa, whereas leaf senescence and shedding occur only when the minimum leaf water potential falls below –2.0 MPa (Constable and Hearn 1978, Turner et al 1978a, Turner and Burch 1982). A dramatic loss of leaves over an 8-day period when the maximum leaf water potential fell from –0.6 to –1.2 MPa and the minimum leaf water potential fell from –2.1 to –2.7 MPa is shown in Figure 1b. Senescence and shedding reduced the leaf area index from 6.0 to 1.2 and reduced evapotranspiration from an average of 10 mm/day to 3.5 mm/day.

A major disadvantage of leaf senescence and shedding is their irreversibility in the event of drought relief. Since yield, at least in sunflowers, is positively correlated with leaf area at flowering (Muriel and Downes 1974, Rawson et al 1980), an irreversible reduction in leaf size due to drought during vegetative



**2.** Relationship between leaf water potential and relative leaf extension rate (—) and relative leaf senescence (--) in green panic. Values are relative to maximum expansion or senescence. Adapted from Ludlow (1975).

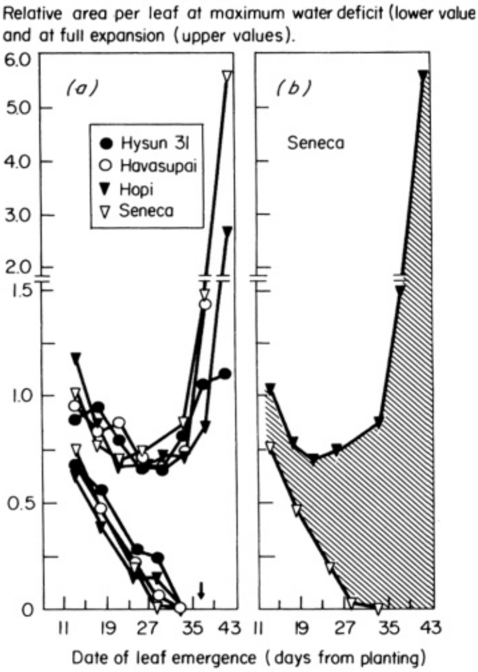
growth will also seriously reduce yields even if drought is relieved during late vegetative and reproductive growth.

Some studies have suggested that leaf expansion may resume on relief of stress. In order to explore the magnitude of this in sunflower, we studied leaf expansion of four cultivars during stress and recovery from stress imposed during vegetative growth (Takami et al 1981). At the time of maximal stress just prior to rewatering, the area of stressed leaves was 65-75% of that of the unstressed controls in the oldest leaves of all 4 sunflower cultivars. The leaves became relatively smaller the later they emerged (lower values in Fig. 3). Because of recommencement of expansion after rewatering, the final areas (upper values in Fig. 3) were very different from those at the time of relief of stress. The maximum reduction from stress in final leaf size, 25-35% in all cultivars, occurred in leaves that emerged 21-36 days after planting (15 days before rewatering) when the turgor pressure decreased below 0.25 MPa. The difference between the upper and lower values in Figure 3a (shown shaded for cultivar Seneca in Fig. 3b) is the degree of recovery after rewatering.

The potential for recovery was smallest in the oldest leaves and greatest in those leaves that emerged after rewatering. The late-emerging leaves of Seneca were significantly larger in stressed plants than the leaves of a similar time of emergence in plants that received no stress throughout their development. Because of the small size of the later, upper leaves in which this phenomenon was observed, the increase in final size of stressed leaves did not compensate for the decrease in size of the earlier, lower leaves during stress.

However, recent field studies have shown that full compensation of leaf area index can occur in sunflower. Leaves that emerge after relief of stress replace the loss of leaf area caused by early stress. This ability to recover from stress is an important drought resistance mechanism worthy of investigation in other species.

*Changes in radiation interception.* An alternate mechanism for adaptation to



**3.** (a) Relationship between date of leaf emergence and relative area of leaves of water-stressed plants at end of 21 days without water (lower set of values) and relative final area of leaves (upper set of data) when plants were rewatered 21 days after stress was imposed in 4 cultivars of sunflower. (b). Same as (a) but for the one cultivar, Seneca; the hatched area shows the recovery of leaf expansion after relief of stress. Values are relative to unstressed controls. Arrow denotes the date of rewatering. Note change in scale of y axis. Experimental details given in Takami et al (1981).

stress without irreversibly affecting leaf area is through changes in leaf angle or orientation. These changes reduce the radiation load on the leaves and allow the plant to dissipate less energy as latent heat. Important features of the mechanisms responsible for changes in leaf orientation are that they operate only during stress and that their recovery is rapid when stress is relieved.

Paraheliotropy refers to the active orientation of leaves to incoming radiation when leaf water content decreases. In legumes, leaflets orient normally to the incident beam in the absence of water deficits but parallel to the incident beam in the presence of water deficits (Begg and Torssell 1974). The mechanism which involves light- and turgor-mediated changes in the pulvini at the base of each leaflet is similar to the rolling of leaves in grasses by specialized bulliform cells in the upper epidermis as a result of loss of turgor. Both mechanisms aid in shedding radiation and reducing the plant's heat load in the middle of the day when stress usually is most severe.

In rice, leaf rolling under controlled environment conditions decreased the rate of transpiration by up to 50% (O'Toole et al 1979a). In the field, reduction in evapotranspiration from an equivalent degree of leaf rolling is likely to be smaller, due to an increase in the sensible heat and vapor pressure deficit within the canopy when the soil surface is dry or because of more rapid evaporation of water when the soil surface is wet.

Passive wilting arising from loss of turgor is also a mechanism for shedding radiation under stress. Gas exchange studies have indicated that transpiration is reduced more than photosynthesis in wilted sunflower leaves allowed to hang vertically than in similar leaves constrained in a horizontal plane (Rawson 1979). However, as with leaf rolling, the increase in leaf and air temperature and the vapor pressure deficit arising from the increase in sensible heat when leaf transpiration is reduced may eliminate any gain in water use efficiency arising from wilting under field conditions. Moreover, leaves that are wilted for any length of time appear to die earlier than those showing no wilting. Thus, one benefit of wilting, its reversibility on relief of stress, is only temporary.

The increased pubescence and waxiness observed under stress in some species and cultivars increases leaf reflectance and reduces water loss (Ehleringer 1980) Increased pubescence as a result of water stress has been reported in wheat (Quarrie and Jones 1977) and sunflower (Turner 1981a). However, using gas exchange techniques, we observed no effect of increased pubescence on water use or water use efficiency in sunflower. Water deficits also have been shown to increase the amount of epicuticular wax in sorghum (Blum 1975). A comparison of photosynthesis and transpiration in bloomed and bloomless non-isogenic lines of sorghum has shown that increased waxiness reduces water loss (Chatterton et al 1975).

*Changes in cuticular resistance.* Even if changes in waxiness fail to change leaf reflectance, they may change the resistance of the cuticle to water loss. O'Toole et al (1979b) reported that differences in cuticular resistance correlated with differences in epicuticular wax deposition in rice. Yoshida and de los Reyes (1976) reported a twofold range in cuticular resistance among rice cultivars and suggested that this resistance accounted for part of the ability of the cultivar to resist drought and perform well under dryland conditions. The measurements were made on mature leaves of adequately watered plants kept in the dark for several hours. Values were lower than those taken during daytime hours on water stressed rice plants.

However, differences have been observed in stomatal closure in the dark among species and cultivars (Hübl 1963, Turner et al 1978a, Muchow et al 1980). Moreover, cuticular resistances measured in the dark and measured on water stressed plants in the light are not correlated. Furthermore, waxiness arising from the development of water deficits may increase. Therefore, these factors make the use of cuticular resistance measured in the dark on unstressed, unadapted leaves to indicate the drought resistance of the cultivar questionable.

## Physiological mechanisms

*Changes in stomatal resistance.* The ability of stomata to regulate water loss provides an important mechanism for reducing water loss during drought. Crop plants show a range in sensitivity of stomata to water deficits. Turner (1974) showed that, under field conditions, stomatal resistance increased markedly at values of leaf water potential ranging from -0.8 MPa in field beans to below –2.7 MPa in cotton. Varietal differences in stomatal response to water stress have been reported in sorghum and wheat (Blum 1974, Jones 1977). However, in many species there is no unique relationship between leaf water potential and stomatal resistance in many species because of the ability of the stomata to adapt to stress

(Ludlow 1980). There does appear to be a unique relationship between turgor pressure and stomatal resistance, with stomatal resistance increasing markedly near zero turgor (Turner 1974), presumably because of the significant increase in abscisic acid near zero turgor (Pierce and Raschke 1980). This is consistent with the observation that adaptation of the stomata to water stress parallels osmotic adjustment of the bulk leaf tissue (Turner et al 1978b, Ludlow 1980). Cultivar differences in response of stomata to leaf and soil water potential may represent different abilities to adjust osmotically.

Stomata also respond to atmospheric humidity (Lange et al 1971) or, more correctly, to leaf-to-air vapor pressure deficit. However, the direct response of stomata to humidity must be distinguished from the indirect response through a lowering of the leaf water potential. This has not been achieved in all studies. Moreover, the degree of responsiveness to humidity depends on the leaf water potential and temperature (Jarvis 1980, Ludlow 1980). Therefore, it is not surprising that conflicting results have been obtained between studies on one species or even within one study on the responses of stomata to humidity (Rawson et al 1977a). Until careful studies are undertaken in which water stress and temperature do not interact with leaf-to-air vapor pressure deficits, comparisons between species and among cultivars will be questionable and the role of the stomatal response to humidity in improving drought resistance will remain unknown.

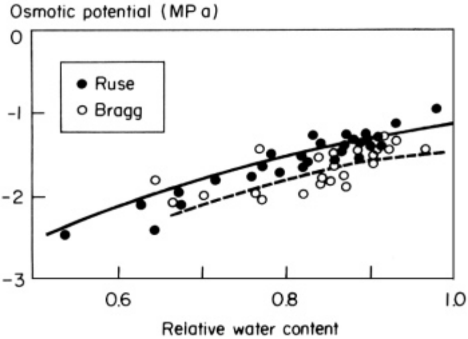
Nevertheless, the ability of stomata to respond directly to humidity in some species provides a mechanism for preventing dehydration and conserving soil moisture on days of extreme evaporative demand, regardless of soil water content. The increase in responsiveness of stomata to humidity as leaf water content decreases (Jarvis 1980) provides a mechanism for conserving water and avoiding dehydration when the water supply decreases.

*Maintenance of turgor.* As water is removed from a cell with the development of water deficits, the solutes inside the plasmalemma are concentrated and the osmotic potential is lowered. The degree of concentration depends on tissue elasticity. For a given change in water potential, the greater the elasticity, the greater the concentration of solutes. In some species, water stress does not merely concentrate solutes; it also induces solute accumulation, a process known as osmotic adjustment (Turner and Jones 1980).

Osmotic adjustment in a range of crop species has been observed in response to diurnal and seasonal changes in water status (Hsiao et al 1976) and led to full or partial turgor maintenance. Turner and Jones (1980) reported that full or partial turgor maintenance during a drying cycle has been shown in the leaves of 14 species, in the root and hypocotyl of 2 more species, and in both the leaves and floral parts of wheat. Cutler et al (1980) demonstrated its occurrence in rice.

However, we observed no osmotic adjustment in two cultivars of soybean slowly stressed in the field during grain filling (Turner et al 1978a). The decrease in osmotic potential with decrease in relative water content, measured in 6 days over a 1-month period as the soil dried, followed the Boyle-van't Hoff relationship expected if concentration of solutes occurred with only loss of water (Fig. 4).

Recently we studied osmotic adjustment in four sunflower cultivars. All four cultivars adjusted osmotically from 0.54 to 0.60 MPa (Takami et al 1981). Figure



**4.** Relationship between leaf osmotic potential and relative water content in 2 cultivars of soybean. The lines give the Boyle-van't Hoff relationship assuming the osmotic potential was –1.3 MPa at a relative water content of 0.9 in Ruse (–) and was –1.7 MPa at a relative water content of 0.85 in Bragg (----). Adapted from Turner et al (1978a).

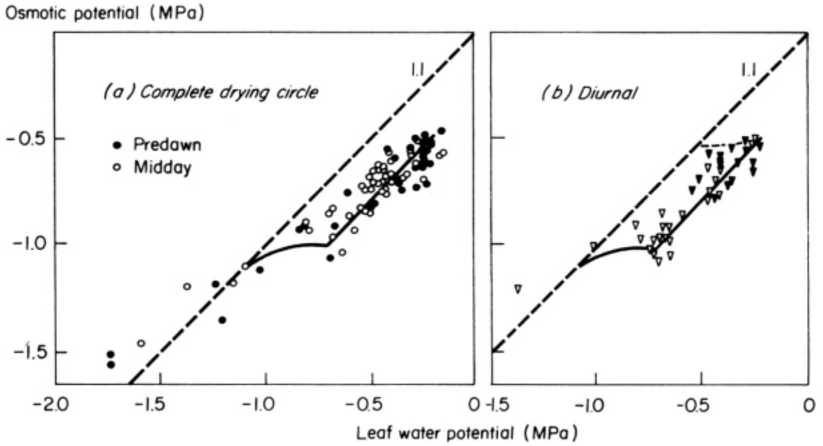
5a shows the changes in osmotic potential as leaf water potential decreased during the stress cycle in Hysun 31. Osmotic adjustment fully maintained turgor as the leaf water potential decreased from 4.2 to –0.7 MPa. Similar results were obtained in the other 3 cultivars, with turgor being fully maintained until the leaf water potential was between 4.6 and –0.7 MPa.

Midway through the drying cycle, diurnal changes in leaf water potential and leaf osmotic potential were observed in all four cultivars (Takami et al 1982). The data for Hysun 31 are shown in Figure 5b. Results were similar in the other three species. The diurnal changes in leaf water and leaf osmotic potential closely followed those observed throughout the complete drying cycle (Fig. 5a, 5b). The dashed line in Figure 5b shows the response expected had Hysun 31 only concentrated the solutes in its leaves at sunrise. It appears that in the well-watered sunflower leaves, osmotic adjustment during the day was approximately 0.25 MPa, almost half that observed throughout the 21-day drying cycle. Diurnal changes in osmotic adjustment also have been observed in maize, sorghum, and soybean (Turner 1975, Hsiao et al 1976, Wenkert et al 1978).

Diurnal changes in osmotic adjustment help maintain physiological processes such as leaf expansion and photosynthesis that otherwise would be impaired by low turgor (Hsiao et al 1976). They also hasten the unrolling of leaves wilted by low turgor (O'Toole and Moya 1978). Osmotic adjustment that occurs during a drying cycle, while rarely fully maintaining physiological functions, slows the rate of loss of physiological activity (Turner and Jones 1980).

Measurements obtained with the four diverse sunflower cultivars indicated no variation in osmotic adjustment. Other studies with sorghum, soybean, and rice also showed no differences among cultivars (Jones and Turner 1978, Turner et al 1978a, Cutler et al 1980). Differences in osmotic adjustment have only been observed among wheat genotypes (Morgan 1980b).

*Changes in dehydration tolerance.* When drought stress becomes prolonged or severe and other mechanisms of adaptation fail or have been exhausted, the ability of tissues to withstand dehydration becomes important. Despite considerable research effort, a unified view of the basis of dehydration tolerance is not available. The evidence suggests that it may involve a complex of mechanisms at the enzyme and membrane levels that reduce protein denaturation and membrane degrada-



5. Relationship between leaf water potential and leaf osmotic potential in sunflower (cultivar Hysun 31) (a) at sunrise or early afternoon at intervals over 21 days during which water was withheld, or (b) at intervals throughout a single day 12 days after water was withheld from the stressed (S ) sunflowers; the diurnal changes for the unstressed (▼) sunflowers is also shown: --- gives the 1:l relationship; —— gives the fitted line assuming osmotic adjustment as the leaf water potential fell from –0.2 to –0.7MPa and thereafter followed the Boyle-van't Hoff relationship [the fitted line from (a) is given in (b)]; --- gives the expected Boyle-van't Hoff relationship for osmotic values measured at sunrise. The Boyle-van't Hoff relationship were calculated using the moisture release curve obtained for sunflower in the same glasshouse (Turner and Long 1980). For experimental details see Takami et al (1982).

tion. Changes in dehydration tolerance occur with different rates of drying. Slow rates of drying enhance dehydration tolerance (Gaff 1980), possibly due to the accumulation of solutes such as sugars and proline that protect proteins and aid in recovery.

The development of simple screening techniques based on exposure of leaf portions or seedlings to heat or severe desiccation has shown that wide variation in dehydration tolerance exists among species and cultivars (Wright and Jordan 1970, Sullivan and Eastin 1974, O'Toole et al 1978). But mechanisms that allow a plant to avoid dehydration can override observations of dehydration tolerance. Moreover, treatments often bear little resemblance to field conditions. Nevertheless, screening for dehydration tolerance has shown that the character is stable from generation to generation, is related to field performance under drought, and is more strongly developed in species and cultivars that have no dehydration avoidance mechanisms (Wright and Jordan 1970, O'Toole et al 1978).

*Changes in allocation of assimilates.* Manipulation of nitrogen and water supplies has been used to demonstrate that excessive growth leading to a depletion of the water supply in the vegetative phase can lead to little reproductive growth and a severe yield reduction (Barley and Naidu 1964, Passioura 1972). Under such circumstances, transfer of nutrients and assimilates stored into roots, stems, and leaves to the grain should reduce the drastic effects of the depleted water reserves. In such severe conditions, the proportion of preflowering assimilates that move to the grain increases from the usual 0-20% (20-40% in rice; Murata and Matsushima 1975) to as high as 60-70% (Gallagher et al 1976, Passioura 1976). However, in all cases in which this phenomenon has been studied, the actual amount of preflowering assimilates transferred to the grain has not increased. Rather, the proportion of postflowering assimilates in the grain has decreased (Passioura 1976, Bidinger et al 1977, Rawson et al 1977b). Although a high harvest index does not necessarily indicate a greater degree of translocation to the grain, the wide variation in harvest index among cultivars does suggest that variation for this character might exist in a broadly based gene pool.

## EVALUATION OF DROUGHT RESISTANCE MECHANISMS IN THE SHOOT

The mechanisms of drought resistance listed in Table 1 are based on current understanding of the ecophysiological responses of both native species and crop plants to drought. Although there has been a considerable advance in our understanding of adaptation to drought in the recent decade, little is known of the influence of these mechanisms on crop yield (Turner and Kramer 1980). This is partly the result of drought being a relative term and partly because more than one mechanism of adaptation usually is displayed under any one drought regime (Turner 1981a).

Nevertheless, the probable value of the various drought resistance mechanisms to crop productivity can be assessed (Table 1). The morphological and physiological mechanisms that enable a plant to avoid water deficits, such as a reduction in leaf area, radiation interception, and an increase in stomatal resistance, have a much greater effect in reducing photosynthesis and productivity than other mechanisms of drought resistance. Drought resistance mechanisms such as an increase in root density and depth and osmotic adjustment also may reduce productivity, but their effects are indirect, less easy to quantify, and likely are smaller than the direct effects of a reduction in leaf area, changes in radiation interception, and stomatal closure.

Also included in Table 1 is an assessment of the reversibility of a drought resistance mechanism once stress is relieved. Characteristics that impose a limitation on crop productivity should be reversible if stress is likely to be relieved. This suggests that, if the rainfall probability increases during a crop's life cycle, radiation shedding and stomatal closure would be of greater benefit than a reduction in leaf area from leaf senescence or shedding.

Blum (1979) has argued that a knowledge of the influence of drought resistance characters on yield is not essential. Rather, if a particular physiological or morphological character can be identified and shown to improve the drought resistance of the crop and if the character and yield are separately inherited (the drought resistance character and yield are not negatively correlated), incorporation of the character into a high yielding line should improve the crop's yield under drought. This has been the basis of a breeding program for dryland sorghum (Blum 1979).

Such a program depends on three factors:

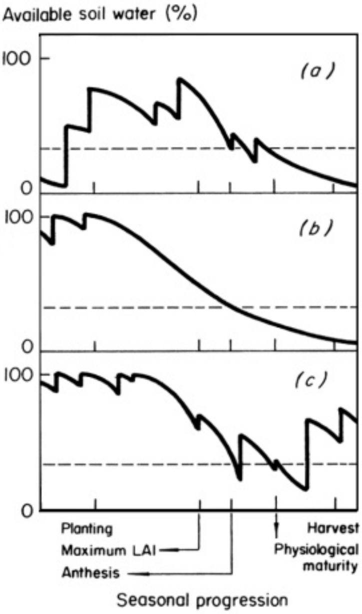
1. Identification of the most suitable physiological and morphological charac-

ters for the expected drought conditions.
2. Screening methods to identify the characters in a wide population.
3. A team of plant scientists — physiologists, crop ecologists, agronomists, and plant breeders — working collaboratively to achieve improved yields under drought.

*Identification of suitable morphological and physiological characters.* The first requirement in starting a drought resistance program is to identify the timing and the length of water stress likely to be encountered. These depend on the soil water store at the beginning of the season in relation to rooting depth, the incidence of rainfall, and the rate of evapotranspiration during the growing season. Ideally a plant/water model in conjunction with climatic analysis should be used (Smith and Harris 1981), but an estimate of the available soil water throughout the growing season often will suffice. Jordan and Miller (1980) provide such an analysis for the principal sorghum growing region of the USA. They posit three soil water availability patterns (Fig. 6).

I have suggested the mechanisms of drought resistance likely to be required in crops for the three conditions (Table 2). For crops with adequate water at sowing but with a declining water supply particularly after flowering (terminal drought), mechanisms to conserve moisture loss (such as leaves whose expansion is sensitive to low water potential) are required during the vegetative phase and mechanisms to adjust to gradually lowering soil and leaf water potential (such as osmotic adjustment and dehydration tolerance) are required during the reproductive phase.

Crops with adequate soil moisture at sowing and a rainfall probability such that water deficits may occur unpredictably at any growth stage, but particularly in the late vegetative and around flowering (unpredictable drought), require a different



**6.** The available soil water in the root zone throughout the season (as a percentage of that in the root zone at field capacity) giving 3 patterns of drought: a) unpredictable and terminal drought, b) terminal drought, and c) unpredictable drought. The dashed line represents the lower limit of soil water availability that will support water loss at potential rates. LAI = leaf area index. From Jordan and Miller (1980).

set of mechanisms. Conservation of water in the vegetative stage is less necessary. With an increasing probability of rainfall in the reproductive phase, a large leaf area at anthesis is desirable to maximize the number of grains set. Leaves whose expansion is insensitive to water deficits and plants with high recovery potential (developmental plasticity) are desirable goals. The leaves should have mechanisms for shedding radiation and stomata should be sensitive to low leafwater potentials to prevent water loss and dehydration during intermittent water deficits.

Where drought is likely to be both unpredictable and terminal, as in many Mediterranean regions, crops require mechanisms that conserve moisture in the vegetative stage and that allow adaptation to water deficits as the soil water is depleted. They need radiation shedding characteristics and stomatal closure when unpredictable stresses arise in the vegetative stage. The drought conditions and mechanisms suitable for these conditions outlined in Table 2 are examples and are not exhaustive. The mechanisms are more fully discussed in Turner (1981a).

*Screening methods to identify drought resistance mechanisms.* Both Blum (1979) and O'Toole and Chang (1979) concluded that before further progress can be made in utilizing morphologically and physiologically based adaptations to drought, suitable screening methods need to be developed. The major problem with many methods developed for physiological and morphological studies is that they are too slow and detailed for use in screening large plant populations.

Current techniques for measuring leaf water potential require 2 persons to measure 30 samples/hour and 2 more persons to measure the stomatal resistance of 20 leaves/hour (Turner 1981b). However, many of these techniques can be modified for use as screening tools. For example, we recently modified our pressure chambers to take three samples simultaneously. With 2 chambers and 3 persons, we have been able to increase the sampling rate to 90 samples/hour. Using an automatic porometer (Delta-T Devices, Cambridge, U.K.), we have increased the number of leaves sampled for stomatal resistance from 20 to 50/hour. This could be doubled if only one leaf surface is sampled. Using a mass flow porometer can increase sampling to 200/hour when the stomata are open or 100/hour when the stomata are closed.

Indirect methods also provide speedy assessment of plant water status. When water deficits induce stomatal closure, leaf temperatures usually rise. Methods of measuring leaf or canopy temperature can be used as indicators of plant water stress. Blum (1979) advocated the use of infrared color photography to screen for leaf hydration, but exposure of soil beneath the crop and variation in the chlorophyll content of the leaves can confound the results. Measurement by infrared thermometry of the leaf-to-air temperature difference may provide a useful technique to screen cultivars for plant water stress. The infrared thermometer needs to be sighted on the canopy and checked to ensure that bare soil is not visible in the field of view. With row crops in which water stress markedly reduces leafsize, such as sunflower, this can be a problem.

In a recent study, we were unable to use the infrared thermometer because the sparse canopy of green leaves meant that the thermometer had to be directed at a single leaf. The temperature relative to the air changed by ± 2° C in a matter of seconds, depending on wind speed. This suggests that infrared thermometry is

**Table 2. Desirable plant characteristics for crops in 3 drought conditions (adapted from Turner 1981a).**

| Terminal drought | Unpredictable drought | Unpredictable and terminal drought |
|---|---|---|
| Rapid establishment of deep roots and sloughing of fine roots in dry soil layers | Indeterminate habit | Rapid germination and early establishment of deep roots |
| Phenological development to suit soil water availability | Developmental plasticity | Indeterminate habit |
| Determinate habit | Radiation shedding by leaves under stress | Rapid phenological development |
| Radiation shedding by leaves under stress | Leaves in which expansion is insensitive to stress | Developmental plasticity |
| Leaf expansion sensitive to water deficits | Stomata sensitive to low leaf water potentials | Radiation shedding by leaves under stress |
| Stomata sensitive only to large vapor pressure deficits and low leaf water potentials | Stomata sensitive to vapor pressure deficits | Leaf expansion highly sensitive to water deficits |
| High degree of osmotic adjustment | Limited root depth | Stomata sensitive only to large vapor pressure deficits and insensitive to low leaf water potentials |
| Large transfer of assimilates from stems to grain | Low degree of osmotic adjustment | Ability to adjust osmotically |
| Dehydration tolerance at grain-filling stage | | Large transfer of assimilates from stem to grain |
| | | Dehydration tolerance particularly at seedling and grain-filling stages |

likely to be useful only in crops with dense canopies and small leaves.

Because many measurements of plant water status change with environmental conditions and stage of crop development, they not only vary from week to week, but also from day to day and hour to hour. Therefore, measurement often is restricted to particular times of day and particular stages of crop and stress development. This restricts the number of lines that can be compared in any one study to between 60 and 100.

To screen a greater number of lines, tests must be undertaken under controlled conditions or visual screening methods need to be devised. O'Toole et al (1978) and Steponkus et al (1980) show how controlled environment facilities can be used to screen large numbers of plants for seedling survival and predawn leaf water potential in rice. Unfortunately, drought conditions in controlled environments often do not adequately simulate those in the field (Begg and Turner 1976). It is also essential to know the physiological basis of visual scores if they are to have any meaning. O'Toole and Moya (1978), Jones (1979a), and Steponkus et al (1980) provide this basis for rice.

Thus far I have discussed only those methods used to measure plant water status. In Table 1, I assess the ease with which the mechanisms of drought resistance can be screened. Multilocation testing with a record of the time to flowering and developmental variation enable the phenological mechanisms to be assessed. Visual screening methods also can readily be devised for changes in leaf area and radiation interception. However, the measurement of stomatal and cuticular resistance requires porometry or water loss studies (Jones 1979b). If cuticular resistance is related to the quantity and quality of cuticular wax over a wide range of genotypes, simple methods for dissolving, weighing, and analyzing waxes are available (O'Toole et al 1979b).

Measurement of root density and depth by field sampling is impossible except in a few lines. Use of $^{32}P$ (Reyniers and Binh 1978) and capacitance techniques (Chloupek 1977) may simplify this. Alternatively, the leaf water potential at sunrise may give an indirect measure of the development and activity of the root system (O'Toole and Moya 1978). However, as the degree of dark stomatal opening, evaporative conditions on the previous day, and as yet unknown variations occur in the predawn leaf water potential, interpretation of only predawn leaf water potential as an indication of rooting behavior should be used with caution.

If differences in hydraulic resistance are associated with a single or a limited number of xylem vessels, microscopic examination of vessels is possible (Richards and Passioura 1981). Alternatively, differences in water potential between covered and uncovered leaves (Begg and Turner 1970) or between maximum and minimum values during the day, taken in conjunction with stomatal resistance measurements, may provide indications of differences in hydraulic resistance among lines. However, this needs confirmation by laboratory or more detailed field studies.

Simple tests for dehydration tolerance are available (Sullivan and Eastin 1974, O'Toole et al 1978), subject to the caution noted. However, in spite of methodologies developed for the field, measurement of allocation of assimilates and of osmotic adjustment (Bidinger et al 1977, Turner 1981b) is not yet feasible except in a few lines.

*A team of plant scientists.* The development of simple physiologically and morphologically based tests for screening drought resistance characters and the development of visual screening techniques that have sound physiological and ecological bases will require crop physiologists and ecologists working in conjunction with agroclimatologists, geneticists, breeders, agronomists, and soil scientists. The interaction of agronomists, physiologists, and breeders working toward a clearly defined plant type produced the first miracle rice that revolutionized rice culture in the developing world (Jennings 1974). The improvement of yields in drought-prone areas will be less easily achieved, but will require the same interdisciplinary team effort.

## CONCLUSION

In order to deal with the dilemma that carbon gained equals water lost, land plants have developed a range of mechanisms to maintain function and ultimately to reproduce in the face of drought. Those mechanisms in the shoot that may be suitable for use in crop improvement in drought-prone areas have been summarized here.

It should be recognized that the utility of many of the mechanisms has not been tested in crops. Such tests require the cooperation of physiologists and breeders in setting up lines or populations isogenic for the character under test. Nevertheless, from current knowledge of the likely effects of the mechanisms on drought resistance, their effects on productivity, and the ability of the character to change on relief of stress, an assessment of their utility under various categories of drought can be undertaken.

With this information and with a knowledge of the drought conditions likely to prevail, a list of the characters most likely to be useful for the crop can be developed.

Clearly, the ultimate test of utility is whether crops containing drought resistant characters yield better in drought-prone environments. This approach is the basis of at least three breeding programs (Blum 1979, O'Toole and Chang 1979, Johnson 1980).

## REFERENCES CITED

Angus, J. F., and M. W. Moncur. 1977. Water stress and phenology in wheat. Aust. J. Agric. Res. 28:177-181.

Barley, K. P., and N. A. Naidu. 1964. The performance of three Australian wheat varieties at high levels of nitrogen supply. Aust. J. Exp. Agric. Anim. Husb. 4:39-48.

Begg, J. E., and B. W. R. Torssell. 1974. Diaphotonastic and parahelionastic leaf movements in *Stylosanthes humilis* H. B. K. (Townsville stylo). Pages 277-283 *in* R. L. Bieleski, A. R. Ferguson, and M. M. Cresswell, eds. Mechanisms of regulation of plant growth. Bull. 12, Royal Society of New Zealand, Wellington.

Begg, J. E., and N. C. Turner. 1970. Water potential gradients in field tobacco. Plant Physiol. 46:343-346.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-167.

Bidinger, F., R. B. Musgrave, and R. A. Fischer. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature (London) 270:431-433.

Black, C. R. 1979. The relationship between transpiration rate, water potential, and resistances to water movement in sunflower (*Helianthus annuus* L.). J. Exp. Bot. 30:235-243.

Blum, A. 1974. Genotypic responses in sorghum to drought stress. I. Response to soil moisture stress. Crop Sci. 14:361-364.

Blum, A. 1975. Effect of the *Bm* gene on epicuticular wax and the water relations of *Sorghum bicolor* L. (Moench). Israel J. Bot. 24:50-51.

Blum, A. 1979. Genetic improvement of drought resistance in crop plants: a case for sorghum. Pages 429-445 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Boyer, J. S. 1971. Resistances to water transport in soybean, bean and sunflower. Crop Sci. 11:403-407.

Boyer, J. S. 1974. Water transport in plants: mechanism of apparent changes in resistance during absorption. Planta 117:187-207.

Burch, G. J., R. C. G. Smith, and W. K. Mason. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. II. Crop evaporation, soil water depletion and root distribution. Aust. J. Plant Physiol. 5:169-177.

Chatterton, N. J., W. W. Hanna, J. B. Powell, and D. R. Lee. 1975. Photosynthesis and transpiration of bloom and bloomless sorghum. Can. J. Plant Sci. 55:641-643.

Chloupek, O. 1977. Evaluation of the size of a plant's root system using its electrical capacitance. Plant Soil 48:525-532.

Constable, G. A., and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. I. Growth, development and yield. Aust. J. Plant Physiol. 5:159-167.

Curtis, D. L. 1968. The relation between the date of heading of Nigerian sorghums and the duration of the growing season. J. Appl. Ecol. 5:215-226.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1980. Influence of water deficits and osmotic adjustment on leaf elongation in rice. Crop Sci. 20:314-318.

Ehleringer, J. 1980. Leaf morphology and reflectance in relation to water and temperature stress. Pages 295-308 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Fischer, R. A. 1980. Influence of water stress on crop yield m semiarid regions. Pages 323-339 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Fischer, R. A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:897-912.

Gaff, D. F. 1980. Protoplasmic tolerance of extreme water stress. Pages 207-230 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Gallagher, J. N., P. V. Biscoe, and B. Hunter. 1976. Effects of drought on grain growth. Nature (London) 264:541-542.

Hsiao, T. C., E. Acevedo, E. Fereres, and D. W. Henderson. 1976. Water stress, growth, and osmotic adjustment. Philos. Trans. R. Soc. London, Ser. B. 273:479-500.

Hübl, E. 1963. Uber das stomatare Verhalten van Pflanzen verschiedener Standorte im Alpengebiet und auf Sumpfweisen der Ebene. Oesterr. Akad. Wiss., Math. Naturwissenschaff. Klass. Sitzungber Abt. 1. 172:1-84.

Jarvis, P. G. 1980. Stomatal response to water stress in conifers. Pages 105-122 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Jennings, P. R. 1974. Rice breeding and world food production. Science. 186:1085–1088.

Johnson, D. A. 1980. Improvement of perennial herbaceous plants for drought-stressed western rangelands. Pages 419-433 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Jones, H. G. 1977. Aspects of the water relations of spring wheat (*Triticum aestivum* L.) in response to induced drought. J. Agric. Sci. 88:267-282.

Jones, H. G. 1979a. Visual estimation of plant water status in cereals. J. Agric. Sci. 92:83-89.

Jones, H. G. 1979b. Stomatal behavior and breeding for drought resistance. Pages 407-428 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Jones, M. M., and N. C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Jordan, W. R., and F. R. Miller. 1980. Genetic variability in sorghum root systems: implications for drought tolerance. Pages 383-399 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Inteerscience, New York.

Krishnamurthy, Ch., S. V. S. Shastry, and W. H. Freeman. 1971. Breeding rice for tolerance to drought salinity. Oryza 8(2) (suppl.):47-54.

Lange, O. L., R. Losch, E. –D. Schulze, and L. Kappen. 1971. Responses of stomata to changes in humidity. Planta 100:76-86.

Ludlow, M. M. 1975. Effect of water stress on the decline of leaf net photosynthesis with age. Pages 123-134 *in* R. Marcelle, ed. Environmental and biological control of photosynthesis. Junk, The Hague.

Ludlow, M. M. 1980. Adaptive significance of stomatal responses to water stress. Pages 123-138 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Morgan, J. M. 1980a. Possible role of abscisic acid in reducing seed set in water-stressed wheat plants. Nature (London) 285:655-657.

Morgan, J. M. 1980b. Osmotic adjustment in the spikelets and leaves of wheat. J. Exp. Bot. 31:655-665.

Muchow, R. C., M. M. Ludlow, M. J. Fisher, and R. J. K. Myers. 1980. Stomatal behaviour of kenaf and sorghum in a semiarid tropical environment. I. During the night. Aust. J. Plant Physiol. 7:609-619.

Murata, Y., and S. Matsushima. 1975. Rice. Pages 73-99 *in* L. T. Evans, ed. Crop physiology: some case histories. Cambridge University Press, Cambridge.

Muriel, J. L., and R. W. Downes. 1974. Effect of periods of moisture stress during various phases of growth of sunflowers in the greenhouse. Pages 127-131 *in* Proc. 6th International Sunflower Conference, 22-24 July 1974, Bucharest, Romania.

O'Toole, J. C., and T. B. Moya. 1978. Genotypic variation in maintenance of leaf water potential in rice. Crop Sci. 18:873-876.

O'Toole, J. C., and T. T. Chang. 1979. Drought resistance in cereals — rice: a case study. Pages 373-405 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

O'Toole, J. C., R. S. Aquino, and K. Alluri. 1978. Seedling stage drought response in rice. Agron. J. 70:1101-1103.

O'Toole, J. C., R. T. Cruz, and T. N. Singh. 1979a. Leaf rolling and transpiration. Plant Sci. Letters 16:111-114.

O'Toole, J. C., R. T. Cruz, and J. N. Seiber. 1979a. Epicuticular wax and cuticular resistance in rice. Physiol. Plant. 47:239-244.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Passioura, J. B. 1976. Physiology of grain yield in wheat growing on stored water. Aust. J. Plant Physiol. 3:559-565.

Passioura, J. B. 1982. The role of root system characteristics in the drought resistance of crop plants. *In* International Rice Research Institute. 1982. Drought resistance in crops, with emphasis on rice. Los Baños, Laguna, Philippines.

Pierce, M., and K. Raschke. 1980. Correlation between loss of turgor and accumulation of abscisic acid in detached leaves. Planta. 148:174-182.

Quarrie, S. A., and H. G. Jones. 1977. Effects of abscisic acid and water stress on development and morphology of wheat. J. Exp. Bot. 28:192-203.

Rawson, H. M. 1979. Vertical wilting and photosynthesis, transpiration, and water use efficiency of sunflower leaves. Aust. J. Plant Physiol. 6:109-120.

Rawson, H. M., and G. A. Constable. 1980. Carbon production of sunflower cultivars in field and controlled environments. I. Photosynthesis and transpiration of leaves, stems and heads. Aust. J. Plant Physiol. 7:555-573.

Rawson, H. M., J. E. Begg, and R. G. Woodward. 1977a. The effect of atmospheric humidity on photosynthesis, transpiration and water use efficiency of leaves of several plant species. Planta 134:5-10.

Rawson, H. M., A. K. Bagga, and P. M. Bremner. 1977b. Aspects of adaptation by wheat and barley to soil moisture deficits. Aust. J. Plant Physiol. 4:389-401.

Rawson, H. M., G. A. Constable, and G. N. Howe. 1980. Carbon production of sunflower cultivars in field and controlled environments. II. Leaf growth. Aust. J. Plant Physiol. 7:575-586.

Reitz, L. P., and S. C. Salmon. 1959. Hard red winter wheat improvement in the plains: a 20-year summary. U. S. Dep. Agric. Tech. Bull. 1192.

Reynien, F. N., and T. Binh. 1978. Screening rainfed rice varieties for rooting depth by a $P^{32}$

absorption technique. Pages 279-284 *in* I. W. Buddenhagen and G. J. Persley, eds. Rice in Africa. Academic Press, London.

Ritchie, J. T. 1974. Atmospheric and soil water influences on the plant water balance. Agric. Meteorol. 14:183-198.

Richards, R. A., and J. B. Passioura. 1981. Seminal root morphology and water use of wheat. II. Genetic variation. Crop Sci. 21. (in press)

Smith, R. C. G., and H. C. Harris. 1981. Environmental resources and restraints to agricultural production in a Mediterranean-type environment. Plant Soil 58:31-57.

Steponkus, P. L., J. M. Cutler, and J. C. O'Toole. 1980. Adaptation to water stress in rice. Pages 401-418 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Sullivan, C. Y., and J. D. Eastin. 1974. Plant physiological responses to water stress. Agric. Meteorol. 14:113-127.

Takami, S., N. C. Turner, and H. M. Rawson. 1981. Leaf expansion of four sunflower (*Helianthus annuus* L.) cultivars in relation to water deficits. I. Patterns during plant development. Plant Cell Environ. 4. (in press)

Takami, S., H. M. Rawson, and N. C. Turner. 1982. Leaf expansion of four sunflower (*Helianthus annuus* L.) cultivars in relation to water deficits. II. Diurnal patterns during stress and recovery. Plant Cell Environ. 4. (in press)

Turner, N. C. 1966. Grain production and water use of wheat as affected by plant density, defoliation and water status. PhD thesis, University of Adelaide, South Australia, Australia.

Turner, N. C. 1974. Stomatal response to light and water under field conditions. Pages 423-432 *in* R. L. Bieleski, A. R. Ferguson, and M. M. Cresswell, eds. Mechanisms of regulation of plant growth. Bull. 12, Royal Society of New Zealand, Wellington.

Turner, N. C. 1975. Concurrent comparisons of stomatal behavior, water status, and evaporation of maize in soil at high or low water potential. Plant Physiol. 55:932-936.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. Pages 343-372 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Turner, N. C. 1981a. Designing crops for dryland Australia: can the deserts help us? J. Aust. Inst. Agric. Sci. 47. (in press)

Turner, N. C. 1981b. Techniques and experimental approaches for the measurement of plant water status. Plant Soil 58:339-366.

Turner, N. C., and G. J. Burch. 1982. The role of water in plants. *In* I. D. Teare and M. M. Peet, eds. Crop-water relations. Wiley Interscience, New York. (in press)

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. Pages 87-103 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Turner, N. C., and P. J. Kramer. 1980. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York. 482 p.

Turner, N. C., and M. J. Long. 1980. Errors arising from rapid water loss in the measurement of leaf water potential by the pressure chamber technique. Aust. J. Plant Physiol. 7:527-537.

Turner, N. C., J. E. Begg, H. M. Rawson, S. D. English, and A. B. Hearn. 1978a. Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leafconductance, $^{14}CO_2$ photosynthesis, and adaptation to water deficits. Aust. J. Plant Physiol. 5:179-194.

Turner, N. C., J. E. Begg, and M. L. Tonnet. 1978b. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata Close. Aust. J. Plant Physiol. 5:597-608.

Wenkert, W., E. R. Lemon, and T. R. Sinclair. 1978. Water content — potential relationship in soya bean: changes in component potentials for mature and immature leaves under field conditions. Ann. Bot. 42:295-307.

Wright, L. N., and G. L. Jordan. 1970. Artificial selection for seedling drought tolerance in Boer Lovegrass (*Eragrostis curvula* Nees). Crop Sci. 10:99-102.

Yoshida, S., and E. de los Reyes. 1976. Leaf cuticular resistance of rice varieties. Soil Sci. Plant Nutr. 22:95-98.

# INTERACTION OF SHOOT AND ROOT CHARACTERISTICS IN THE RESPONSE OF MILLET TO DROUGHT

P. J. GREGORY

The physiological processes responsible for grain yield are similar in most cereals. This paper examines the response of pearl millet to drought and attempts to extract some principles for improving rice. Crops of millet grown on stored soil moisture in India and Niger illustrate the response to atmospheric demand for water in terms of the interaction between the ability of roots in supplying water and the behavior of stomata in regulating water loss.

Measurements of crop growth, root growth, water use, and stomatal conductance are presented. The results indicate that grain yields might be increased in three ways: 1) by increasing the size of the root system to exploit deeper water reserves, 2) by managing the existing water reserves more efficiently, and 3) by increasing the quantity of assimilates moved to fill grain.

Transpiration results from the interaction of the evaporative demand of the atmosphere, physiological factors within the plant, and the supply of water from the soil. This continuum for water movement forms the basis of most modern approaches to crop-water relations (Cowan 1965, Nimah and Hanks 1973). It also provides a conceptual framework for investigating the drought tolerance of crops and determining traits likely to produce higher yields.

To understand the responses of crops to drought, it is necessary to specify the environmental conditions during growth. For example, models of water uptake by

---

Department of Soil Science, University of Reading, London Road, Reading, Berks, England.

crops rely on values of inflow (uptake per unit length of root per unit of time) that depend on soil hydraulic properties, density of rooting, the atmospheric demand for water, and the conductance of stomata. This means that for any program of crop improvement, it is necessary to know the likely sequence of weather and the hydraulic properties of the soil so that information gathered in one series of experiments may be safely extrapolated to another area.

A variety of weather and soil combinations is possible but one that lends itself readily to experimentation starts with a soil profile close to field capacity, then allows the crop to deplete the water reserve. The two experiments with pearl millet (*Pennisetum typhoides*) reported here used this arrangement to investigate the interaction between shoot and root environments and growth and yield.

In the experiment in India, a comparison with an irrigated crop was made. In the experiment in Niger, the effects of plant density on the interaction were examined.

## EXPERIMENT AT HYDERABAD, INDIA

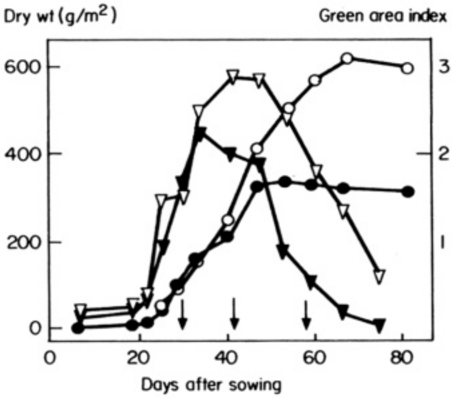
The experiment at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India, during the postrainy (rabi) season compared the growth of crops with access to different amounts of soil water. Pearl millet (BK560) was sown on 13 October 1977 on a medium-deep Alfisol in rows 37.5 cm apart. Thinning 13 days after sowing (DS) spaced plants 10 cm apart within rows.

Eight 15- × 9-m plots were set aside for measurements. Four plots received no irrigation other than the 30 mm shortly after sowing and 20 mm at 13 DS required to produce the initial stand (dry crop). The remaining four plots received an additional 30 mm of water at 30, 42, and 58 DS (irrigated crop). After a few light showers at the beginning of November (19 DS), the weather remained almost continuously dry and warm, although a cyclonic storm in late November caused some light showers (8 mm), cooler weather, and strong winds. Evaporation from a class A pan was 300 mm between 18 and 82 DS.

### Crop growth

Total root dry weight of the dry crop reached 48 $g/m^2$ at 40 DS and thereafter remained unchanged. Root dry weight of the irrigated crop increased to 63 $g/m^2$ at 54 DS. In contrast, total root length was unaffected by irrigation. It was 134 m/plant at 40 DS and decreased to 113 m/plant at final harvest. Root length was unaffected by irrigation because the root axes produced by irrigated plants 40 DS were thick and unbranched, contributing to an increase in dry weight but not length. Roots were confined to the upper 1 m of soil and their distribution was only slightly affected by water treatment. Irrigation increased root length in the surface layers (0-20 cm). Root densities, which were 0.7 cm root/$cm^3$ soil in the top 40 cm, decreased to 0.4 at 60 cm and to <0.1 at 1 m.

Figure 1 shows shoot growth. The smaller green leaf area index ($m^2/m^2$) ofthe dry crop resulted from the reduced size of the upper two or three leaves, which also senesced more rapidly. Although both crops produced a similar number of tillers,



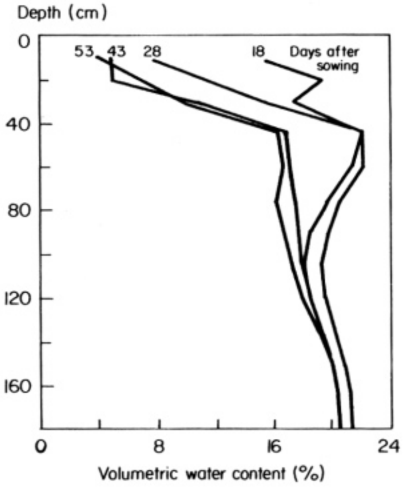
**1.** Crop dry weight (circles) and green leaf area index (triangles) for dry (black) and irrigated (white) crops of pearl millet. Arrows indicate times of irrigation.

fewer survived in the dry crop, which led to the marked differences in growth evident at 47 DS. Dry matter accumulation of the dry crop ceased at 47 DS. Growth of the irrigated crop continued until about 70 DS.

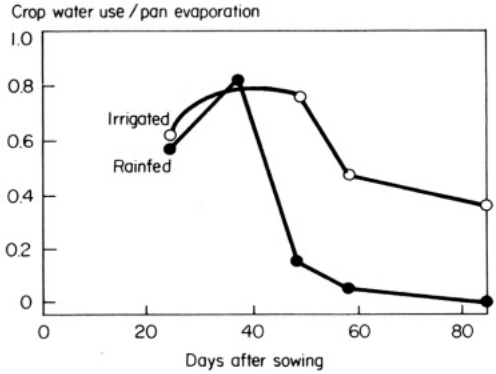
Despite the constant postanthesis weight of the dry crop, panicles continued to grow and an increase in panicle dry weight was reflected in an equal decrease in stem dry weight. In the irrigated crop, changes in stem and panicle dry weights after anthesis were almost identical. Grain yield was 1.1t/ha for the dry crop and 1.9 t/ha for the irrigated crop. Details of crop growth have been published elsewhere (Gregory and Squire 1979).

## Water use

Figure 2 shows changes in soil volumetric water content with depth and time under the dry crop. Drying occurred almost without interruption. During the first 40 DS, water was extracted mainly from the upper 80 cm. Interpretation of the



**2.** Extraction of soil water beneath the dry crop of pearl millet at 53, 43, 28, and 18 days after sowing.

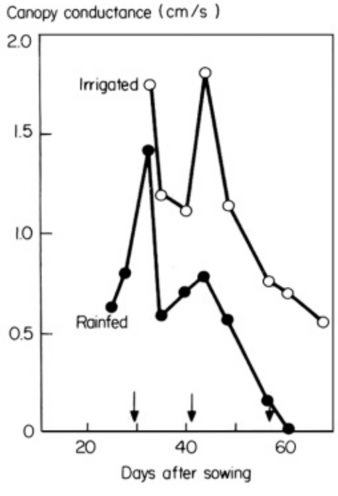


**3.** Changes in the ratio of crop water use to pan evaporation for dry and irrigated crops of pearl millet.

profile below 90 cm was complicated by the early accretion of water, but measurements of soil water potential made with tensiometers indicated that changes in water content in the soil below 120 cm after 32 DS was attributable to drainage. Water extraction after 40 DS was primarily between 60 and 120 cm and virtually ceased at 55 DS. In comparison with the irrigated crop (Fig. 3), extraction was severely restricted after 36 DS. The pattern of soil water use was different in the irrigated crop, where more water was used from the surface layers than from below 60 cm. Total water use during growth was 102 mm in the dry crop and 204 mm in the irrigated crop.

## Canopy conductance

Measurements of stomatal conductance made with a diffusion porometer combined with measurements of green leaf' area index allowed the calculation of canopy conductance ($g_c$) (Fig. 4). In the dry crop, $g_c$ depended largely on the



**4.** Seasonal changes in canopy conductance. Values are the means of at least 3 hourly averages measured between 0900 and 1400 hours. Arrows indicate the times of irrigation.

amount of light intercepted by the canopy and was closely related to the green leaf area index for much of the crop's life. At about 50 DS, stomatal closure in the dry crop resulted in very low $g_c$ values, but stomata in the irrigated crop continued to respond to radiation until about 70 DS. A more thorough treatment of the results has been presented by Squire (1979).

## Interaction of water use and crop growth

The restricted soil water supply in the dry crop after 36 DS was manifested in a rapid reduction in green leaf area index, followed by a decline, then cessation, of dry matter production at about 47 DS. Measurements with soil thermocouple psychrometers showed that, when the water supply became restricted, soil water potential ( $Y_s$ ) was greater than –0.1 MPa in much of the root zone and lower (–0.6 MPa) only in the top 30 cm. By 47 DS, $Y_s$ was –1.5 MPa in the top 20 cm and leaf water potential ( $Y_L$ ) was –1.9 MPa at midday. Values in the irrigated crop were >–0.1 MPa for $Y_s$ and –1.2 MPa for $Y_L$ (ICRISAT 1978, Squire and Gregory 1981).

These measurements pointed to the interaction of factors that result in reduced crop growth during drought. When water is in short supply, the green leaf area intercepting radiation is liable to senesce, lowering $g_c$ but also restricting dry matter production. Full stomatal closure follows and prevents carbon dioxide entry to the leaves and further dry matter accumulation. To increase dry matter production, the water supply also must be increased.

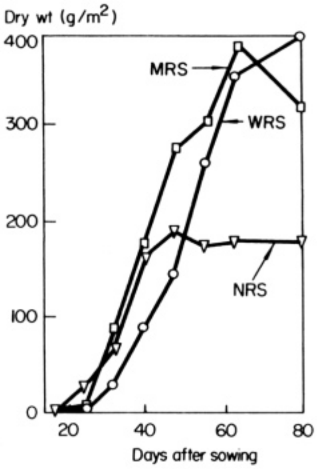
Figure 2 shows that at the conclusion of the experiment there was still a considerable quantity of unused water below 1 m. Root length results showed only small lengths of root deeper than 60 cm. Breeding varieties that produce deeper root systems has often been proposed as an answer to this problem (Hurd 1974), but in cereals, root growth often appears to cease at about anthesis (Gregory et al 1978). This means that any increased root growth must occur during the vegetative phase of growth. Varieties with a faster rate of root extension must be selected. In regions with very limited reserves of soil water, increasing the accessibility of water during vegetative growth may itself have undesirable consequences (Passioura 1972) if water is used before grain growth occurs.

These results indicate that millet may be well adapted to its drought-prone environment. As long as it has sufficient water to flower, the movement of stored assimilates to fill the grain will result in some yield.

While breeding may offer some hope for increasing the amount of water available to a crop, management of plant populations may provide an alternate strategy for using a limited supply of water more effectively.

## EXPERIMENT AT NIAMEY, NIGER

The experiment at the World Meteorological Organization (W.M.O.) AGRHYMET Center, Niamey, Niger (13°29'N; 2° 10'E) during the postrainy season determined how the balance between water supply and demand is controlled or affected by spacing in stands of millet. Pearl millet (BK560) was sown on deep sand at narrow (37.5 cm), medium (75 cm), and wide (150 cm) row spacings



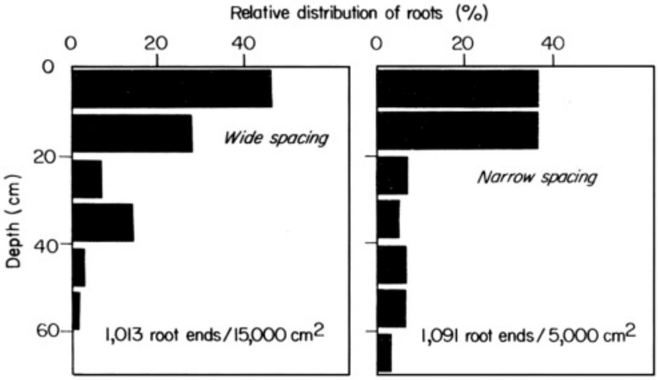
**5.** Crop dry weight for wide (WRS), medium (MRS), and narrow (NRS) spaced millet.

on 18 October 1980. Thinning 20 DS spaced plants 20 cm apart within rows.

The site (75 m × 25 m) was divided into 4 equal blocks, each containing 14 rows (12.5 m long) of each spacing treatment. All blocks were sprinkler-irrigated to field capacity to a depth of 2 m before sowing. No additional water was supplied beyond that necessary to establish the crop (completed at 14 DS). There was no rain during the experiment and the weather remained warm throughout. Evaporation from class A pan was 365 mm between 14 and 60 DS.

## Crop growth

Figure 5 shows total shoot weight for the three crops. The narrow and medium spaced crops grew faster than the wide spaced crop. The narrow spaced crop stopped growing 40 DS, but the medium spaced crop continued growing for another 15 days. Despite its initial slower growth, the wide spaced crop grew for a



**6.** Root distribution below narrow and wide spaced millet at 32 days after sowing longer time and eventually weighed more than the narrow or medium spaced crops.

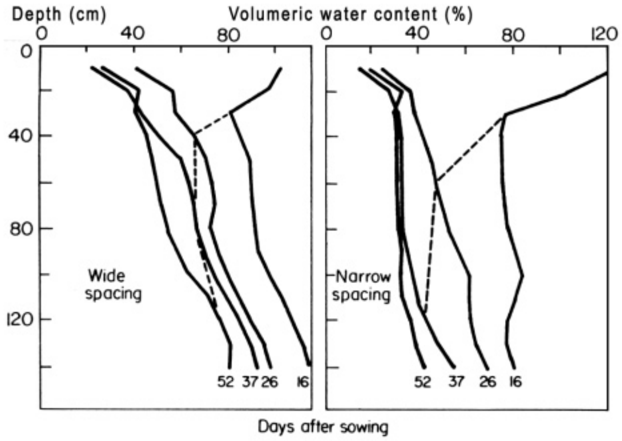
Root growth also was affected by plant density. Figure 6 compares the relative distribution of roots for narrow and wide spaced crops 32 DS. The root distribution was obtained by digging a pit and washing away a thin layer of soil to expose the root ends. A grid was placed against the washed face and the root ends in each grid square were counted. The narrow and wide spaced crops had similar numbers of root ends, but the roots of the narrow spaced crop were confined in a volume of soil one-third that of the wide spaced crop. At depths below 40 cm, the narrow spaced crop had 11.3% more roots than the wide spaced crop. This tendency for fewer deep roots as row width increased was confirmed 38 DS when soil axes from both the medium and the wide spaced crops were collected and their roots washed. The wide spaced crop had only half the root length of the medium spaced crop at depths below 50 cm.

### Water use

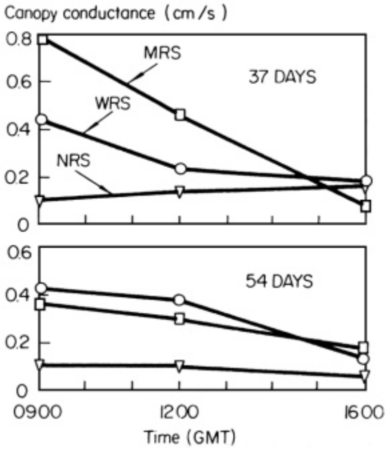
Water use was measured with a neutron probe using appropriate spacings of access tubes to discern possible gradients of water use across rows in the wide row spacing. Figure 7 shows the mean water use in the narrow and wide spaced crops. The drainage component was determined from tensiometer profiles of hydraulic potential. The pattern of water use clearly is different. The narrow spaced crop lost little water after 37 DS, while the wide spaced crop used water throughout the measurement period.

### Canopy conductance

Response of the stomata to the soil water supply is shown in Figure 8. At 37 DS, when the supply of soil water in the narrow spaced crop was also depleted, both canopy conductance and stomatal conductance values were small, indicating that the stomata were closed. In contrast, during the morning and early afternoon canopy conductance in the wide spaced crop was larger because the stomata were



**7.** Extraction of soil water below narrow and wide spaced millet. Dashed line shows the changing zero flux plane.



**8.** Changes in canopy conductance for wide (WRS), medium (MRS), and narrow (NRS) spaced millet at 37 and 54 days after sowing.

open. This difference between treatments also was evident at 54 DS, when the conductance of the narrow spaced crop remained small while that of the wide spaced crop, although smaller than previously, was still about four times larger.

## Interaction of water use and crop growth

These preliminary analyses again show the interaction between soil water supply, stomatal opening, and production of crop dry matter. The changes in rooting habit caused by the different row spacings eventually changed the quantity of water available to the crops. Altering plant density when the water supply is limited can have an important effect on the amount of crop dry matter produced.

## RELEVANCE TO RICE IMPROVEMENT

These results were obtained with pearl millet, but there are certain similarities between cereals in their response to drought. These have been characterized for rice in terms of avoidance and tolerance (Yoshida 1975). Drought avoidance, permitting a crop to grow longer in a given enviroment, usually is effected by either stomatal closure or reduced leaf area or by exploitation of a deeper reserve of soil water. The experiments reported here show that these factors interact. Growth and yields in the Indian experiment were related closely to the amount of water used so that increasing the supply of water might offer a way to improve yields. However, the variation in rooting depth between varieties is still largely undetermined and, although breeding may give the potential to root deeply, the actual rooting depth will depend on the physical and chemical conditions of the soil.

Characteristics of drought avoidance often are developed at the expense of photosynthesis. Tolerance for drought offers an alternative basis for improvement. For example, in the Indian experiment where drought occurred during grain filling, movement of materials from the stem enhanced grain yield. Other varieties may be even better at using previously accumulated reserves of carbohydrate to sustain grain yields.

The physiological responses affecting yield vary during a growing season (Boyer and McPherson 1975), so the timing of drought is important. The Niger experiment illustrates the combination of factors that result in yield differences when planting density is altered. However, management and breeding will result in improved crops only when both are based on a thorough understanding of the balance of evaporative demand relative to soil supply and the likely consequences of any imbalance on crop behavior.

## REFERENCES CITED

Boyer, J. S., and H. G. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23.

Cowan, I. R. 1965. Transport of water in the soil-plant-atmosphere system. J. Appl. Ecol. 2:221-239.

Gregory, P. J., M. McGowan, P. V. Biscoe, and B. Hunter. 1978. Water relations of winter wheat. I. Growth of the root system. J. Agric. Sci. Camb. 91:91-102.

Gregory, P. J., and G. R. Squire. 1979. Irrigation effects on roots and shoots of Pearl Millet (*Pennisetum typhoides*). Exp. Agric. 15:161-168.

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. Agric. Met. 14:39-55.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1978. Report of work 1977-78. Environmental physics, farming systems research program. Hyderabad, India.

Nimah, M. N., and R. J. Hanks. 1973. Model for estimating soil water, plant, and atmospheric interrelations: 1. Description and sensitivity. Soil Sci. Soc. Amer. Proc. 37:522-527.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Squire, G. R. 1979. The response of stomata of Pearl Millet (*Pennisetum typhoides*) to atmospheric humidity. J. Exp. Bot. 30:925-933.

Squire, G. R., and P. J. Gregory. 1981. Water use by rainfed and irrigated Pearl Millet. In preparation.

Yoshida, S. 1975. Factors that limit the growth and yields of upland rice. Pages 46-71 *in* International Rice Research Institute. Major research in upland rice. Los Baños, Philippines.

# SHOOT CHARACTERISTICS OF RICE FOR DROUGHT RESISTANCE

K. S. MURTY AND G. RAMAKRISHNAYYA

Shoot characters associated with moisture stress resistance and recovery vigor of rice under field conditions were assessed. Drought-resistant cultivars, such as Lalnakanda 41, CR143-2-2, TNl/T65, and Kiran, were characterized by late wilting and early recovery, tolerance for heat, continuous tiller production even during drought, high leaf water potential, high dry matter production at flowering, and greater contribution of stem carbohydrates to grain filling.

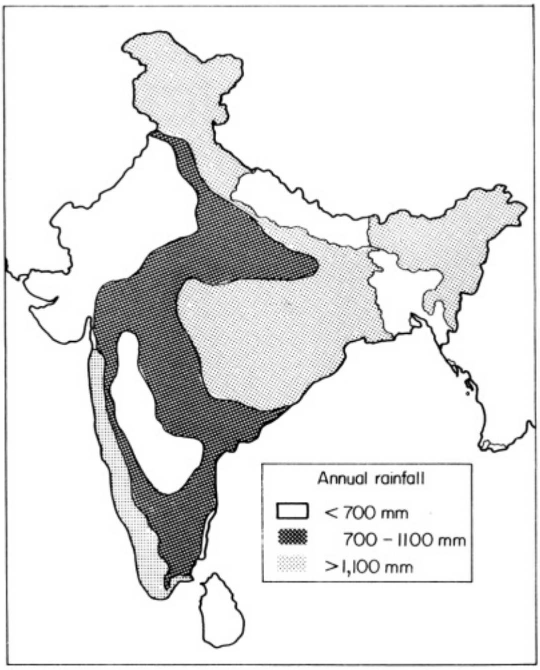
Treatment of seeds with sodium phosphate (358 ppm) prior to seeding and foliar spray of kinetin (10 ppm) and CCC (500 ppm) at vegetative and reproductive stages promoted drought resistance.

Six million hectares of rice are grown in India under rainfed dryland conditions with moderate rainfall (700-1,100 mm) over a 3-month period (July-September) (Fig. 1). Generally, early-maturing rice cultivars (80-110 days total duration) are planted. Although the early crop receives adequate rainfall to mature, it often is subjected to periodic droughts which last up to 10 days/cycle (Table 1) (George et al 1974).

The moisture stress situation is: 1) unpredictable drought, 2) poor nutrient availability, 3) inadequate crop stand, 4) low moisture retention, and 5) poor recovery rate. This situation demands that varieties with desirable plant characteristics be selected.

---

Central Rice Research Institute, Cuttack, India.



**1.** Drought prone rice areas (700-1,100 mm annual rainfall) in India (George et al 1974).

**Table 1. Number of breaks in the monsoon rains in 80 years in India (George et al 1974).**

| Duration of break (days) | Breaks (no.) | | |
|---|---|---|---|
| | July | August | July-August |
| 3- 4 | 28 | 25 | 2 |
| 5- 6 | 10 | 12 | — |
| 7- 8 | 8 | 9 | 1 |
| 9-10 | 3 | 4 | — |
| 11-12 | 2 | 3 | 1 |
| 13-16 | 1 | 1 | — |
| 17-21 | 1 | 1 | 1 |
| Total | 53 | 55 | 5 |

Investigations were conducted at the Central Rice Research Institute (CRRI), Cuttack, and the All India Coordinated Rice Improvement Project (AICRIP), Hyderabad, to determine the reaction of rice varieties to induced moisture stress conditions during the dry season, to identify characters associated with resistance to such stress, and to devise ameliorative measures to reduce the adverse effects of drought (Murty and Venkateswarlu 1978). This paper discusses shoot characters associated with moisture-stress resistance and recovery vigor in rice.

## DROUGHT TOLERANCE AT DIFFERENT GROWTH STAGES

Unpredictable drought spells can occur at any growth stage of a rice crop.

### Germination

Rainfed dryland rice normally is seeded in anticipation of the monsoon season. If initial rains are scanty or rain fails soon after sowing, the germination and stand of the crop are adversely affected. In general, coarse-grain type cultivars with slow germination rates resisted moisture deficiency better than other types (CRRI 1966). Pretreatment of seeds with 358 ppm sodium phosphate ($Na_2HPO_4$) for 12-14 hours helped germination and stand uniformity of seedlings even under stress conditions (Chatterjee 1980).

### Seedling stage

Early seedling stage is the most vulnerable to moisture stress. Drought injury is manifested either by wilting (rolling) or by drying of leaves. Leaf drying is common among short-statured varieties (CRRI 1971). At AICRIP, 21-day-old seedlings were tested in the greenhouse for the relationship between wilting and recovery (AICRIP 1979). Cultivars were grouped by observations into four categories:

1) slow wilting and quick recovery — MW10, CR143-2-2, Akashi.
2) fast wilting and quick recovery — IET6148, IET6155, Bala.
3) slow wilting and slow recovery — IET2685, IET4106, IET4107, IET5859, IET5850.
4) fast wilting and slow recovery — Cauvery.

Group 1 plants had both greater resistance and early recovery. Group 2 wilted fast but recovered quickly through an avoidance mechanism. Group 4 was not suitable for moisture stress conditions.

The relationship of wilting behavior to thermal injury or heat resistance of leaf tissue (52° C for 15 minutes), as indicated by electrolytes discharged in the water medium, also was examined. Cultivars CR143-2-2, MW10, and Akashi showed a high degree of heat resistance through delayed wilting and rapid recovery (AICRIP 1979).

The stability of chlorophyll to heat, which is considered an index of drought resistance, was fairly high in drought-tolerant types (Majumder and Murty 1962).

Tests for proline accumulation in drought-stressed leaves in the field showed low levels of free proline in drought-resistant cultivars such as Lalnakanda 41, CR143-2-2, and Kiran (Table 2). On relief of stress, free proline increased in these cultivars. In drought-susceptible types such as Co 13, the increase was not apparent (CRRI 1976). However, under rapid stress at 5-10 bars of polyethylene-glycol (PEG), proline accumulation was higher in drought-resistant than in drought-susceptible cultivars, indicating that the reaction of rice varieties to proline accumulation under stress is not consistent but varies with the mode and duration of induced stress (CRRI 1975).

Recovery speed after drought stress was associated with high leaf water content during the stress period (Bhattacharjee et al 1971). Under extreme desiccation and

**Table 2. Effect of induced field drought$^a$ at tillering stage on free proline content in the penultimate leaf (CRRI 1976).**

| Cultivar | Free proline content (µg/g fresh wt) | | |
|---|---|---|---|
| | W | D | Recovery 24 h after irrigation |
| Lalnakanda 41 (DR) | 73 | 54 | 216 |
| CR143-2-2 (DR) | 86 | 96 | 227 |
| CR141-192 (DR) | 70 | 100 | 212 |
| Co 13 (DS) | 49 | 141 | 93 |

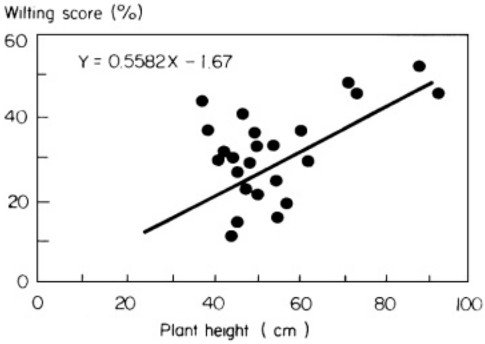
[a] DR = drought resistant, DS = drought susceptible, W = normal irrigation, D = drought (stress from 30 to 50 days after sowing. Soil moisture depleted to 1/3 field capacity by end of drought period).

complete leaf-drying, seedling recovery was higher in types with high leaf sheath succulence. Leaf sheath moisture also showed good association with root regenerating ability (Murty and Venkateswarlu 1978).

## Tillering stage

Drought at the tillering stage reduced plant height and leaf length, induced leaf rolling or drying, and prolonged the vegetative stage even after drought stress was removed (Fig. 2).

Drought-resistant cultivars such as Bala, Bala/JBS508, and Lalnakanda 41 were less affected under drought (CRRI 1978). Drought (50% field capacity) for a 15-day period at early tillering enhanced the yield in drought-resistant cultivars such as Mtu 17, Lalnakanda 41, and Mtu 17 Mutant 2 by the promotion of productive tillers soon after the stress was relieved (CRRI 1975). Total nitrogen concentration in both leaf and stem increased under drought. This was reflected in a corresponding increase in protein-N in drought-resistant cultivars and in ammoniacal-N in drought-susceptible cultivars. The accumulated protein-N under drought induced continuous tiller production even under stress and vigorous tillering soon after removal of stress in the drought-resistant cultivars (CRRI 1973).



**2.** Relation between rice cultivar height and wilting score under field drought at tillering stage (CRRI 1978).

**Table 3. Leaf moisture. moisture extraction, and yield of high-yielding cultures under soil moisture stress (CRRI 1972).**

| Variety | Leaf moisture (%) | Total moisture extracted (%) | Grain yield (t/ha) |
|---|---|---|---|
| Bala | 277 | 5.82 | 3.28 |
| CR125-12-1-2 | 281 | 6.44 | 5.73 |
| CR115-54-62 | 252 | 6.34 | 4.44 |
| CR115-79 | 172 | 8.98 | 2.93 |
| CR44-3b | 253 | 6.44 | 2.76 |
| CR113-18 | 252 | 8.19 | 4.88 |
| CR125-12-3-3 | 281 | 6.69 | 3.76 |
| CR1134 | 252 | 7.29 | 5.29 |
| CR113-31 | 252 | 8.79 | 2.95 |
| Lalnakanda 41 | 289 | 8.07 | 4.00 |

In early types, normally grown in drought-prone dryland areas, most tillers produced up to 40-45 days after sowing (DS) were productive. Recovery vigor in tiller production was relevant only up to that stage. Only tillers with 500 mg dry weight at 45 DS and those that attained a height of 60% of the main shoot supported panicles. Small tillers formed later were sterile (Rao and Murty 1975).

Studies on moisture extraction pattern and water use efficiency for grain production in the drought-adapted varieties indicated two types of reaction: 1) low water requirement with moderate leaf water content, such as in Bala, and 2) moderate water requirement with high leaf moisture, such as in CR125 (Table 3). Type 1 cultivars exhibited resistance mechanisms while type 2 showed adaptive mechanisms, evident in their extensive root proliferation (CRRI 1972).

Foliar spray of kinetin (10 ppm) during the drought phase promoted rapid recovery and normal growth and yield (Ramakrishnayya and Murty 1979).

**Table 4. Effect of drought[a] on stem sugars at booting and flowering stages (Bhattacharjee et al 1971).**

| Variety | Sugar (%) | | | |
|---|---|---|---|---|
| | Nonreducing | | Total | |
| | W | D | W | D |
| | *Booting* | | | |
| Lalnakanda (DR) | 4.0 | 4.5 | 9.1 | 5.1 |
| TN1/T65 (DR) | 5.1 | 7.9 | 4.5 | 11.3 |
| Co 13 (DS) | 1.2 | 4.3 | 2.4 | 14.7 |
| | *Flowering* | | | |
| Lalnakanda 41 (DR) | 5.3 | 6.6 | 10.1 | 12.5 |
| TN1/T65 (OR) | 3.4 | 5.8 | 5.1 | 8.0 |
| Co 13 (DS) | 4.0 | 4.0 | 8.3 | 9.7 |

[a] DR = drought resistant, DS = drought susceptible, W = normal irrigation, D = drought.

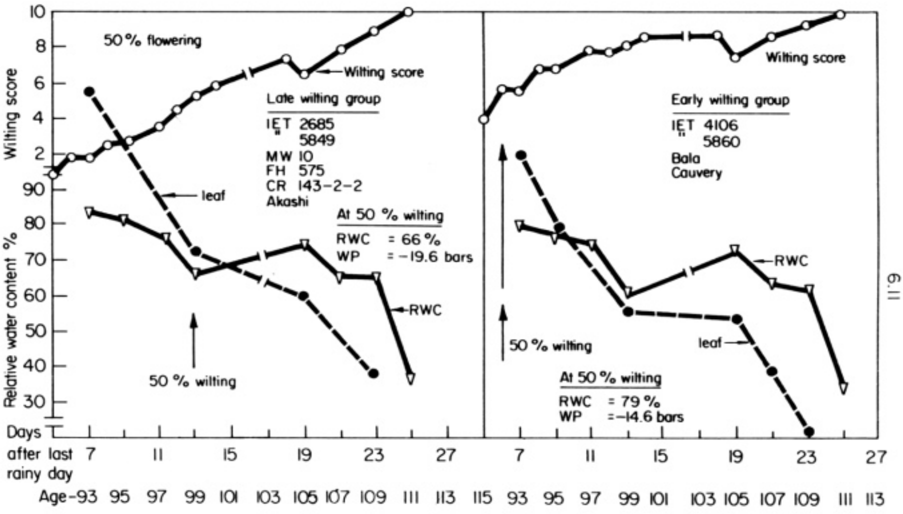
## Booting and flowering stages

Moisture stress at booting and flowering reduces height and dry matter production, delays panicle exsertion, and induces uneven flowering. Photosynthetic efficiency is impaired, resulting in less dry matter accumulation and a low concentration of nonreducing sugars in the stem (Table 4). In general, varieties with high stem sugars resisted drought better than others because sugars translocated from stem to panicle promoted normal grain filling under stress (Bhattacharjee et al 1971).

Useful results on drought resistance at reproductive and ripening stages have been obtained at AICRIP. Two groups—late wilting and early wilting types—were identified. The late-wilting group showed low relative water content (RWC) (66%) and water potential (WP)(-19.6 bars) in leaf while the early-wilting group showed relatively higher RWC (79%) and WP (–14.6 bars). The late-wilting group exhibited resistance mechanisms while the early-wilting group showed avoidance mechanisms (Fig. 3). The drought-resistant types also showed high osmotic concentration, particularly in the shoot, which helped to maintain high water content under drought (Rajagopalan 1957).

Certain varieties exposed to drought at the vegetative stage failed to produce normal panicles even when stress was relieved far ahead of the flowering stage (Jaya and other medium types). This indicated further consideration of genotypes as drought-injury persisting and nonpersisting types. In general, varieties with high dry matter production at flowering gave better yields under dryland conditions because of a considerable contribution of reserve carbohydrates to grain filling (Murty and Venkateswarlu 1978).

Foliar spray of cycocel (CCC)(500 ppm) before flowering helped to reduce drought injury at the reproductive stage (Rao and Murty 1980).



**3.** Pattern of change in relative water content (RWC), leaf water potential (Ψ leaf), and wilting score (WS) with increasing drought stress duration under field conditions (AICRIP 1979).

## Ripening stage

Drought during the ripening stage induced sterility of spikelets and premature lodging of the crop. Maintenance of high leaf water potential and delayed leaf senescence are desirable traits during this stage. The drought-resistant cultivars such as Lalnakanda 41 and TN1/T65 were characterized by high stem weight losses during the ripening stage, indicating the contribution of stem carbohydrates to grain filling.

Many rice varieties can tolerate drought at the vegetative stage by a sustaining mechanism and recovery vigor. However, even reputed drought-resistant cultivars such as Lalnakanda 41 and Bala become susceptible to drought at the flowering stage, indicating the need to identify superior donors for drought resistance at reproductive and flowering stages and the need to transfer this character to modern high yielding rice cultivars.

An overview of the shoot characters associated with drought resistance and recovery vigor indicates the important traits for better performance under moisture-stress situations (Rao et al 1971, Murty and Venkateswarlu 1978):

- Early duration (85-100 days) with less extended vegetative period under stress.
- Medium height (80-100 cm) with less reduction in height under stress.
- Moderate, synchronized tillering at early growth stages, normal tillering even during drought phase, high, ratio of productive tillers.
- Seedling vigor with rapid buildup of leaf area index at early stages (Krishnamurthy 1975). Thick, medium long, and erect or moderately droopy leaves (Yoshida 1975), normal leaf elongation with slow leaf senescence, maintenance of high water potential in leaf with low transpiration ratio (Paul et al 1974) and high photosynthetic efficiency (Murty et al 1976), and high leaf sugar and protein content.
- High root-shoot ratio, resistance to internal water stress with ability to recover and grow rapidly on hydration, thick stem with high leaf sheath succulence (Rao et al 1971), late wilting and early recovery with resistance mechanism to withstand low water potential in leaf (high dry matter accumulation by flowering).
- Long dense panicles with high harvest index and greater contribution of shoot dry matter to panicle and grain yield.
- Stability and synchronization of flowering with full expression of panicle (less sterility of spikelets).

The usefulness of breeding varieties for a nonspecific stress such as drought is evident in the set of traits governing productivity on drought-prone dryland areas. The traits appear to be different from those governing productivity of wetland rices grown with adequate moisture (Venkateswarlu 1977, Prasad 1977). An interdisciplinary approach by breeders, physiologists, and soil chemists is essential to understanding rice plant response to drought stress and to improving yield potential.

## REFERENCES CITED

AICRIP (All India Coordinated Rice Improvement Project). 1979. Progress report of All India Coordinated Rice Improvement Project, Hyderabad, kharif 1979. Physiol. 6:3-1.

Bhattacharjee, D. P., G. Ramakrishnayya, and S. C. Paul. 1971. Physiological basis of drought conditions. Oryza 8 (2 suppl.):61-68.

Chatterjee, B. N. 1980. Upland direct seeded rice production through pretreated seeds under rainfed conditions. In Proc. Group Meet. Res. Priorities in Rice for Drought Prone Areas, May 16-17, 1980, Cuttack, India.

CRRI (Central Rice Research Institute). 1966. Annual progress report of the scheme —Breeding rice varieties for drought areas. Cent. Rice Res. Inst., Cuttack, India.

CRRI (Central Rice Research Institute). 1971. Annual report of 1971. Cent. Rice Res. Inst., Cuttack, India.

CRRI (Central Rice Research Institute). 1972. Annual report of 1972. Cent. Rice Res. Inst., Cuttack, India.

CRRI (Central Rice Research Institute). 1973. Annual report of 1973. Cent. Rice Res. Inst., Cuttack, India.

CRRI (Central Rice Research Institute). 1975. Annual report of 1975. Cent. Rice Res. Inst., Cuttack, India.

CRRI (Central Rice Research Institute). 1976. Annual report of 1976. Cent. Rice Res. Inst., Cuttack, India.

CRRI (Central Rice Research Institute). 1978. Annual report of 1978. Cent. Rice Res. Inst., Cuttack, India.

George, C. T., P. E. Moray, and V. P. Athyankar. 1976. Meteorological monograph Agromet, India 6:4-5.

Krishnamurthy, C. H. 1975. Upland rice. Proc. AICRIP Workshop, Hyderabad.

Majumder, S. K., and K. S. Murty. 1962. Modification of technique for determination of chlorophyll stability index in relation to studies of drought resistance in rice. Current Sci. 31:470-471.

Murty, K. S., S. K. Nayak, G. Sahu, G. Ramakrishnayya, K. V. Janardhan, and R. S. V. Rai. 1976. Efficiency of $^{14}$C photosynthesis and translocation in local and high-yielding rice varieties. Plant Biochem-J 3:67-71.

Murty, K. S., and B. Venkateswarlu. 1978. Physiological constraints on growth and productivity in rice during Kharif season. Pages 45-65 *in* Nat. symp. increasing rice yield in kharif. ICAR/ CRRI, Cuttack.

Paul, S. C., V. K. Vamadevan, G. B. Manna, and R. N. Pati. 1974. Consumptive use and moisture extraction pattern of upland direct sown rice as influenced by variety, nitrogen and spacing. Oryza 11:99-101.

Prasad, S. C. 1977. Upland rice. Paper presented at AICRIP Workshop, Hyderabad, April 1977.

Rajagopalan, K. 1957. Osmotic concentration of cell sap in shoot and root and drought resistance. Rice Res. Newsl. 5(2):7-13.

Ramakrishnayya, G., and K. S. Murty. 1979. Amelioration of drought injury in rice by chemical sprays. Current Sci. 48:264-265.

Rao, C. N., and K. S. Murty. 1975. Effect of split application of nitrogen on tiller survival and yield in direct seeded upland rice. Indian J. Agric. Sci. 45:183-188.

Rao, C. N., and K. S. Murty. 1980. Paper presented in group meeting on research priorities in rice for drought-prone areas. Cuttack, May 1980.

Rao, M. J. B. K., S. Sampath, and K. S. Murty. 1971. Breeding varieties for special situations. Indian Farming 21(7):45-52.

Venkateswarlu, B. 1977. Breeding rice for tolerance to drought. Paper presented at AICRIP Workshop, Hyderabad, April 1977.

Yoshida, S. 1975. Factors that limit growth and yields of upland rice. Pages 46-71 *in* Major research in upland rice. Int. Rice Res. Inst., Los Baños, Philippines.

# EFFECT OF DROUGHT ON SHOOT GROWTH: SIGNIFICANCE OF METABOLISM TO GROWTH AND YIELD

S. K. SINHA, R. KHANNA-CHOPRA, P. K. AGGARWAL,
G. S. CHATURVEDI, AND K. R. KOUNDAL

Shoot growth and yield are dependent upon the development of source and yield components. The influence of water stress on source components affects the development of yield components according to the determinate or indeterminate nature of the crop species. Metabolic effects are induced in a relatively short time and disappear relatively quickly on recovery. Therefore, metabolic effects could have an immediate effect only on those source or yield components developing at that time. Plant metabolism should be evaluated through such effects.

The adverse effects of water deficit on crop plants and the development of management practices or genotypes that can partially or fully overcome those effects are of worldwide concern (Mussell and Staples 1979, Turner and Kramer 1980, Paleg and Aspinall 1981). Such studies can be grouped as research on the effects of water deficit on:

- the free amino acid pool, particularly proline content, activity of nitrate reductase, ribulose-1, 5 biphosphate (RuBP), phosphoenolpyruvate (PEP) carboxylase, protein synthesis, and solute accumulation. Most of these studies are based on seedlings, excised plant parts or tissues.
- morphological characters such as leaf and shoot growth and regrowth, mostly in grasses. Many of these studies include effects on stomatal behavior, transpiration, changes in water potential, and turgor and osmotic adjustment.

---

Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110012.

- yield components in controlled environments.

These studies provide insight into the functioning of plant processes. Often responses observed at one stage have been used to determine correlations and predict selection criteria for drought resistance. But three points need clarification through case studies on the effects of water deficit on crop productivity:

1. What is the nature of water deficit under field conditions?
2. What are the distinct phases of growth and what are their relationships?
3. How do metabolic events influence growth and yield?

## NATURE OF WATER DEFICIT

The duration and intensity of water deficit is location specific and can vary from year-to-year because of the rainfall pattern. When monsoon- and winter-season rainfall in India are considered, the probability of water deficit is predictable. In northern India, rainfall starts in late June and ends by September. Crops are sown in early July, with a second crop in October or November, depending on the ambient temperature and stored soil moisture.

Under certain rainfall patterns, such as when 5-20 day dry spells occur during the rainy season, a water deficit could develop in the preanthesis period. But it generally occurs after anthesis, when it influences grain development. In the winter season, wheat or chickpea can experience water deficit during differentiation or in the postanthesis period. Although water stress intensity varies from year to year, there is usually enough water stress under field conditions to reduce leaf expansion and vegetative growth. Therefore, it is important to establish a relationship between reduced vegetative growth and reproductive growth (particularly the yield components).

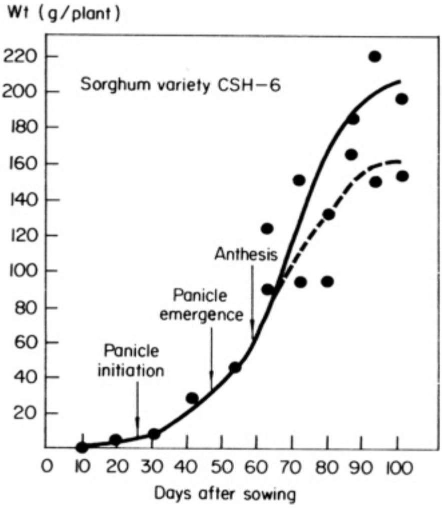
## RELATIONSHIP OF GROWTH PHASES UNDER DROUGHT

The growth pattern of two crops, sorghum *Sorghum vulgare* and pigeonpea *Cajanus cajan* grown in the rainy season and wheat *Triticum vulgare* and chickpea *Cicer arietinum* grown in winter, are shown in Figures 1-4. The main points to consider are: These crops have the normal S-shaped curve (Fig. 5). If stress at any point is followed by rain to support growth, how much compensation is possible in comparison with the normal curve? To what extent would the metabolic effects influence immediate recovery and compensate in the final yield?

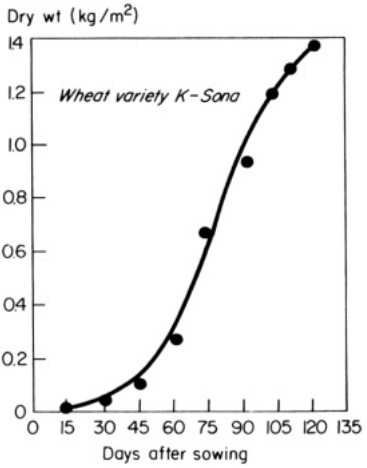
### Vegetative growth, yield components, and yield

The grain yield of a crop usually depends on the final yield components, such as the number of panicle-bearing shoots/m$^2$, grains/spikelet per panicle, and grain weight/panicle in wheat, rice, and other cereals (Ishizuka 1969, Sinha and Khanna 1975). In pulses and oilseed crops, the number of pods, seeds per pod, and seed weight are the major components. The development of these components is vital for crop yields.

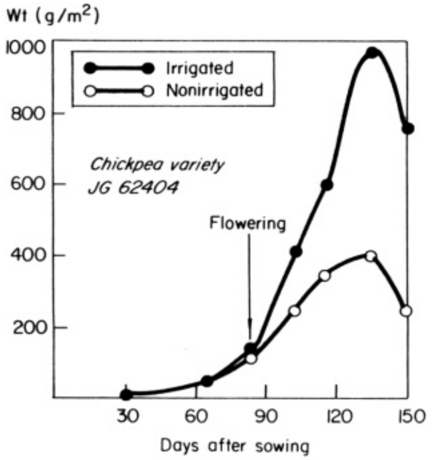
Plant breeders generally have emphasized yield components, although the development of source components is equally important. The complementation of



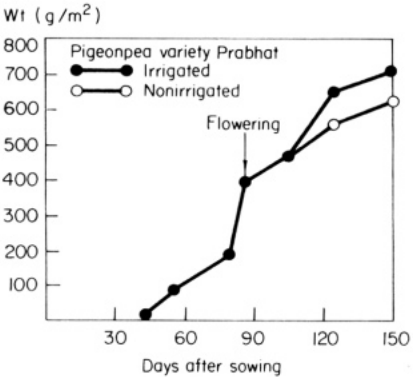
1. Growth curve of sorghum from emergence to harvest.



2. Growth curve of wheat from emergence to harvest.

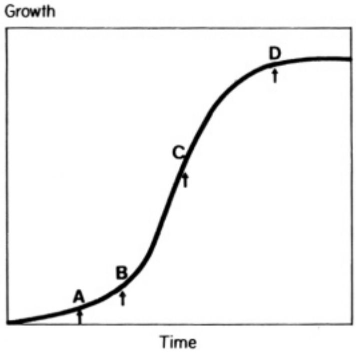


3. Growth curve of chickpea from emergence to harvest.



4. Growth curve of pigeonpea from emergence to harvest.

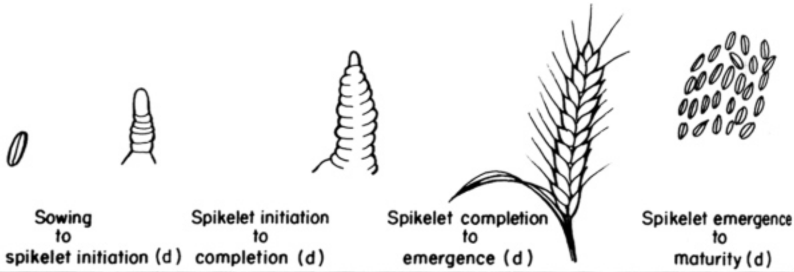
these source and sink components leads to higher grain yield (Sinha and Khanna 1975). Figure 6 illustrates the timetable for the development of wheat components at Delhi. The main features of this timetable are the duration of spikelet differentiation, development and emergence of spikelet, and grain filling. When wheat is irrigated 26 days after sowing (DS), leaf area expands and tillers develop. We observed that an increase in leaf area of the mother shoot slightly increased the number of spikelets that emerged (Table 1), although it did not significantly affect



**5.** A normal S-shaped growth curve with possible points where stress could come.

spikelet production (Table 2).

When the apex differentiates into a spikelet in wheat, flag leaf initiation has already begun. A stress period at this stage could influence the size of the flag leaf. In some varieties, the size of flag leaf was reduced more than in others (Chaturvedi et al 1981). However, a decrease in grain yield of the panicle was not commensurate with the reduction in leaf area, which suggests compensation for photosynthesis, perhaps by increasing the leaf thickness. Therefore, an event at the time of spikelet differentiation eventually would directly or indirectly affect grain yield. The importance of morphological responses and metabolic events becomes obvious. If a metabolic adaptation leads to restoration of flag-leaf size or spikelet number, the genotype would be stable. But once the final spikelet number or leaf



| Cultivar treatment | Sowing to spikelet initiation (d) | Spikelet initiation to completion (d) | Spikelet completion to emergence (d) | Spikelet emergence to maturity (d) |
|---|---|---|---|---|
| C 306 irrigated | 25 | 30 | 32 | 50 |
| C 306 nonirrigated | 25 | 25 | 30 | 50 |
| K – Sona irrigated | 24 | 25 | 33 | 53 |
| K – Sona nonirrigated | 23 | 17 | 33 | 48 |

**6.** Development of a wheat spikelet.

**Table 1. Relationship between leaf area and spikelet number.**[a]

| Group | Leaf area from spikelet initiation to completion | | | Spikelets observed (no.) | | | Spikelets expected (no.) | | |
|---|---|---|---|---|---|---|---|---|---|
| | $I_0$ | $I_1$ | $I_2$ | $I_0$ | $I_1$ | $I_2$ | $I_0$ | $I_1$ | $I_2$ |
| *T. aestivum* | 19.88 | 21.48 | 22.33 | 14.28 | 19.71 | 20.93 | 18.58 | 20.07 | 20.93 |
| *T. durum* | 16.23 | 20.07 | 26.20 | 13.84 | 18.79 | 20.82 | 12.88 | 15.93 | 20.82 |
| Triticale | 17.04 | 21.58 | 27.26 | 16.64 | 22.76 | 25.80 | 16.08 | 20.36 | 25.80 |
| *H. vulgare* | 43.72 | 50.35 | 43.51 | 16.70 | 20.89 | 21.00 | 21.12 | 24.32 | 21.00 |
| Average | 24.22 | 28.37 | 29.82 | 16.11 | 20.54 | 22.14 | 17.16 | 20.17 | 22.14 |

[a] $I_0$ = nonirrigated, $I_1$ = presowing irrigation, $I_2$ = recommended irrigation.

**Table 2. Effect of water stress on the number of spikelets in wheat.**

| Cultivar | Treatment | Spikelets (no.) | |
|---|---|---|---|
| | | Initiated | Emerged |
| Kalyansona | Irrigated | 22.7 ± .4 | 23.0 ± .4 |
| | Nonirrigated | 21.3 ± .5 | 21.5 ± .7 |
| C306 | Irrigated | 24.8 ± .6 | 24.7 ± .5 |
| | Nonirrigated | 23.0 ± .4 | 22.7 ± .5 |

size has been determined, the advantage of metabolic adaptation might become insignificant for these components.

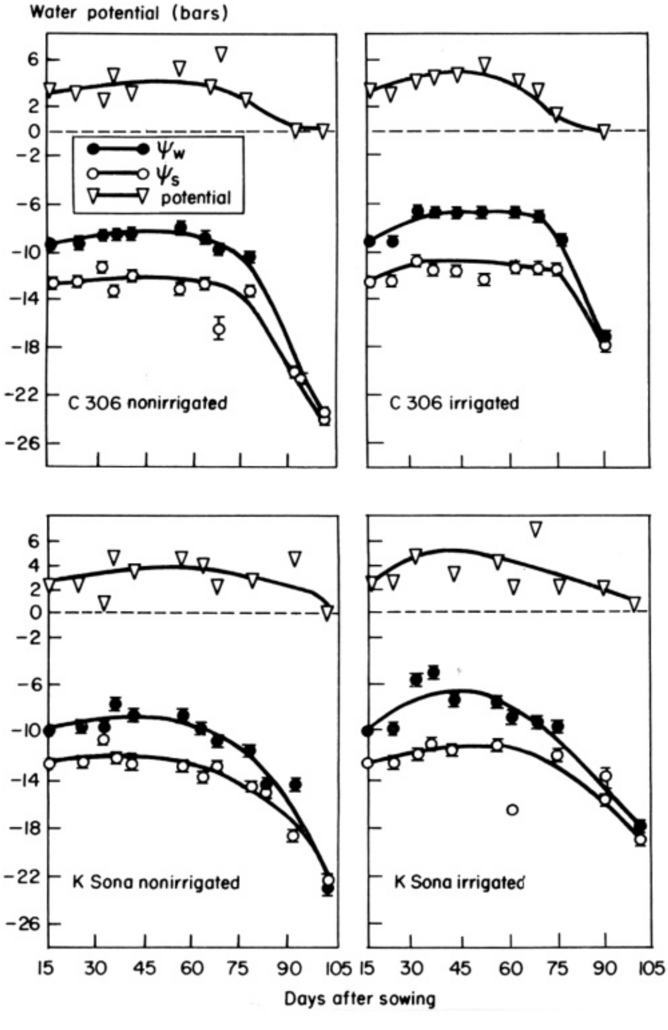
What should the measure of stress be? Fischer (1980) points out that, while it had been based on soil moisture content, stress is now measured by plant water potential (y). Does plant y provide a measure of water deficit and stress throughout the life cycle of the plant? Changes in leaf y of wheat and chickpea are given in Figures 7 and 8. Obviously leaf y, as well as plant y continue to decline as the plant grows under field conditions. This decline is sharper after panicle emergence in wheat and from flowering in chickpea. This is not a small change because leaf y drops from –6 to –8 bars to –20 bars. Most authors report that at –20 bars, leaf y indicates almost severe stress in crop plants, a condition that impairs most physiological and biochemical activities (Hsiao 1973, Boyer and McPherson 1975). Under field conditions, the postflowering phase has considerable physiological activity because a larger amount of dry matter is produced at this time (Aggarwal et al 1981, unpubl.). Even the suggestion for using turgor pressure as a stress index may be inadequate, because leaves usually have zero turgor at this stage. Thus we suggest the need to develop a more suitable measure of stress under field conditions.

## Effects of indeterminate plants

Chickpea is an indeterminate but photoperiod-sensitive plant. Growth reduction before flowering is reflected in the number of secondary and tertiary branches that bear pods. Figure 3 compares irrigated and nonirrigated chickpea grown in the field and indicates that a lag in dry-matter accumulation from 60 DS was reflected in grain yield.

Chickpea is peculiar in its response to water availability after flowering. In wheat, Passioura (1976) showed a linear increase in grain yield as water availability increased after anthesis. But in chickpea, a slight excess ofwater increases vegetative growth further. Thus biomass — but not grain yield — increases. However, a mutant with relatively better response to water availability has been identified that yields better than its parent (Sinha and Swaminathan 1981). In this species, when plants were stressed before flowering but subsequently given water equal to the control, the plants yielded almost equally (Table 3).

In *Lupinus,* plants stressed during the preflowering stage or during the full flowering period had the lowest seed yield (Withers and Ford 1979). This showed a greater possibility of compensation for adverse effects before flowering in an

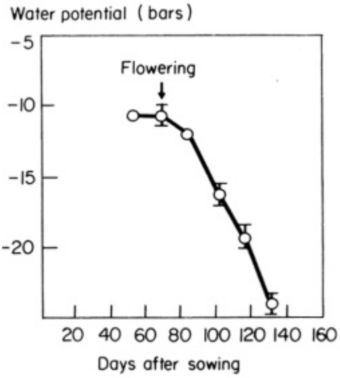


**7.** Water potential of wheat during growth and development.

indeterminate plant such as chickpea.

In *Brassica,* the amount of leaf area at bolting is related to the size of the bolt (Bhargava, unpubl.) Plants stressed in the seedling stage could compensate for the loss and reach the same bolt size as the control. Plants under water stress at bolting lacked the capacity to compensate for loss, which resulted in a small bolt size. This effect was essentially through the expansion and senescence of leaves (Table 4).

These examples indicate that the effects of water stress on yield are the consequences of several events that occur earlier than the period of actual yield formation. The effects on factors such as leaf area development or senescence are relatively short compared with the total time of yield formation. If we follow the



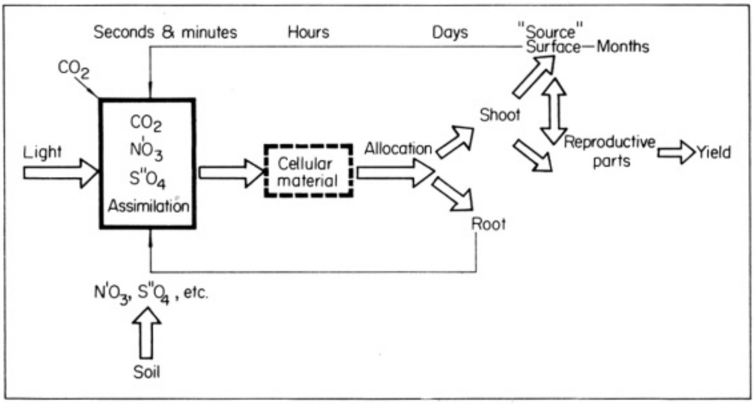
**8.** Water potential of chickpea during growth and development.

effects on leaf area expansion and senescence further, we find those effects are caused by even shorter processes related to the assimilation of $CO_2$, $NO_3$, and $SO_4$ and to the allocation of assimilates (Fig. 9).

## EFFECTS ON METABOLISM

Changes occur in metabolites and enzymes associated with assimilatory and degradative reactions in plants placed under water stress. Studies have been done on carbohydrate and nitrogen balance and metabolism in plants exposed to stress through osmotica such as polyethylene glycol (PEG), mannitol, or forced wilting. The results obtained through induced short-term stress and natural field stress are not comparable. Yet effects due to PEG-induced stress or obtained in controlled environments have often been used to explain plant behavior in field situations. The types of experiments used to evaluate the importance of metabolic studies in relation to water deficit are:

- Applying stress to excised parts in plants raised in controlled environments and studying changes in metabolites and enzymes;



**9.** The relationship of metabolism, growth, and yield in a time scale.

**Table 3. Effect of water stress at different stages on dry matter and yield components in *Cicer arietinum* (av of 12 plants).**

| Stress treatment | Dry matter[a] (g) | Pod wt (g) | Pods (no.) | Seeds (no.) | Seed wt (g) |
|---|---|---|---|---|---|
| No stress | 13.50 ± 1.75 | 8.08 ± 1.14 | 55 ± 3.20 | 65 ± 6.49 | 6.39 ± 1.02 |
| At vegetative stage | 13.33 ± 0.33 | 7.64 ± 0.42 | 50 ± 7.89 | 52 ± 10.28 | 6.14 ± 0.37 |
| At flowering stage | 8.00 ± 0.28 | 3.83 ± 0.36 | 30 ± 2.64 | 29 ± 0.57 | 2.29 ± 0.05 |
| At pod setting | 12.50 ± 0.76 | 5.25 ± 0.57 | 42 ± 7.45 | 38 ± 0.85 | 4.07 ± 0.37 |
| At pod maturity | 12.67 ± 1.33 | 7.35 ± 0.37 | 49 ± 4.58 | 51 ± 5.69 | 5.99 ± 0.81 |

[a] Fallen leaves not included

**Table 4. Effect of water stress at two stages on compensation in *Brassica*.[a]**

| Stage, treatment | Leaf Ψ | Leaf area | | Bolt ht (cm) | | Silique on main shoot |
|---|---|---|---|---|---|---|
| | | Prestress | Recovered | Prestress | Recovered | |
| Seedling | | | | | | |
| Control | –8.5 | 100 | 100 | 100 | 100 | 100 |
| Stressed | –21.0 | 59 | 84 | 48 | 112 | 89 |
| Bolting | | | | | | |
| Control | –8.5 | 100 | 100 | 100 | 100 | 100 |
| Stressed | –21.2 | 50 | 74 | 50 | 71 | 57 |

[a] Source: A. Goel, S.C. Bhargava, and S.K. Sinha (unpubl.)

- raising plants in controlled environments, then applying PEG to the root systems and analyzing the shoots; and
- raising plants under field conditions and using their aerial parts for studying the effects of water stress through osmotica application.

Two major factors could cause profound differences in field-grown plants and other systems:

- Metabolites in field-grown plants can be redistributed among different plant parts. Therefore, a balance between aerial parts and underground parts should be an important consideration.
- Field-grown plants have greater capacity for osmotic adjustments than plants grown in a controlled environment.

## Protein synthesis

In an actively metabolizing cell, there is a continuous turnover of proteins involved in various cellular processes. When plants are subjected to stress, recovery of important processes such as respiration and photosynthesis upon rewatering may be of little value unless the cells can renew protein synthesis. Few studies have been conducted on transcription and translation, two major components of protein synthesis.

Under moisture stress, tomato retained the ability to synthesize ribonucleic acid (RNA), but the rate of RNA destruction increased (Gates and Bonner 1959). In maize, minor changes were observed in leaf RNA when leaves were exposed briefly to drought but protein synthesis greatly declined. This was attributed to the dissociation of polysomes into subunits (Genkel et al 1967).

The activity of RNA-hydrolyzing enzymes increases RNAs in severely stressed tissue (Bozenkov 1968). A new type of ribonuclease was produced during water stress (Genkel et al 1974). These studies were done in crude extracts. Using a purified enzyme preparation in wheat, Yi and Todd (1979) found identical ribonuclease enzymes in severely stressed and in nonstressed tissue. The subcellular distribution between soluble and particulate fraction was not changed by water stress treatment. Although the dry weight of treated plants was less, the total quantity of ribonuclease per plant was similar in the control and water-stressed plants. Hence, the activity per gram was significantly higher. Crude extracts contained a ribonuclease inhibitor; a greater amount was present in control leaves. Loss in protein synthesis is linked to the loss of polysomes (Bewley 1972, Hsiao 1970).

Under water stress, protein synthesis decreases as measured by incorporation of amino acids into protein in photosynthetic tissues (Benzioni et al 1967) and nonphotosynthetic tissues (Nir et al 1970, Dhindsa and Cleland 1975a). Qualitative changes in the type of protein produced during stress also were demonstrated in Avena coleoptiles, although the underlying mechanism is not understood (Dhindsa and Cleland 1975b). The water stress in the tissue was quantified as either root water potential or water potential of the osmoticum. It is not understood how water stress exerts its effects. Water stress might operate directly by mechanisms involving a reduction in chemical potential of water, through a reduction in cell turgor potential, or through an increase in cell solute concentration. Alternatively, water stress could act indirectly, its effect being mediated by hormones that become increasingly available or unavailable during water stress and that then inhibit protein synthesis. These individual effects were studied in Avena coleoptile. Water stress was found to reduce the rate and to change the pattern of protein synthesis but abscisic acid (ABA) reduced the rate and did not alter the pattern of protein synthesis. The effect of hydrostatic pressure depends on the gas used. With a 19:1 mixture of nitrogen and air, the rate of protein synthesis is increased in stressed but not in turgid tissues (Dhindsa and Cleland 1975a). The differences in response led to the conclusion that water stress does not affect protein synthesis via ABA or reduced hydrostatic pressure.

Conclusions from studies with detached nonphotosynthetic tissues involving osmoticum-induced stress cannot easily be extended to intact plants where organ interaction and osmotic adjustment play important roles in response to water deficits. Furthermore, it would be interesting to know the effect of water stress and recovery on protein synthesis in different cell organelles such as the chloroplasts and the mitochondria. Overall protein-synthesis inhibitors will mask stress effects on protein synthesis in different organelles.

In wheat, growth, differentiation, and protein synthesis in the immature apex were concomitantly reduced by water stress of –12 bars (Barlow et al 1977). Although polyribosomes disappeared from the stressed apex, there appeared to be no net loss of ribosomes during stress. That implies that, although the protein synthetic mechanisms were partly dismantled, the potential for recovery remains. Such studies highlight the differential responses of plant organs to water stress and recovery.

The processes involved in translation are more sensitive to water stress than those involved in transcription, although translation effects are manifested only at severe stress levels.

## Nitrogen balance

Most experiments have demonstrated that total nitrogen and protein nitrogen decrease as amino nitrogen increases in shoots of plants under stress (Hsiao 1973, Tully et al 1979). In an intact maize plant it is possible to transfer metabolites, including nitrogen, from the aerial parts to roots (Aggarwal and Sinha 1981 unpubl.). On rewatering or revival, part of the nitrogen is remobilized back to the shoot and part can be lost through leaching. This transfer of reduced nitrogen and other metabolites could influence protein synthesis in aerial parts during recovery and become a basis of adaptation. It is difficult, however, to visualize such an adaptation on the basis of studies with plant parts where overall balance could not be examined. The importance of total nitrogen balance and other metabolites on a plant basis also has been emphasized by other studies.

## Proline accumulation

Accumulation of proline in plant parts during water stress is an important observation (Palfi 1968, Kemble and McPherson 1954, Singh et al 1972). Varietal differences in proline accumulation in barley were observed and correlated with a stability index by Singh et al (1973). But several studies have indicated that proline accumulation may not be related to drought resistance (Sinha and Rajagopal 1978, Krishnasastry et al 1979, Stewart and Hanson 1980). Krishnasastry et al (1979) showed the importance of proline accumulation in groundnut where the crop experienced short-duration intermittent water stress because of a break in the rainfall. Stewart and Hanson (1980) also showed that proline accumulation related to leaf firing is indicative of injury effects. Nevertheless, proline does accumulate in potentially higher metabolic tissue organs such as pollen grain (Britikov and Musatova 1964). Absence of proline in pollen generally is associated with sterility. Furthermore, when leaves are water stressed (Rajagopal and Sinha 1980), the tissues infiltrated with proline retain higher relative water content than controls. In turgid leaves, proline stimulates the activity of nitrate reductase (Sinha and Rajagopal 1981) or protects the loss of this enzyme activity during stress (Sinha and Rajagopal 1974). These observations suggest proline could provide metabolic advantages within limits of water stress. Depending upon the stage of plant growth and the chance of recovery from the water stress, the advantage may or may not be reflected in source or yield components. Proline accumulation could provide metabolic advantage on recovery in cultivars where accumulation starts at low or moderate stress (Stewart and Hanson 1980). Therefore, further studies on proline accumulation and metabolism in relation to water stress and recovery from stress may be important.

## Nitrate reductase

Nitrate reductase (NR) is an important enzyme for the assimilation of nitrate and growth (Hageman et al 1967). This enzyme loses its activity when plants experience stress (Mattas and Pauli 1965, Sinha and Nicholas 1981). The decrease in NR is accompanied by an increase in free amino acids and a decline in protein synthesis. It appears that under such conditions further nitrate reduction is of little value to the plant. Varieties differ in the loss of this enzyme activity (Balasubramaniam et al 1974), but the enzyme activity is never completely lost (Mattas and Pauli 1965). It has been suggested that a part of the enzyme could be inactivated (Sinha and Nicholas 1981) but a large amount could be degraded as suggested by Morilla et al (1973) and Hageman et al (1967). Stress relief could reactivate the inactivated enzyme. Depending on the revival of leaf area development, the NR activity could quickly restore nitrate assimilation (Khanna-Chopra et al 1980).

Although there are few critical studies on the relationship between growth and NR in plants experiencing water deficit, inhibition in growth appears to precede reaction in NR activity. Therefore, quicker loss in the activity of this enzyme during water stress and its activation on rewatering may be of adaptive importance.

## Effect on photosynthesis, respiration, and photorespiration

Among the assimilatory processes, photosynthesis is important for determining growth and yield. The total photosynthate production is the result of multiplicative interaction between the photosynthetic rate and leaf area or the photosynthetic surface.

*Leaf area.* Mild to moderate water stress is sufficient to reduce leaf area in most crop species (Begg and Turner 1976). A drop in leaf y is coupled with a decline in leaf turgor potential (P) unless the species has the property of osmotic adjustment (Turner and Jones 1980). Positive turgor potential is essential for growth and expansion (Hsiao 1973). Hence, leaf expansion is sensitive to decline in leaf y (Boyer and McPherson 1975), although this relationship differs among plants grown in controlled environments and those grown in the field. A complete cessation in leaf expansion was observed in plants grown under controlled environments at –8 bars leaf y, while the leaf expansion of field-grown maize plants continued to –9 bars leaf y (Begg and Turner 1976). This difference is attributed to the variation in the osmotic potential values of leaves grown under controlled environments and in the field.

An early buildup of crop canopy is essential for interception of the incident radiation in the field. When barley was intermittently stressed between emergence and harvest, the main factor reducing yield under all treatments was a decrease in intercepted radiation (Legg et al 1979). In determinate crops, the effect of reduction in leaf area is permanent because there is no scope for compensation through an increase in leaf number. But in an indeterminate crop like chickpea, in which vegetative growth continues even after flowering, compensation in leaf area can occur even if water stress comes after the vegetative growth stage. Water stress can also affect leaf area by speeding the rate of leaf senescence (Begg and Turner 1976).

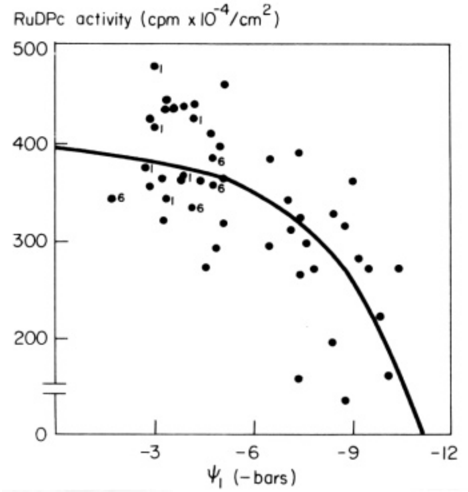
*Photosynthesis rate.* Photosynthesis has two major components, the stomatal and the nonstomatal. Nonstomatal components include activities of the photosynthetic enzymes and light reactions.

Water stress affects both the stomatal and nonstomatal components of photosynthesis. Scientists now generally accept that initial photosynthetic reduction is due to an increase in plant moisture stress arising from a decrease in the conductance of $CO_2$ through the stomata. The threshold for stomatal closure varies in different field crops and ranges from –7 to –19 bars (Begg and Turner 1976). It also is suggested that stomatal conductance may be better related to leaf turgor potential (P) than leaf y.

Contrary to earlier belief, moderate water stress of –6 to –8 bars leaf does inhibit several biochemical functions in the chloroplast in bean, cotton, and spinach (O'Toole et al 1976, Jones 1973, Plaut and Bravdo 1973, Plaut 1971). In these studies, gas exchange analysis was combined with enzyme assay of RuBPcase. In bean plants (Fig. 10), RuBPcase activity started declining at –5 to –6 bars leaf y with a rapid decrease at –8 to –9 bars leaf y (O'Toole et al 1976). It is emphasized that RuBPcase activity should be used as an indicator of biochemical response to water stress in addition to the measurement of mesophyll resistance by gas exchange studies because the term mesophyll resistance has been too liberally interpreted in the literature.

Water stress affects the primary photochemical events in sunflower and soybean (Mohanty and Boyer 1976). Quantum yield in sunflower was reduced from 0.076 to 0.020, as leaf y dropped from –4 to –15 bars. After recovery to a leaf y potential of –5 bars, quantum yield also rose to 0.060.

Net photosynthesis is a balance of gross photosynthesis, respiration, and photo-



**10.** Relationship between RuBP-case and leaf water potential in bean (O'Toole et al 1976).

respiration if present. The effect of PEG-induced stress was studied on the true photosynthesis, apparent photosynthesis, and photorespiration in wheat and sunflower leaves by gas exchange measurements and $^{14}$C activity pattern in photosynthetic intermediates (Lawlor and Fock 1975,1977; Lawlor 1976a, b). True photosynthesis and apparent photosynthesis decreased linearly from maximum at –4 bars leaf y, to 0 at about –18 bars leaf y. At lower leaf y, $CO_2$ evolved from the leaf. However, this is unlikely to occur in nature because in field-grown soybean net photosynthesis does not become 0 even at –25 bars leaf y (Rawson et al 1978). Photorespiration decreased linearly with stress, and at –18 bars was 30% of the control plant. Respiration of leaves through the tricarboxylic acid (TCA) cycle remained almost constant with changing y. More $CO_2$ was derived from reserve materials and less from immediate photosynthate. It was concluded that desiccation decreased photosynthesis by decreasing the stomatal conductance to $CO_2$ diffusion and by changing the balance between $CO_2$ assimilation and production in the leaf. Consequently, carbon flux through glycolate pathway decreased; so did the rate of $CO_2$ produced by it. However, TCA cycle respiration in the light increased with stress so that total photorespiration remained high. Results from gaseous exchange studies were further confirmed following the pattern of $^{14}$C in photosynthetic intermediates.

To conclude, water stress reduces net photosynthate availability by reducing leaf area and increasing stomatal resistance. This is followed by a decrease in the activities of enzymes such as RuBPcase and in the photochemical activity of the chloroplast. Relief of stress would change the revival capacity of the components determining net photosynthate availability. This would be dependent on the degree of stress and the stage at which stress occurs. But the revival in photosynthesis rate could be earlier than the compensation in leaf area. This information needs to be obtained.

## CONCLUSION

A crop's yield depends on processes occurring at different times during plant growth and development. Some processes, such as leaf area growth, intensity of flowering, and root growth, can be influenced rapidly. Depending on the stage of development, however, these source components influence sink components. The metabolic effects can largely be due to the effects on such processes that require shorter duration for expression, but have long-term influence. Therefore, it could be a coincidence that any relationship between metabolism and yield is established under water stress conditions. More information is needed on the relationship between solute accumulation during stress and its subsequent utilization during recovery for growth or realization of sink components.

## REFERENCES CITED

Balasubramanian, V., V. Rajagopal, and S. K. Sinha. 1974. Stability of nitrate reductase under moisture and salt stress in some crops. Indian J. Genet. 34A:1055-1061.

Barlow, E. W. R., Ranna Munns, N. Steele Scott, and A. H. Reisner. 1977. Water potential, growth and polyribosome content of the stressed wheat apex. J. Exp. Bot. 28(105):909-916.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

Ben-zioni, A., A. C. Itai, and Y. Vaadia. 1967. Water and salt stresses, kinetin and protein synthesis in tobacco leaves. Plant Physiol. 42:361-365.

Bewley, J. D. 1972. The conservation of polyribosomes in the moss *Tortula ruralis* during total desiccation. J. Exp. Bot. 23:692-698.

Boyer, J, S., and H. T. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:11-23.

Bozenkov, V. P. 1968. Effect of Al and Co on nucleic acid content and RNase activity in the growing points of sunflower plants under water deficit conditions. Sov. Plant Physiol. 15:94-99.

Britikov, E. A., and N. A. Musatova. 1964. Proline in the reproductive system of plants. Fiziol. Rast. 11:464-472.

Chaturvedi, G. S., P. K. Aggarwal, and S. K. Sinha. 1981. Effect of water availability on the stability of leaf size of wheat, triticale & barley. Indian J. Agric. Sci. 51(8). (in press)

Dhindsa, R. S., and R. E. Cleland. 1975a. Water stress and protein synthesis. I. Differential inhibition of protein synthesis. Plant Physiol. 55:778-781.

Dhindsa, R. S., and R. E. Cleland. 1975b. Water stress and protein synthesis. II. Interaction between water stress, hydrostatic pressure and abscisic acid on the pattern of protein synthesis in Avena coleoptiles. Plant Physiol. 55:782-785.

Fischer, R. A. 1980. Influence of water stress on crop yield in semi-arid regions. Page 323 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Gates, C. T., and J. Bonner. 1959. Response of the young tomato plant to a brief period of water shortage. IV. Effects of water stress on the RNA metabolism of tomato leaves. Plant Physiol. 34:49-55.

Genkel, P. A., N. A. Satarova, G. I. Blekhman, and E. K. Tvorus. 1974. Effect of water deficit on the functional activity of cytoplasmic ribosomes in wheat leaves and isozyme spectrum of cytoplasmic RNase. Sov. Plant Physiol. 21:91-96.

Genkel, P. A., N. A. Satarova, and E. K. Tvorus. 1967. Effect of drought on protein synthesis and the state of ribosomes in plants. Fiziol. Rast. 14:754.

Hageman, R. H., E. R. Leng, and J. W. Dudley. 1967. A biochemical approach to corn breeding. Adv. Agron. 19:45-86.

Hsiao, T. C. 1970. Rapid changes in levels of polyribosomes in *Zea mays* in response to water stress. Plant Physiol. 46:281-285.

Hsiao, T. C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.

Izhizuka, Y. 1969. Engineering for higher yields. *In* J. D. Eastin, F. A. Haskins, C. Y. Sullivan, and Ian Bavel, eds. Physiological aspects of crop yield. C. H. M. American Society of Agronomy, USA.

Jones, H. G. 1973. Moderate term water stresses and associated changes in some photosynthetic parameters in cotton. New Phytol. 72:1095-1105.

Kemble, A. P., and H. T. McPherson. 1954. Liberation of amino acids in perennial ryegrass during wilting. Biochem. J. 58:46-49.

Khanna-Chopra, R., G. S. Chatruvedi, P. K. Aggarwal, and S. K. Sinha. 1980. Effect of potassium on growth and nitrate reductase during water stress and recovery in maize. Physiol. Plant. 49:495-500.

Krishnasastry, K. S., V. P. Sashidhar, and A. A. Mehkri. 1979. Validity of proline accumulation under stress as a measure of relative drought tolerance in bunch types of groundnut. *In* Plant responses to water availability. New Delhi.

Lawlor, D. W. 1976a. Water stress induced changes in photosynthesis, photorespiration, respiration and $CO_2$ compensation concentration of wheat. Photosynthetica 10(3):378-387.

Lawlor, D. W. 1976b. Assimilation of carbon into photosynthetic intermediates of water-stressed wheat. Photosynthetica 10(4):431-439.

Lawlor, D. W., and H. Fock. 1975. Photosynthesis and photorespiratory $CO_2$ evolution of water stressed sunflower leaves. Planta 126:247-258.

Lawlor, D. W;, and H. Fock. 1977. Photosynthetic assimilation of $^{14}CO_2$ by water stressed sunflower leaves at two $O_2$ concentrations and the specific activity of products. J. Exp. Bot. 28(103): 320-328.

Legg, B. T., W. Day, D. R. Lawlor, and K. T. Parkinson. 1979. The effects of drought on barley growth models and measurements showing the relative importance of leaf area and photosynthetic rate. J. Agric. Sci. 92(3):703-716.

Mattas, R. E., and A. W. Pauli. 1965. Trends in nitrate reduction and nitrogen fractions in young corn (*Zea mays* L.) plants during heat and moisture stress. Crop Sci. 5:181-184.

Mohanty, P., and J. S. Boyer. 1976. Chloroplast response to low leaf water potentials. IV. Quantum yield is reduced. Plant Physiol. 57:704-709.

Morilla, C. A., J. S. Boyer, and R. H. Hageman. 1973. Nitrate reductase activity and polyribosome content of corn (*Zea mays* L.) having low leaf water potentials. Plant Physiol. 51:817-824.

Mussell, H., and R. C. Staples. 1979. Stress physiology in crop plants. Wiley Interscience, New York.

Nir, I., A. Poljakoff-Mayber, and S. Kleins. 1970. The effect of water stress on the polysome population and the ability to incorporate amino acids in maize root tips. Israel J. Ot. 19:451-462.

O'Toole, J. C., R. E. Crookston, K. J. Treharne, and J. L. Ozbun. 1976. Mesophyll resistance and carboxylase activity. A comparison under water stress conditions. Plant Physiol. 57:465-468.

Paleg, L. G., and D. Aspinall. 1981. Physiology and biochemistry of drought resistance. Academic Press, New York.

Palfi, G. 1968. Changes in the amino acid content of detached wilting leaves of *Solanum laciniatum* Ait. in the light and in the dark. Acta Agron. Acad. Sci. Hung. 17:381-388.

Passioura, J. B. 1976. Physiology of grain yield in wheat growing on stored water. Aust. J. Plant Physiol. 3:559-565.

Plaut, Z. 1971. Inhibition of photosynthetic carbon dioxide fixation in isolated spinach chloroplasts exposed to reduced osmotic potential. Plant Physiol. 48:591-595.

Plaut, Z., and B. Bravdo. 1973. Response of carbon dioxide fixation to water stress. Plant Physiol. 52:28-32.

Rajagopal, V., and S. K. Sinha. 1980. Influence of exogenously supplied proline on the relative water content in wheat and barley. Indian J. Exp. Biol. 18(12): 1523-1524.

Rawson, H. M., N. C. Turner, and J. E. Begg. 1979. Agronomic and physiological responses of soybean and sorghum crops to water deficits. IV. Photosynthesis, transpiration and water use efficiency of leaves. Aust. J. Plant Physiol. 5:195-209.

Singh, T. N., D. Aspinall, and L. G. Paleg. 1972. Proline accumulation and varietal adaptability to drought in barley: a potential metabolic measure of drought resistance. Nature (New Biol.) 236:188-190.

Singh, T. N., L. G. Paleg, and D. Aspinall. 1973. Nitrogen metabolism and growth in the barley plant during water stress. Aust. J. Biol. Sci. 26:45-56.

Sinha, S. K., and V. Rajagopal. 1974. Proline slows down the loss of nitrate reductase in moisture stressed plants. Plant Physiol. Suppl. 56(2):22.

Sinha, S. K., and R. Khanna. 1975. Physiological, biochemical and genetic basis of heterosis. Adv. Agron. 27:123-170.

Sinha, S. K., and V. Rajagopal. 1978. Effect of moisture stress on proline accumulation in sorghum and wheat. Pages 158-163 *in* S. P. Sen, Y. P. Abrol, and S. K. Sinha, eds. Nitrogen assimilation and crop productivity. Associated Publishing Company, New Delhi.

Sinha, S. K., and J. D. Nicholas. 1981. Nitrate reductase in relation to water stress. *In* L. G. Paleg and

D. Aspinall, eds. Physiology and biochemistry of drought resistance. Academic Press, New York.

Sinha, S. K., and V. Rajagopal. 1981. Proline stimulates nitrate reductase in turgid tissues. Indian J. Exp. Biol. 19:195-196.

Sinha, S. K., and M. S. Swaminathan. 1981. New parameters and selection criteria in plant breeding. Pergamon Press, New York.

Stewart, C. R., and A. D. Hanson. 1980. Proline accumulation as a metabolic response to water stress. *In* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Tully, R. E., A. D. Hanson, and R. E. Nelson. 1979. Proline accumulation in water stressed barley leaves in relation to translocation and the nitrogen budget. Plant Physiol. 63:518-523.

Turner, N. C., and P. J. Kramer. 1980. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustments: a review and evaluation. Pages 87-104 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Withers, K. J., and B. J. Ford. 1979. Effects of water stress on *Lupinus albus.* III. Response of seed yield and vegetative growth to water stress imposed during two or three growth stages. N. Z. J. Agric. Res. 22:463-474.

Yi, C., and G. W. Todd. 1979. Changes in ribonuclease activity of wheat plants during water stress. Physiol. Plant 46:13-18.

# ABSCISIC ACID AND DROUGHT RESISTANCE IN WHEAT, MILLET, AND RICE

R. B. AUSTIN, I. E. HENSON, AND S. A. QUARRIE

There is good evidence that abscisic acid (ABA) is involved in mediating responses to drought. There is genetic variation in wheat, rice, and pearl millet in drought-induced capacity for ABA accumulation. In wheat and millet, this capacity is highly heritable.

ABA promotes stomatal closure and reduces leaf extension. Genotypes appear to differ in the sensitivity of these processes to ABA. In wheat, high ABA accumulation appears to be associated with reduced sensitivity to ABA, but in rice, the reverse may be the case. In pearl millet, the stomata of low and high ABA accumulators appear equally sensitive to the hormone.

Present knowledge does not permit us to predict with any certainty the consequences for yield and water use of modified ABA physiology. It is necessary to prepare genotypes contrasting in aspects of ABA physiology and study their yield and water use under conditions of controlled water supply. Work toward attaining these objectives is described.

Abscisic acid (ABA), first identified in young cotton bolls (Ohkuma et al 1963) is present in plants belonging to many families. Its concentration in leaves increases rapidly during water stress, often by as much as 40-fold, as first shown by Wright

---

Financial support from the UK Overseas Development Administration.

---

Plant Breeding Institute, Maris Lane, Trumpington, Cambridge, UK.

(1969) for wheat. ABA causes stomatal closure, thus reducing transpiration (Mittelheuser and Van Steveninck 1969). Mutants lacking the capacity to synthesize normal amounts of ABA (Tal and Nevo 1973) are unable to regulate their transpiration and become severely wilted unless kept at high atmospheric humidity.

In view of these relations between water stress, ABA, and stomatal closure, it has been suggested that drought resistance could be improved by selecting for modified ABA accumulation (Larque-Saavedra and Wain 1976). Our interest in this possibility was strengthened by the findings of Quarrie and Jones (1977) that ABA applied to well-watered wheat plants modified growth and morphology in the same way as drought does.

We recognize that ABA is only one of many attributes claimed to be associated with drought resistance. However, such claims have seldom been verified by rigorous studies with suitably defined, contrasting genotypes.

The objective of the work outlined here is to assess the significance for drought resistance of genetic modifications in aspects of ABA physiology.

## A MODEL FOR THE INVOLVEMENT OF ABSCISIC ACID IN MEDIATING RESPONSES TO DROUGHT

Although abscisic acid (ABA) probably is involved in regulating stomatal closure, drought resistance may not necessarily be increased by selecting for high ABA content or for high stomatal sensitivity to ABA. The appropriate stomatal response required to maximize growth and yield depends on the timing and severity of the drought and on other environmental factors that vary with season and site (Jones 1976). ABA affects not only the stomata, but also leaf expansion and other processes (Quarrie and Jones 1977). These effects have further consequences for drought reaction.

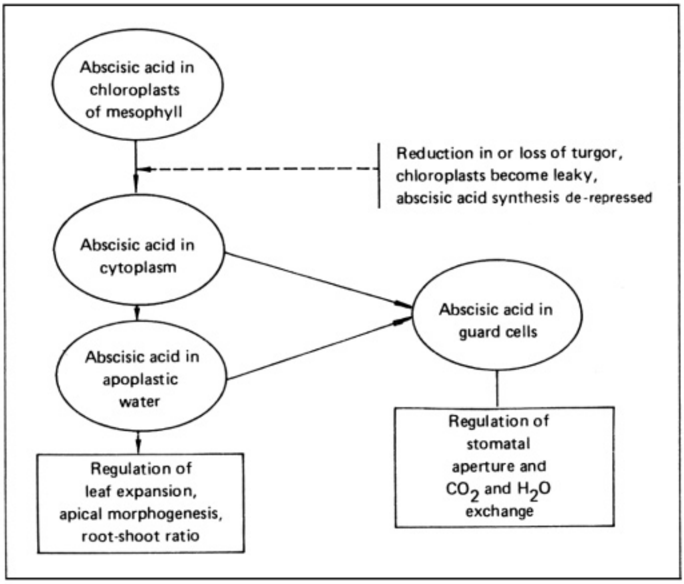
It may be supposed that low levels of ABA in nonstressed plants influence growth processes and patterns of development. Effects of these low levels represent inherent responses. For example, inherent responses of reduced leaf development and shortened life cycle would predispose a plant to escape a drought late in the growing season. Such responses would be in addition to the induced or adaptive responses brought about by the high levels of ABA accumulated in stressed plants.

The model we used in formulating our research (Fig. 1) led us to ask:

1. Can genetic variation in drought-induced ABA accumulation be detected? If so, what would be the consequences for stomatal behavior, growth, development processes, and yield in different drought regimes?
2. Can genetic variation in the sensitivity of stomatal closure or leaf extension to applied ABA be detected? If so, what would be the consequences for growth, development, and yield in different drought regimes?

## GENETIC VARIATION IN DROUGHT-INDUCED ABA ACCUMULATION

Initially, we chose to investigate question 1 because we assessed it to be simpler than question 2. A combined thin layer chromatography - gas liquid chromatography (TLC-GLC) method for the rapid assay of free ABA in leaf tissue was



**1.** Postulated relationships involving abscisic acid (ABA). (For fuller discussion of possible mechanisms, see Davies et al 1980, and Milborrow 1980.)

developed (Quarrie 1978). Samples of 100-1,000 mg of fresh leaf material were processed and the ABA content of subsamples of the extracts determined. The overall accuracy of the measurements of ABA present in water-stressed leaves was better than ± 10%.

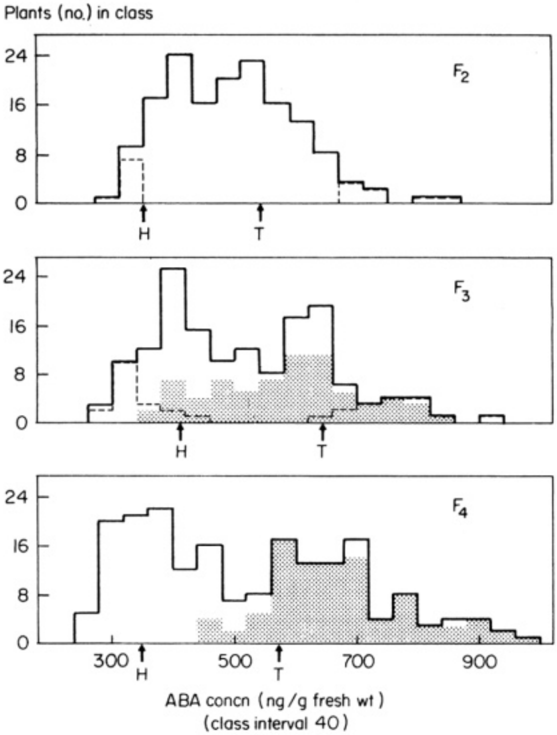
A detached leaf test was used so that genotypic comparisons would not be confounded with environmental and other effects on ABA accumulation. Genotypes to be compared were grown under standardized conditions in controlled environments. When the ligule of the leaf to be sampled appeared, the leaf was detached and placed in an airstream until it had lost a given percentage of its initial fresh weight. It was incubated in a closed tube in the dark for a standard length of time prior to assay for ABA.

In each species, accumulation of ABA was influenced by leaf age, the environment (particularly the humidity) in which the plants were grown, the degree to which excised leaves were desiccated, and the time and temperature of incubation (Henson and Quarrie 1981, Quarrie and Henson 1981).

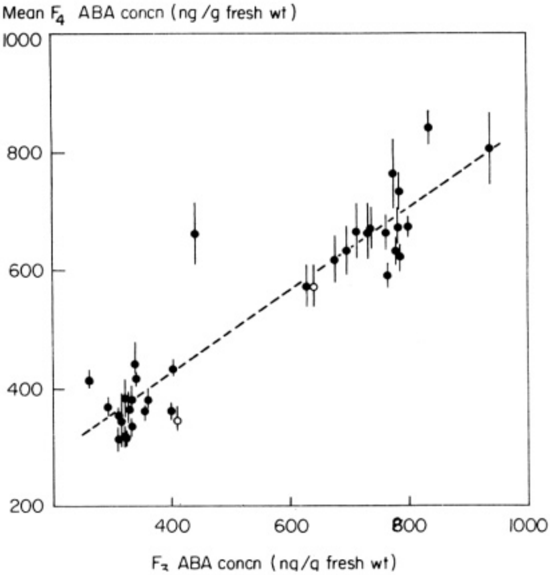
The conditions for genotype comparisons were those that gave maximum ABA concentrations in tests with one or two genotypes. In the two genotypes of spring wheat studied intensively (TW 269/9 and Highbury), differences in ABA accumulation were maintained over a wide range of conditions which varied both before and after leaf excision. Table 1 shows that, in each species, some genotypes accumulated significantly more ABA than others. The range in accumulation was 2.7-fold for wheat, 2.8-fold for rice, and 4.8-fold for pearl millet. Because only

**Table 1. Genotypic variation in drought-induced ABA accumulation in spring wheat, rice, and millet.**

| ABA accumulation | Cultivar | ABA concentration (ng/g fresh-leaf wt) |
|---|---|---|
| | Spring wheat | |
| More than average | Ngezi | 410 |
| | Limpopo | 400 |
| | Sonora 64 | 870 |
| | TW269/9 | 350 |
| Less than average | Kharkovskaya 93 | 210 |
| | Hope | 190 |
| | Lee Mida | 170 |
| | Chinese Spring | 150 |
| Mean of 21 genotypes | | 280 |
| | Rice | |
| More than average | IR20 | 890 |
| | Rikuto Norin 21 | 760 |
| Less than average | Bala | 410 |
| | 63-83 | 320 |
| Mean of 16 genotypes | | 580 |
| | Millet | |
| More than average | Serere 39 | 430 |
| | WC9-27 | 330 |
| | 1/2 HK | 320 |
| Less than average | KG40 | 123 |
| | BK560 | 90 |
| Mean of 16 genotypes | | 210 |



**2.** Frequency distributions of abscisic acid (ABA) content in stressed leaves of $F_2$, $F_3$, and $F_4$ spring wheat individuals from the cross TW269/9 × Highbury. Arrows indicate the mean ABA content of Highbury (H) and TW269/9 (T) grown with each generation. Individuals within the dashed lines at low and high ABA contents in the $F_2$ and $F_3$ distributions were used for the succeeding generation. Dark area indicates $F_3$ and $F_4$ indi. viduals from high ABA parents. Light area indicates $F_3$ and $F_4$ individuals from low ABA parents



**3.** Relation between abscisic acid (ABA) content of an $F_3$ individual and the mean ABA content of its $F_4$ progeny. The regression line is given. Bars indicate ± standard deviations for each $F_4$ family mean and the parents of the cross. Open circles indicate the parents Highbury and TW269/9.

such deviations are similar to chose of the parents, which suggests that homozygosity for ABA accumulation was approached by the $F_4$.

Similar studies with pearl millet and rice are in progress. High heritability of ABA accumulation in pearl millet is indicated by a regression coefficient of 0.60 for $F_3$ on $F_2$ data.

## GENETIC VARIATION IN RESPONSIVENESS TO ABA

Studies on sensitivity to ABA are fraught with difficulties. The form of ABA available commercially is the racemate (±)-ABA, whereas the naturally occurring enantiomer is (+)-ABA. It is uncertain whether the (–) form is always as physiologically active as the natural form. Other difficulties—determining the most appropriate method, dose, and timing of ABA presentation—have to be resolved. Furthermore, differences between genotypes in response to ABA application could result not only from differences in responsiveness *per se* but also from differences in uptake of the presented dose, in its transport from the site of application, or in its metabolism and sequestration by intervening tissues.

Despite these problems, there is evidence of considerable variation between species in the concentration of ABA required to cause a 50% reduction in transpiration or stomatal conductance, with values ranging from $4 \times 10^{-4}$ to $10^{-7}$ M (Quarrie 1982). However, uncertainty about the growth and testing conditions used by researchers makes it difficult to interpret differences within species. We have studied the effects on stomatal conductance of ABA either injected into the leaf sheaths of young plants or absorbed through the cut end of detached leaves. The injection method also has been used in studying the effects of ABA on leaf extension growth.

With the use of detached leaves, significant genotypic variation in the depression of stomatal conductance by ABA at $3.8 \times 10^{-6}$ M was detected in wheat (Table 2). In general, genotypes with the greatest stomatal sensitivity to ABA accumulated less of the hormone in response to water stress and *vice versa.* Therefore, in spring wheat a given stress in the leaves may result in different ABA accumulations but have the same net effect on stomatal behavior.

In studies with rice genotypes, ABA (5 µg) injected into the leaf sheaths of young plants reduced leaf conductance in the short term to between 70 and 40% of the control values (Table 2). When detached leaves were allowed to imbibe $10^{-6}$ M (±)-ABA, transpiration was reduced by 50%, on the average. Reductions in transpiration correlated well ($r$ = 0.72, d.f. = 11) with those in stomatal conductance assessed independently using intact plants. Among genotypes tested, those whose stomatal sensitivity and ABA accumulation capacity were positively correlated could be selected. Thus, in contrast to spring wheat, the two responses in rice might reinforce each other in their effect on water-use efficiency.

The stomata of pearl millet appeared less sensitive to ABA than those of rice and wheat. The concentration of ABA required to reduce stomatal conductance in millet by 50% was about 400-fold greater than that needed to achieve the same effect in rice and wheat. Furthermore, 16 genotypes tested showed no differences in stomatal response to applied ABA, as assessed by conductance or transpiration

**Table 2. Genotypic variation in sensitivity of stomata to abscisic acid.**

| Sensitivity | Cultivar | Conductance (% of control) |
|---|---|---|
| | *Spring wheat (detached leaves)* | |
| Most sensitive | TW161 | 26 |
| | Highbury | 29 |
| Least sensitive | TW269/9 | 49 |
| | Kleiber | 53 |
| Mean of 25 genotypes | | 42 |
| | *Rice (intact plants)* | |
| Most sensitive | IR20 | 40 |
| | IR8 | 43 |
| Least sensitive | IR36 | 65 |
| | Kinandang Patong | 68 |
| | 63-83 | 71 |
| Mean of 16 genotypes | | 56 |

measurements.

In view of the association between low ABA accumulation and high stomatal sensitivity to ABA in wheat, particular attention was given to two millet genotypes, Serere 39 and BJ104, which contrasted in their capacity to accumulate ABA. Supplying a range of ABA concentrations ($10^{-7}$ to $10^{-3}$ M) to detached leaves revealed no difference in stomatal sensitivity between these genotypes.

As with stomatal responses, the effects of an application of ABA on leaf extension rate (LER) were transitory, probably because ABA was metabolized rapidly. To examine the effects of ABA on leaf extension, either LER was measured over the 1-2 days after ABA application or ABA was applied frequently over the period of leaf extension, and final leaf size was compared with controls. Repeated applications were used to examine influences on other aspects of development, such as time of anthesis in wheat.

Leaf expansion in rice genotypes was affected differentially by ABA (Table 3), with a 1.7-fold response difference. In pearl millet, a 2.0-fold variation among genotypes was observed in ABA depression of leaf extension rates. In wheat, preliminary studies indicated genotypic variation in the sensitivity of leaf expansion to ABA and in the extent to which anthesis dates were advanced by ABA.

## CONSEQUENCES ON YIELD AND WATER USE OF MODIFIED ABA PHYSIOLOGY

Increased ABA content at a given water potential may lead to reduced transpiration, photosynthesis, and leaf expansion and to modified assimilate distribution and apical morphogenesis. It should, in general, improve water use efficiency (Davies et al 1980). However, the effect on yield in a given environment would depend on the degree to which each process was affected and the way in which each contributed to final yield. For example, if leaf expansion was the most

**Table 3. Genotypic variation in sensitivity of leaf growth to abscisic acid.**

| | Cultivar | Leaf area (% of control) |
|---|---|---|
| | Rice | |
| Most sensitive | Khao Dawk Mali | 57 |
| | Sigadis | 62 |
| | IR480-5-9-3 | 65 |
| Least sensitive | Bala | 94 |
| | Kinandang Patong | 100 |
| Mean of 16 genotypes | | 82 |
| | Millet | |
| Most sensitive | Serere Composite 1 | 27 |
| Least sensitive | Serere 39 | 53 |
| Mean of 4 genotypes | | 42 |

affected, water would be conserved in the long term and more water would be available during grain filling. This could minimize the effects of water shortage on grain yield. If only stomatal closure was substantially affected, a similar water economy might be achieved initially. However, the larger leaf area would put the plant in greater danger in the event of continued drought and the resulting high ABA accumulation might seriously lower yield potential. Although these general relationships can be deduced from the available information, better prediction of the consequences of any particular change is impossible because the detailed relationships are inadequately quantified and understood. In this respect, ABA physiologists are in no worse a position than those concerned with other systems controlling growth and development.

For these reasons, we believe that the only way to assess with certainty the effect of modified ABA physiology is to compare water use and yields of sets of experimental genotypes that differ in a particular attribute (e.g. in the capacity for ABA accumulation) and in pleiotropically related ones, but that are similar in all other respects.

In wheat, sets of lines selected only for low and high ABA accumulation, now at the $F_5$, are being studied in field experiments at the Plant Breeding Institute. These lines approached homozygosity for ABA accumulation capacity in the $F_4$ (Fig. 3). It was possible to make a preliminary assessment of attributes likely to be pleiotropically associated with low and high ABA accumulation (Table 4). Plants were grown in the glasshouse and in the field and were well-watered. Therefore, the differences between the sets of lines were of the kind referred to as inherent, as distinct from *induced.* Table 4 shows that high-ABA lines reached anthesis earlier than low-ABA lines. They had fewer leaves on the main stem and fewer spikelets per ear. These characteristics are shown by low-latitude wheats with reduced sensitivity to photoperiod. We are examining the low and high lines for differences in sensitivity to photoperiod. Such differences would suggest that ABA is involved in determining response to photoperiod in wheat.

**Table 4. Some characteristics of $F_4$ lines from the spring wheat cross TW269/9 × Highbury (parents contrast in drought-induced ABA accumulation).**

| Characteristic | Where grown | 17 low-ABA lines | 17 high-ABA lines |
|---|---|---|---|
| Leaf 4 dry wt (mg) | Glasshouse | 101 | 87*** |
| Stomatal conductance of leaf 5 (cm/s) | Glasshouse | 0.83 | 0.87 |
| Main stem leaves[a] (no.) | Glasshouse | 7.3 | 6.2*** |
| Flag leaf area ($cm^2$) | Field | 49 | 47 |
| Ears (no./plant) | Field | 3.54 | 3.78 |
| Days to ear emergence | Glasshouse | 54.9 | 47.1*** |
| | Field | 79.1 | 75.5*** |
| Days to anthesis | Field | 83.0 | 81.4*** |
| Spikelets (no./ear) | Glasshouse | 20.6 | 18.4*** |
| | Field | 17.5 | 16.6** |
| 1000-grain wt (g) | Field | 40.9 | 43.7** |

[a] $F_5$ selections.
**, *** indicate differences significant at the 1 and 0.1 % levels of probability, respectively.

In relation to one expected effect of high ABA accumulation — greater stomatal closure at a given level of water stress — the high accumulator TW269/9 has stomata that are less sensitive to ABA than those of the low accumulator Highbury (Table 2). Whether this difference in stomatal sensitivity is an adaptive response to ABA concentration is not known. It appears that in wheat, at least, it could negate any benefits derived from stomatal control of transpiration which might accrue from high ABA accumulation. As mentioned earlier, this is not likely in the lines of rice or millet that have been examined.

We hope within the next few years to be able to carry out critical experiments with defined genotype sets of wheat, millet, and rice. The experiments should answer the questions we have posed. The results presented here have encouraged us to continue the work. Although they must be regarded with caution, indications from varietal comparisons in wheat are that resistance to late drought is associated with low ABA accumulation capacity. In a set of 13 rice genotypes, good drought resistance assessed visually (Chang et al 1974) was also associated with low ABA accumulation ($r$ = 0.62). However, pearl millet, a $C_4$ species, appears to differ from wheat and rice in ABA physiology. Yields from droughted plots of five genotypes, expressed as a percentage of control yields, were *positively* correlated ($r$ = 0.95) with accumulation of ABA. Studies are needed to determine whether these associations involve causal relationships and, if they do, how they operate in each case.

## REFERENCES CITED

Chang, T. T., G. C. Loresto, and O. Tagumpay. 1974. Screening rice germ plasm for drought resistance. SABRAO J. 6:9-16.

Davies, W. J., T. A. Mansfield, and A. R. Wellburn. 1980. A role for abscisic acid in drought endurance and drought avoidance. Pages 242-253 *in* F. Skoog, ed. Plant growth substances 1979. Proceedings of the 10th international conference on plant growth substances, Madison, Wisconsin. Springer-Verlag, Berlin-Heidelberg-New York.

Henson, I. E., and S. A. Quarrie. 1981. Abscisic acid accumulation in detached cereal leaves in response to water stress. I. Effects of incubation time and severity of stress. Z. Pflanzensphysiol. 101:431-438.

Jones, H. G. 1976. Crop characteristics and the ratio between assimilation and transpiration. J. Appl. Ecol. 13:605-622.

Larqué-Saavedra, A., and R. L. Wain. 1976. Studies on plant growth regulating substances XLII. Abscisic acid as a genetic character related to drought tolerance. Ann. Appl. Biol. 83:291-297.

Milborrow, B. V. 1980. Regulation of abscisic acid metabolism. Pages 262-273 *in* F. Skoog, ed. Plant growth substances 1979. Proceedings of the 10th international conference on plant growth substances, Madison, Wisconsin. Springer-Verlag, Berlin-Heidelberg-New York.

Mittelheuser, C. J., and R. F. M. Van Steveninck. 1969. Stomatal closure and inhibition of transpiration by (RS)-abscisic acid. Nature 221:281-282.

Ohkuma, K., J. L. Lyon, F. T. Addicott, and O. E. Smith. 1963. Abscisin II, an abscission-accelerating substance from young cotton fruit. Science 142:1592-1593.

Quarrie, S. A. 1978. A rapid and sensitive assay for abscisic acid using ethyl abscisate as an internal standard. Anal. Biochem. 87:148-156.

Quarrie, S. A. 1981. Genetic variability and heritability of drought-induced abscisic acid accumulation in spring wheat. Plant, Cell and Environment 4:147-152.

Quarrie, S. A. 1982. Genetic differences in abscisic acid physiology and their potential uses in agriculture. *In* F. T. Addicott, ed. Abscisic acid. Praeger, New York. (in press)

Quarrie, S. A., and H. G. Jones. 1977. Effects of abscisic acid and water stress on development and morphology of wheat. J. Exp. Bot. 28:192-203.

Quarrie, S. A., and I. E. Henson. 1981. Abscisic acid accumulation in detached cereal leaves in response to water stress. II. Effects of leaf age and leaf position. Z. Pflanzenphysiol. 101:439-446.

Tal, M., and Y. Nevo. 1973. Abnormal stomatal behaviour and root resistance, and hormonal imbalance in three wilty mutants of tomato. Biochem. Genet. 8:291-300.

Wright, S. T. C. 1969. An increase in the "inhibitor-*ß*" content of detached wheat leaves following a period of wilting. Planta 86:10-20.

# OSMOTIC ADJUSTMENT IN RICE

PETER L. STEPONKUS, KEVIN W. SHAHAN, AND J. M. CUTLER

Drought conditioning of dryland rice results in alterations in the internal water relations of the leaves. As a result of osmotic adjustment (a net increase in solute concentration) solute potential ($y_s$) is decreased by as much as 5 bars in conditioned leaves. The maximum extent of osmotic adjustment is dependent on the conditioning stress intensity and independent of the rate of stress development or the number of drought cycles imposed. After subsequent irrigation, osmotic adjustment persists for up to 14 days, depending on the stress-conditioning regime. Diurnal fluctuations in $y_s$ of up to 5 bars also occur. Little diversity in these aspects of osmotic adjustment was observed in the cultivars studied.

Drought conditioning decreased the sensitivity of leaf elongation to subsequent water stress. Although this effect commonly is considered as the result of the maintenance of turgor potential at lower water potentials, this may not be appropriate. As the primary cellular consequence of osmotic adjustment is a decrease in the chemical potential of water, continued cell expansion and leaf elongation may be described on the basis of maintenance of gradients in water potential. Thus, osmotic adjustment will diminish the extent of cellular dehydration in fully expanded cells at any given water potential level less than zero and a net influx of water in expanding cells will continue to lower water potentials.

---

Department of Agronomy, Cornell University, Ithaca, NY 14853, USA.

Drought resistance in rice, as in any other crop species, results from a multiplicity of phenological, morphological, anatomical, and physiological characteristics. A particular cultivar is considered drought resistant if these characteristics can effectively modulate the internal water status under the edaphic and climatic conditions that constitute a drought, enabling growth and development to proceed to culminate in a yield judged to be acceptable.

Although adaptation to drought is the result of long-term phylogenetic evolution of different ecotypes, there is considerable plasticity in the characteristics that contribute to drought resistance. Acclimation in response to environmental stimuli may occur within a single life cycle. Thus, after exposure to a moderate drought, many crop species are less sensitive to a later, but more severe, drought (Maximov 1929). This phenomenon is referred to as drought hardening or drought conditioning.

Drought conditioning may alter characteristics associated with water uptake, such as a greater root-shoot ratio. Alternatively, characteristics associated with water conservation — for instance increased stomatal and cuticular resistance, leaf rolling, or overall canopy architecture — may be altered. Such alterations will influence the internal water status relative to the prevailing edaphic and climatic conditions and minimize internal water deficits. In addition, drought conditioning may alter internal water relations or the tolerance of various growth and developmental processes to internal water deficits. Tolerance of water deficits must be defined ultimately at the cellular level and must be considered a function of cellular water status. Because crop plants generally grow under conditions of internal water deficits, some basal level of tolerance is implicit.

## OSMOTIC ADJUSTMENT

Osmotic adjustment, generally considered as the net increase in intracellular solutes, usually occurs in response to various environmental stresses (Steponkus 1980). Lidforss (1907) was among the earliest to document an increase in soluble carbohydrates in response to cold acclimation. Rosa (1921) established that cold, drought, or saline conditioning caused increases in the sugar and amino acid contents in several species. Iljin (1929) concluded that plants grown in dry habitats contain more sugar than those grown in moist habitats. Increases in osmotic pressure during drought often were reported (Clements 1937, Schmidt 1939, Whiteside 1941, Eaton and Ergle 1948). In one instance, the increase in osmotic pressure paralleled the reputed order of drought resistance in four wheat varieties (Bartel 1947).

Interest in the phenomenon of osmotic adjustment in response to water deficits has been renewed and investigated in many crop species (Acevedo 1975; Simmelsgaard 1976; Hsiao et al 1976; Morgan 1977,1980; Jones and Turner 1978; Cutler and Rains 1978; Turner and Jones 1980). Interest was renewed partly because most early reports failed to demonstrate that the increase in solute concentration was not due solely to a lower water content (Hsiao et al 1976). More important, however, recent interest in osmotic adjustment may be attributed to growth (Greacen and Oh 1972, Meyer and Boyer 1972) and the suggestion (Hsiao 1973, Hsiao and Acevedo 1974, Hsiao et al 1976) that turgor potential is the primary transducer between internal water deficits and expansive growth. As a result of Hsiao's (1973) analysis of the sensitivity of growth processes to water deficits, the influence of osmotic adjustment on turgor maintenance has been of major concern.

The possibility of improving the drought resistance of a crop species on the basis of differences in osmotic adjustment was bolstered by the demonstration of substantial genotypic diversity in this phenomenon among wheat genotypes (Morgan 1977). In contrast, Jones and Turner (1978) found no differences in the extent of osmotic adjustment in two sorghum varieties reputed to differ in drought resistance.

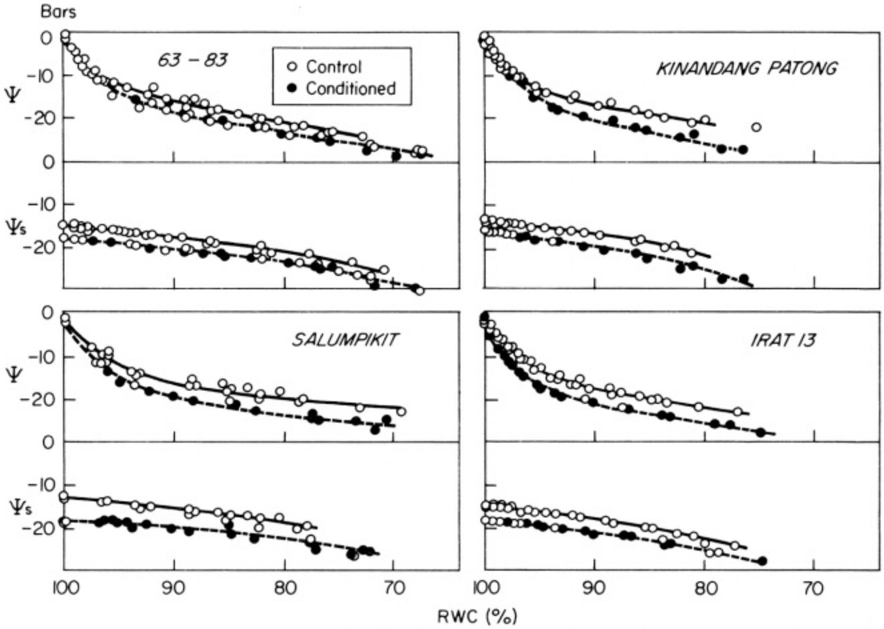
A comprehensive analysis of osmotic adjustment in dryland rice cultivars in response to drought hardening (conditioning) has been completed (Cutler et al 1979, 1980a,b,c,d; Shahan 1980; Steponkus et al 1980). One objective of these studies was to determine whether aspects of osmotic adjustment could be exploited in the development of drought-resistant dryland rice cultivars. In these studies, drought conditioning was effected by withholding water until the plant water status — determined as predawn leaf water potential ($\Psi$) — declined to a prescribed value. Internal water relations were determined by pressure-volume relations (Cutler et al 1979).

## ALTERATIONS OF INTERNAL WATER RELATIONS BY DROUGHT CONDITIONING

The influence of drought conditioning on the internal water relations of dryland rice cultivars 63-83, Salumpikit, IRAT-13, and Kinandang Patong has been reported (Cutler et al 1980a). Changes in the internal water relations of recently matured leaves were evident in the relationship between relative water content (RWC) and Y or in the relationship between RWC and solute potential ($\Psi_s$) or turgor potential ($\Psi_p$) (Fig. 1). At maximum hydration, $Y_s$ of leaves from conditioned plants was 3–5 bars lower than that of leaves from well-watered plants. No significant differences in the extent of osmotic adjustment were observed among the four cultivars. The $\Psi_s$ ranged from–12.5 to –14.4 bars for well-watered plants and from –16 to –18 bars for conditioned plants. A corresponding increase in $\Psi_p$ at maximal hydration was inferred. In all cultivars, loss of turgor occurred in the range of 88 to 92% RWC. This relationship was not altered by drought conditioning in any of the cultivars. Thus, the decrease in solute potential altered the internal water relations such that conditioned plants maintained a greater RWC at a given $\Psi$. That is, the extent of cellular dehydration was mitigated.

## DYNAMICS OF OSMOTIC ADJUSTMENT

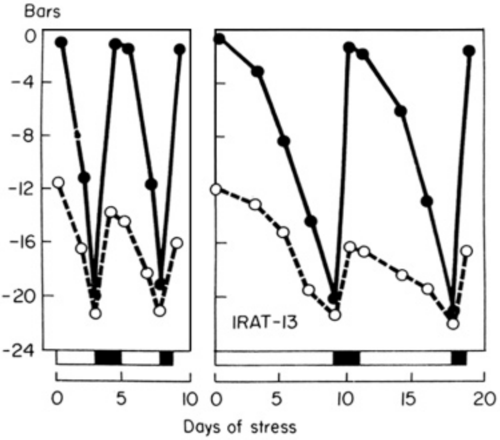
As osmotic adjustment occurs in response to water deficits (drought conditioning), the dependence of osmotic adjustment on the rate of stress development, its intensity, and its duration requires elaboration. Begg and Turner (1976) suggest that the response of field-grown plants differs from that of container-grown plants



**1.** Relation between leaf water potential (y) or solute potential (y s) and relative water content (RWC) for individual leaves of conditioned and control rice plants (from Cutler et al 1980a).

because the rate of stress development differs. Recently, however, Jones and Rawson (1979) observed a similar extent of osmotic adjustment in container-grown sorghum plants if water deficits developed at either a slow (1.5 bars/day) or intermediate (7 bars/day) rate while the extent of adjustment was less if water deficits developed extremely rapidly (12 bars/day).

The maximum extent of osmotic adjustment in rice plant leaves is independent of the rate of stress development (measured as a change in predawn y) over a range of 0.5 to 6 bars/day. For example, Cutler et a1 (1980b) compared the extent of osmotic adjustment in leaves of 3 dryland cultivars, IRAT-13, Kinandang Patong, and Rikuto Norin, grown in large soil bins (0.7 × 1.0 × 0.45 m) at a density of 70 plants/m$^2$, or in 10-liter pots. In the larger soil mass, predawn y declined to–12 to –16 bars in 20–22 days. In pots, a similar decline in predawn y was achieved in 4-6 days. In both cases the minimum $y_s$ values were similar — about –18 bars. Similarly, Shahan (1980) observed that in cultivars IRAT-13 and Kinandang Patong grown in soil volumes of 5 or 12 liters, where the rate of stress development was 6 bars/day in the 5-liter pots and 2 bars/day in the 12-liter pots, $y_s$ declined to –20 bars when predawn y values in the –18 to –20 bar range were attained (Fig. 2). In both treatments, the rate of osmotic adjustment was a function of the stress intensity rather than the rate of stress development. The extent of osmotic adjustment was not a simple function of the duration of the stress if duration was considered simply as the number of days over which the stress was imposed.



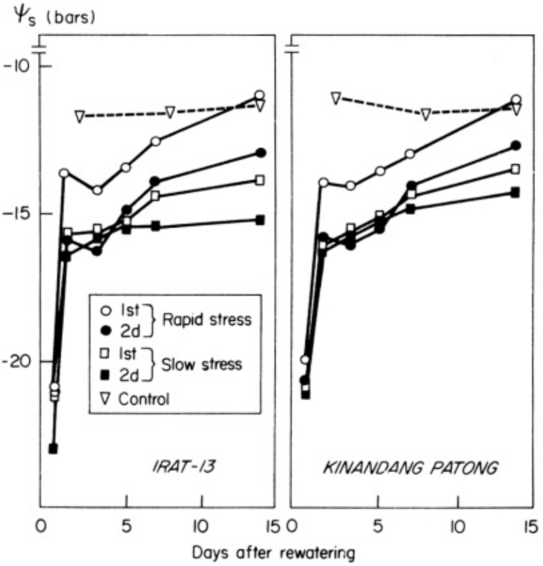
**2.** Changes in water potential (y, solid line) and solute potentials ($y_s$, broken line) during consecutive rapidly (3 = bars/day) or slowly (● = 2 bars/day) developed stress cycles. Bars at bottom indicate irrigation regime: light, no irrigation; dark, irrigation twice a day (from Shahan 1980).

The maximum extent of osmotic adjustment in rice is independent of the number of stress cycles imposed. Cutler et al (1980b) observed that the extent of adjustment achieved in plants subjected to one rapid conditioning cycle, which occurred in 4 days, was equal to that elicited by 3 conditioning cycles. Shahan (1980) reported that the maximum extent of adjustment was the same whether the plants were subjected to one stress cycle or to two, regardless of whether stress was imposed rapidly (6 bars/day) or slowly (2 bars/day) (Fig. 2). A difference in rate of adjustment during the two stress cycles was observed. Such a difference was only apparent because the maximum extent of adjustment was independent of the number of stress cycles and because $y_s$ increased during rewatering between stress cycles. Thus, a different rate of adjustment resulted because $y_s$ was lower at the start of the second cycle. In both studies, the maximum extent of adjustment was similar (–20 to –22 bars) in the small range of cultivars examined — IRAT-13, Salumpikit, Kinandang Patong, and Rikuto Norin.

The maximum extent of adjustment observed in these rice cultivars was similar to that in *Dactylis glomerata* (Gavande and Taylor 1967) and in several wheat genotypes (Morgan 1977). Asimilar extent ofosmotic adjustment (5 to 8 bars) has been reported for sorghum (Turner and Jones 1980), although plants were grown under diverse climatic and edaphic conditions.

## PERSISTENCE OF OSMOTIC ADJUSTMENT

The increased solutes concentration accrued in response to drought hardening is dissipated when the plants are rewatered. This transience of osmotic adjustment is observed in a wide variety of species and occurs in a similar time scale of about 10 days (Turner and Jones 1980). In several dryland rice cultivars, osmotic adjustment persists slightly longer — up to 14 days (Shahan 1980). Persistence of the osmotic adjustment was a function of the conditioning stress imposed. Plants subjected to either one or two conditioning stresses had the same extent of osmotic



**3.** Change in solute potentia (ψs) in leaves of rice after resumption of normal irrigation.

adjustment ($\psi_s$=–20 to –22 bars in the final days of stress) whether the conditioning stress was rapid (2 bars/day) or slow (6 bars/day).

After rewatering, however, the persistence of osmotic adjustment differed considerably (Fig. 3). In all treatments, a large increase in $\psi_s$ occurred in the first 24 hours after rewatering. The extent of this initial decay was greatest (6.5 bars) in plants exposed to a single, rapid conditioning stress, compared with a lower initial decay (3.5-4.0 bars) in the other treatments. During the next 5 days under well-watered conditions, plants in all treatments increased in solute potential at about 1 bar/day. After 5 days, the rate of decay diminished in the plants subjected to 2 slow stresses, and $\psi_s$remained at–15 bars for up to 14 days after rewatering. In contrast, $\psi_s$ continued to increase in plants subjected to a single, rapid conditioning stress. After 14 days, $\psi_s$was –11 bars. The $\psi_s$ in plants exposed to either two rapid stresses or a single, slow stress was between the two values.

In a subsequent experiment, the persistence of osmotic adjustment was a function of the number (0, 1, 2, or 3) of conditioning cycles imposed. Osmotic adjustment persisted the longest in leaves that underwent the greatest number of stress cycles.

These results indicate that the stress-conditioning regime significantly influences persistence of the adjusted state. More importantly, they also suggest a degree of complexity not evident in studies that consider only the final extent of adjustment. The biphasic decay in $\psi_s$ suggests that osmotic adjustment may be attributable to one component that is readily inducible and reversible and its induction is intensity dependent, whereas induction of the other component, which decays less rapidly, is dependent on stress duration. Whether the biphasic decay is attributable to biochemical differences in the interconversions of osmotically active compounds with osmotically inactive compounds or to structural changes is not known. However, Ackerson (1981) recently reported biochemical differences in osmotic adjustment of young versus old cotton leaves. Older leaves from adapted plants contained up to five times more starch than nonadapted leaves. In contrast, osmotic adjustment in younger leaves did not affect starch accumulation.

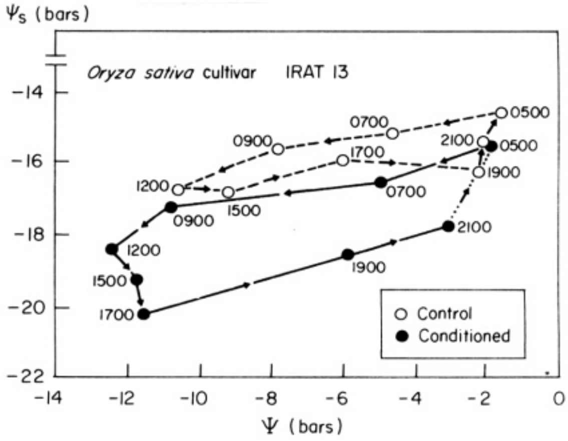
## DIURNAL ALTERATIONS IN $y_s$

Diurnal fluctuations in $y_s$ have been reported in the leaves of several crop species, including maize (Turner 1975, Hsiao et al 1976), wheat (Millar and Denmead 1976), cotton (Cutler et al 1977), sorghum (Fereres et al 1978), and soybean (Wenkert et al 1978). In maize, the diurnal fluctuation was greatest in leaves of plants exposed to low soil potentials (Turner 1975). The minimum $y_s$ was attained 2 hours after the minimum $y$ had been reached (Hsiao et al 1976). In both studies, the diurnal fluctuation was about 7 bars.

In rice (IRAT-13), $y_s$ varied between –15.5 and –20.2 bars in leaves of conditioned plants but only between –14.6 and 16.8 bars in leaves of well-watered plants (Shahan 1980). Because the measurements were made after both groups of plants were irrigated twice daily for 3 days, diurnal fluctuations in $y$ were similar (–10 bars) in both treatments. The minimum $y_s$ in conditioned plants occurred 5 hours after the minimum $y$ was achieved. In contrast, the minimum $y_s$ in control plants coincided with the minimum $y$. In both treatments, hysteresis in the relation between $y_s$ and $y$ was observed during the diurnal cycle, with the degree of hysteresis greater in conditioned plants (Fig. 4). Such hysteretic behavior strongly supports the contention that diurnal fluctuations were due to the active concentration of solutes.

## CONSEQUENCES OF OSMOTIC ADJUSTMENT

As previously stated, recent interest in osmotic adjustment in relation to drought



**4.** Diurnal relation of solute potential ($y_s$) to water potential ($y$) in leaves of conditioned and control plants (from Shahan 1980).

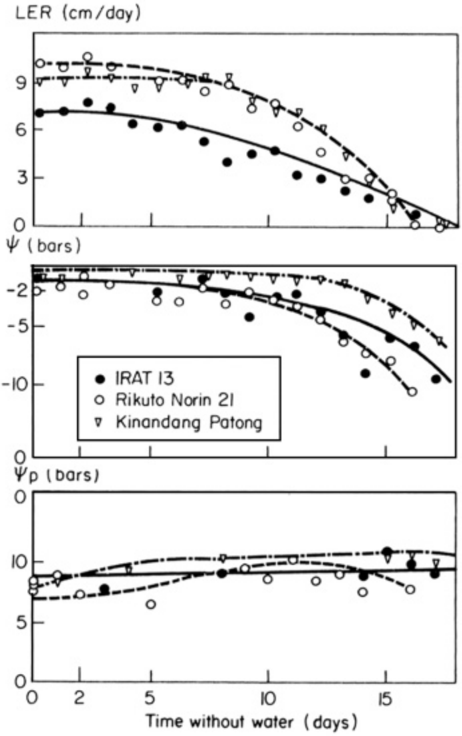
resistance was stimulated by Hsiao's analysis of the sensitivity of plant responses to water deficits (Hsiao 1973). From this analysis, Hsiao concluded that cell expansive growth was the process most sensitive to water deficits. Subsequently, the sensitivity of cell expansion served as a nucleus around which the effects of water deficits on other less sensitive processes were considered and provided an explanation for the effect of drought on yield (Hsiao and Acevedo 1974).

Because expansive growth was considered to be mediated by turgor potential interactions with cell wall elastic properties (Lockhart 1965, 1967; Hsiao et al 1976) and other consequences of cellular dehydration (reduced activity of water, concentration of macromolecules, and solutes, changes in spatial relations in membranes, and the highly speculative effects on water of hydration of macromolecules) could not explain the effects of moderate water deficits on chemical or physiological processes, turgor potential became the most probable candidate for the role of the primary transducer between internal water status and growth. Osmotic adjustment in response to water deficits therefore could preclude the loss of turgor and allow the maintenance of turgor-mediated processes in spite of reductions in plant water potential.

Observations indicating that osmotic adjustment in response to water deficits resulted in a nearly constant turgor potential in pea roots (Greacen and Oh 1972) and soybean hypocotyls (Meyer and Boyer 1972) exposed to water stress provided additional substance to the proposal. As a result, the major consequence of osmotic adjustment is attributed to the maintenance of turgor potential at lower water potentials. In some instances (Turner and Jones 1980), turgor maintenance has become nearly synonymous with osmotic adjustment.

Recently, Turner and Jones (1980) considered limitations to osmotic adjustment and noted that adjustment does not fully maintain physiological processes despite the maintenance of turgor. For example, they replotted the data of Meyer and Boyer (1972) to demonstrate that, although turgor was kept nearly constant by osmotic adjustment, the growth rate of soybean hypocotyls declined. Meyer and Boyer (1972) attributed this decrease to either an increase in the turgor threshold for growth or a decrease in the yielding tendency of the cell walls as was elaborated by Green et al (1971). Turner and Jones (1980) noted that an increase in the turgor threshold for growth was contrary to that reported in soybean leaves (Bunce 1977). Although it was not explicitly stated, the purpose of the Turner and Jones (1980) discussion appears to have been to note that osmotic adjustment, and presumably turgor maintenance, is not a universal panacea to drought stress when turgor-mediated processes (expansive growth and stomatal resistance) are considered. However, one may question whether the maintenance of turgor as a consequence of osmotic adjustment is of primary importance in drought conditioning.

Cutler et al (1980c) noted that, despite apparent turgor maintenance, leaf expansion rates of rice were markedly reduced (Fig. 5). Conditioning apparently did not alter the turgor threshold. This study, however, is subject to the criticism that inferred values of $\Psi_p$ from bulk measurements of predawn $\Psi$ and $\Psi_s$ are not appropriate indicators of internal water relations in the elongating zone. While the appropriate technology to directly determine $\Psi_p$ in the elongating region of the leaf has not yet been developed, similar limitations have precluded the direct verifica-



**5.** Comparison of leaf elongation rate (LER), predawn water potential (y), and predawn turgor potential ($y_p$) during a slowly developing stress period (from Cutler et a1 1980c).

tion of the turgor-mediated hypothesis in higher plant tissues. In *Nitella,* where $y_p$ was directly measured (Green 1968, Green et a1 1971), growth rate was zero at $y_p$ of 2 bars or less, roughly proportional to $y_p$ between 2 and 5 bars, and independent of $y_p$ above 5 bars.

In Hsiao's synthesis (Hsiao et a1 1976), turgor pressure is assigned a critical role in cell growth. It is considered the physical force needed to sustain enlargement and therefore is a prerequisite to cell enlargement. Such a model has not been without criticism. Burstrom (1971) criticized turgor-dependent cell expansion models for their failure to include the generation or maintenance of y gradients requisite for growth. Although Ray et al (1972) based their response to this criticism on Lockhart's (1965, 1967) conceptualization of plastic extension, it is still intuitively attractive to consider turgor as a consequence of impeded volumetric expansion. Although Cram (1974) accepts turgor as the driving force for expansive growth, he argues that turgor does not necessarily regulate the rare of growth. In a more comprehensive analysis, Shahan (1980) concludes that turgor-dependent cell expansion models are not well documented and, therefore, conceptual models of drought resistance based on such turgor dependence are not either.

In considering alternatives, it is important to note that the primary cellular consequence of osmotic adjustment is to decrease the chemical potential of water. It might be more prudent to concentrate on this primary consequence rather than on the secondary effect on turgor potential. In addition, cellular water status in response to a drought stress most often is considered in terms of cellular dehydration. Such a perspective is not entirely appropriate. For example, although the mitigation of cellular dehydration is of primary concern in fully expanded tissues, expansive growth is dependent on continued cellular dehydration — the continued influx of water into the growing regions. As water movement in plant tissues is proportional to gradients in the chemical potential of water and inversely proportional to resistances in the path, any factor that influences the chemical potential of water will influence cellular water status. Thus, lowered $Y_s$ resulting from osmotic adjustment in fully expanded cells will diminish the extent of cellular dehydration at any given water potential less than zero. In expanding cells, a net *influx* of water will continue at lower external water potentials. In both cases, $Y_s$ may be considered as the gear ratio between cellular water content and water potential.

From such a perspective, Cutler et al (1980d) have suggested that responses of cell enlargement and leaf elongation to alterations in water status may be described without explicit reference to turgor. Quite simply, cell enlargement is due to the accumulation of solutes in the vacuole and the subsequent influx of water. Thus, continuous expansion requires a continual accumulation of solutes. Boyer and Wu (1978) found that elongation of soybean hypocotyl was strongly related to the magnitude of the water potential gradient between the elongation zone and the substrate and bore little relation to the absolute value of $Y_p$ in the elongation zone. Molz and Boyer (1978) also were able to predict the magnitude of $Y$ gradients expected in growing tissue and found that these corresponded closely with the measured gradients. Cutler et al (1980d) conclude that, in a cell expansion model based on gradients in water potential, osmotic adjustment reduces the sensitivity to water stress because gradients for water uptake are maintained. In rice leaves, a gradient of 2-3 bars was sufficient to allow elongation, which was similar to the gradient predicted and observed in expanding soybean tissues by Molz and Boyer (1978).

Considerations of osmotic adjustment from the perspective of a turgor-based hypothesis for drought stress may be questioned for another reason. Selection of turgor as the transducer was arrived at *a priori.* Other effects resulting from cellular dehydration were eliminated by default because of insufficient information (Hsiao 1973, Hsiao et al 1976). That was especially true for the consideration of the effects of water deficits on alterations in the spatial relations in cellular membranes.

Recently, studies of the effects of severe cellular dehydration incurred by isolated protoplasts indicated that large surface areal contractions resulting from cellular dehydration effect a change in the resilience of the plasma membrane (Steponkus and Wiest 1978, 1979; Steponkus et al 1981). These observations prompted an analysis of the stress-strain relationship of the plasma membrane (Wolfe and Steponkus 1981). These studies indicate that surface areal deformations resulting from volumetric contraction and expansion have a significant impact on the resting tension ($g_r$) of the plasma membrane. Upon volumetric contraction, surface tension relaxes to zero, but upon expansion surface tension increases. In both cases the untensioned membrane area is changed. However, $g_r$

is reestablished within minutes. Hence, the existence of a reservoir into or from which membrane material is transferred during contraction and expansion was proposed (Wolfe and Steponkus 1981). While small areal changes ( ≅ 1%) are largely reversible, only a small portion of the change in the membrane area may be achieved by intrinsic contraction or expansion of the membrane area. Exchange of material between the reservoir and the plasma membrane follows a surface energy law which is influenced by the surface tension of the plasma membrane. As volumetric contraction and expansion perturb the surface tension, cellular hydration and dehydration will affect the incorporation and deletion of plasma membrane material. Repercussions on expansive growth, which requires the incorporation of new plasma membrane material and presumably the transport of cell wall material via a plasma membrane shuttle, are possible.

## COSTS OF OSMOTIC ADJUSTMENT

Turner and Jones (1980) have considered the costs of osmotic adjustment. Implicit in such an analysis is the connotation that the accumulation of osmotically active solutes is at the expense of some growth process. Surely there is a metabolic expenditure for osmotic adjustment, but this is not to say that it is an optional expense. Instead, osmotic adjustment in response to drought stress may result because of impediments to the use of metabolites. Hence, the accumulation of solutes in itself is not necessarily an option, it is merely a consequence of impeded growth and development. Conditioning or acclimation effected by either drought, salinity, or cold results in osmotic, adjustment. It is accompanied by growth impairment in all cases. For drought conditioning, growth impairment is induced by water deficits. In the case of cold acclimation, growth is impeded because of temperature limitations. Therefore, it is doubtful that there is a specific transducer for sensing water deficits which effects osmotic adjustment, although caution must be exercised in oversimplifying this point.

## CONCLUSIONS

Hsiao et a1 (1976) concluded that ". . . plant reactions to water stress cannot be interpreted as simple responses to changes in $\psi$ , with $\psi_s$ remaining relatively constant, with $\psi_p$, changing in phase with $\psi_s$ ," and "in spite of the strong theoretical and experimental evidence of a close relationship between growth and $\psi_p$ ,simple expressions stating this relationship have limited applicability. . ." These conclusions hold true, but it should be added that osmotic adjustment cannot be interpreted as the simple maintenance of $\psi_p$. Alternatives to the $\psi_p$--based model for drought injury are emerging. Such models and the $\psi_p$--based model require direct experimental validation.

Drought resistance of a crop species has been defined as "the ability of a crop species or variety to grow and yield satisfactorily in areas subjected to periodic water deficits" (Turner 1979). Such a definition exemplifies the arbitrary and relative nature of drought resistance, which at best is an ill-defined characteristic sought by many, found by few, and explained by no one. Considering the task of addressing the complexities of growth, development, and yield within a framework of varied water status, the question as to whether increased water-use efficiency in crop species is a mirage (Reitz 1974) is not surprising. If the adage that "you can breed for drought resistance simply by selecting for low yield" (Blum 1980) is correct, one can query whether drought resistance is a delusion—a belief in something contrary to fact or reality. In the least some aspects of drought resistance of crop species may be illusions—the false perception of something that has objective significance—for example, osmotic adjustment.

## REFERENCES CITED

Acevedo, E. 1975. The growth of maize (*Zea mays* L.) under field conditions as affected by its water relations. Ph D thesis, University of California, Davis.

Ackerson, R. C. 1981. Osmoregulation in cotton in response to water stress. Plant Physiol. 67:489-493.

Bartel, A. T. 1947. Some physiological characteristics of four varieties of spring wheat presumably differing in drought resistance. J. Agric. Res. 74:97-112.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

Blum, A. 1980. Genetic improvement of drought adaptation. Pages 450-452 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York.

Boyer, J. S., and G. Wu. 1978. Auxin increases the hydraulic conductivity of auxin sensitive hypocotyl tissue. Planta 130:227-237.

Bunce, J. A. 1977. Leaf elongation in relation to leaf water potential in soybean. J. Exp. Bot. 28:156-161.

Burstrom, H. 1971. Wishful thinking of turgor. Nature 234:488.

Clements, H. F. 1937. Studies in the drought resistance of the sunflower and the potato. Res. Stud. Stn. Coll. Washington 5:81-98.

Cram, W. J. 1974. The regulation of concentration and hydrostatic pressure in cells in relation to growth. Pages 183-189 *in* R. L. Bieleski, A. R. Ferguson, and M. M. Creswell, eds. Mechanisms of regulation of plant growth. Bull. 12, Royal Soc. New Zealand, Wellington.

Cutler, J. M., D. W. Rains, and R. S. Loomis. 1977. Role of changes in solute concentration in maintaining favorable water balance in field-grown cotton. Agron. J. 69:773-779.

Cutler, J. M., and D. W. Rains. 1978. Effects of water stress and hardening on the internal water relations and osmotic constituents of cotton leaves. Physiol. Plant. 42:261-268.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1979. Characterization of internal water relations of rice by a pressure-volume method. Crop Sci. 19:681-685.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1980a. Alteration of the internal water relations of rice in response to drought hardening. Crop Sci. 20:307-310.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1980b. Dynamics of osmotic adjustment in rice. Crop Sci. 20:310-314.

Cutler, J. M., K. W. Shahan, and P. L. Steponkus. 1980c. Influence of water deficits and osmotic adjustment on leaf elongation in rice. Crop Sci. 20:314-318.

Cutler, J. M., P. L. Steponkus, M. J. Wach, and K. W. Shahan. 1980d. Dynamic aspects and enhancements of leaf elongation in rice. Plant Physiol. 66:147-152.

Eaton, F. M., and D. R. Ergle. 1948. Carbohydrate accumulation in the cotton plant at low moisture levels. Plant Physiol. 23:169-187.

Fereres, E., E. Acevedo, D. W. Henderson, and T. C. Hsiao. 1978. Seasonal changes in water potential and turgor maintenance in sorghum and maize under water stress. Physiol. Plant. 44:261-267.

Gavande, S. A., and S. A. Taylor. 1967. Influence of soil water potential and atmospheric evaporative demand on transpiration and the energy status of water in plants. Agron. 59:4–7.

Greacen, E. L., and J. S. Oh. 1972. Physics of root growth. Nature New Biol. 235:24-25.

Green, P. B. 1968. Growth physics in *Nitella:* a method of continuous in *vivo* analysis of extensibility based on a micro-manometer technique for turgor pressure. Plant Physiol. 43:1169-1184.

Green, P. B., R. O. Erickson, and J. Buggy. 1971. Metabolic and physical control of cell elongation rate. *In vivo* studies in *Nitella.* Plant. Physiol. 47:423-430.

Hsiao, T. C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570.

Hsiao, T. C., and E. Acevedo. 1974. Plant responses to water deficits, water-use efficiency and drought resistance. Agric. Meteorol. 14:59-84.

Hsiao, T. C., E. Acevedo, E. Fereres, and D. W. Henderson. 1976. Water stress, growth and osmotic adjustment. Phil. Trans. R. Soc. London, B, 273:479-500.

Iljin, W. S. 1929. Der Einfluss der Standortsfeuchtigkeit auf den osmotischen Wert bei Pflanzen. Planta 7:45-58.

Jones, M. M., and N. C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Jones, M. M., and H. M. Rawson. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use and osmotic potential in sorghum. Physiol. Plant. 45:103–111.

Lidforss, B. 1907. Die wintergrune Flora. Lund Universitat Arsskrift, N. F. 2, Afd. 2, No. 13 (cited by Maximov, 1929, original not seen).

Lockhart, J. A. 1965. An analysis of irreversible plant cell elongation. J. Theor. Biol. 8:264-275.

Lockhart, J. A. 1967. Physical nature of irreversible deformation of plant cells. Plant Physiol. 42:1545-1552.

Maximov, N. A. 1929. Internal factors of frost and drought resistance in plants. Protoplasma 7:259-291.

Meyer, R. F., and J. S. Boyer. 1972. Sensitivity of cell division and cell elongation to low water potentials in soybean hypocotyls. Planta 108:77-87.

Millar, B. D., and O. T. Denmead. 1976. Water relations of wheat leaves in the field. Agron. J. 68:303-307.

Molz, F. J., and J. S. Boyer. 1978. Growth-induced water potentials in plant cells and tissues. Plant Physiol. 62:423-429.

Morgan, J. M. 1977. Differences in osmoregulation between wheat genotypes. Nature 270:234-235.

Morgan, J. M. 1980. Differences in adaptation to water stress within crop species. Pages 369-382 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York.

Ray, P. M., P. B. Green, and R. Cleland. 1972. Role of turgor in plant cell growth. Nature 239:163-164.

Reitz, L. P. 1974. Breeding for more efficient water use — is it real or a mirage? Agric. Meteor. 14:3-11.

Rosa, J. T. 1921. Investigation of the hardening process in vegetable plants. Miss. Agric. Exp. Stn. Res. Bull. 48:1-97.

Schmidt, H. 1939. Plasmazustand and Wasserhaushalt bei *Laminium maculatum.* Protoplasma 33:25-43.

Shahan, K. W. 1980. Facultative drought-induced alterations of internal water relations in rice (*Oryza sativa* L.). M Sc thesis, Cornell University, Ithaca, New York. 207 p.

Simmelsgaard, S. E. 1976. Adaptation to water stress in wheat. Physiol. Plant. 37:167-174.

Steponkus, P. L. 1980. A unified concept of stress in plants? Pages 235-255 *in* D. W. Rains, R. C. Valentine and A. Hollaender, eds. Genetic engineering of osmoregulation. Plenum Press, New York.

Steponkus, P. L., and S. C. Wiest. 1978. Plasma membrane alterations following cold acclimation and freezing. Pages 75-91 *in* P. H. Li and A. Sakai, eds. Plant cold hardiness and freezing stress. Academic Press, New York.

Steponkus, P. L., and S. C. Wiest. 1979. Freeze-thaw induced lesions in the plasma membrane. Pages 231-254 *in* J. M. Lyons, D. Graham, and J. K. Raison, eds. Low temperature stress in crop plants. Academic Press, New York.

Steponkus, P. L., J. M. Cutler, and J. C. O'Toole. 1980. Adaptation to water stress in rice. Pages 401-418 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York.

Steponkus, P. L., J. Wolfe, and M. F. Dowgert. 1981. Contraction and expansion induced stresses during a freeze-thaw cycle: considerations from a membrane perspective. *In* J. Morris and A. Clark, eds. Effects of low temperature on biological membranes. Academic Press, London. (in press)

Turner, N. C. 1975. Concurrent comparisons of stomatal behavior, water status, and evaporation of maize in soil at high and low water potentials. Plant Physiol. 55:932-936.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. Pages 343-372 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley-Interscience, New York.

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. Pages 87-103 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York.

Wenkert, W., E. R. Lemon, and T. R. Sinclair. 1978. Water content-potential relations in soya-bean: changes in component potentials for mature and immature leaves under field conditions. Ann. Bot. 42:295–307.

Whiteside, A. G. O. 1941. Effect of soil drought on wheat plants. Sci. Agric. 21:320–334.

Wolfe, J., and P. L. Steponkus. 1981. The stress–strain relation of the plasma membrane of isolated protoplasts. Biochim. Biophys. Acta 643:663–668.

# ADAPTATION OF RICE TO DROUGHT-PRONE ENVIRONMENTS

J. C. O'TOOLE

Rice is cultured in environments that are hydrologically marginal for semiaquatic species. Evidence of the occurrence of adaptive mechanisms in the rice germplasm induced by drought stress is reviewed. Adaptive mechanisms of root and shoot systems are discussed in terms of selection pressure characteristics and resulting effects on crop water relationships, growth, and yield. The relevance of specific growth stages is illustrated and some interactions among adaptive mechanisms are discussed. Given the goal of agricultural productivity in contrast to natural selection, an imaginative reassessment of the suitability of adaptive mechanisms for future breeding of rainfed rice cultivars is suggested.

The world's rainfed rice crop covers an estimated 65-75 million hectares and occupies an extremely diverse array of ecological niches. Rainfed rice is cultivated across wide ranges of photoperiod, temperature, and solar radiation (Yoshida 1977). But water is the predominant ecological factor affecting growth and yield. The hydrological conditions of a region interact strongly with edaphic, biotic, agronomic, and other climatic factors. The variability of these interactive effects across locations, across seasons, and within seasons, illustrates the potential complexity of rainfed rice ecology (O'Toole and Chang 1979).

Rainfed rice is grown in three generalized nonirrigated habitats: dryland, where

---

The International Rice Research Institute, Los Baños, Philippines.

water input is directly by rainfall (pluvial); wetland, where water input is from rainfall, surface flow, and subsurface interflow (phreatic); and deepwater, where surface flow (fluxial) is the paramount water input.

Rainfed rice germplasm has adapted to the broadest range of hydrological conditions of any crop species. Rice, because of its adaptation to submerged anaerobic soils, is considered a semiaquatic species best suited for wetland habitats. However, cultivars may be found within the germplasm bank that exhibit varying degrees of adaptation to anaerobic dryland conditions. Indeed, some dryland rice cultivars do not grow well in anaerobic wetland fields.

The literature on the evolutionary origin of semiaquatic monocots is laden with controversy. The argument related to our subject is whether rice evolved from a dryland or a wetland adapted ancestor. Hughes (1976) states that there is no evidence in recent times of a dryland plant invading a wetland habitat. Most evidence supports migration in the opposite direction (Hughes 1973). The view that higher plants such as the monocotyledons now adapted to wetland habitats arose by re-entry of dryland species into the aquatic habitat is equally espoused (Takhtajan 1969, Crawford 1978).

The vast majority of cultivars in the world rice germplasm collection at IRRI appear to be adapted to wetland habitats. Although all are capable of dryland culture at high soil moisture content, less than 4% appear strongly adapted to dryland culture. Whether these genotypes are the progenitors of modern rice ecotypes or the most recently evolved is not our immediate concern. That these genotypes are indeed different in the water related qualities of their adaptation is the focus of this discussion.

Of particular relevance is the adaptation of rice to drier environments within the species' range. It will become apparent that the entire agroclimatic or edaphic range of rice is wetter than that of any other dryland adapted food crop species. However, the relative differences within the range of rice are still very wide and the result in terms of crop adaptation to drought will be better appreciated after this discussion.

Man's efforts to expand the range of rice into marginal hydrologic conditions over several millennia have resulted in intense selection pressure, leading to an expectation of a spectrum of cultivars possessing varying degrees of adaptation to particular water stress conditions. In this single species we find a model system for investigating both the water relations of semiaquatic vegetation and the adaptive mechanisms involved in the evolution of a species from semiaquatic to terrestrial habitats. Research on the adaptation of rice to drought-prone environments uniquely combines ecophysiological research with an immediate application of its results to the improvement of a major food crop.

## ADAPTIVE MECHANISMS

The diversity of physical conditions characterizing drought-prone rainfed rice environs makes discussion of each mechanism's interaction with other factors impossible. An evaluation of each mechanism's role would be equally academic. For that reason, this discussion will concentrate on illustrating characteristics relevant to the adaptation of rice ecotypes to habitats hydrologically marginal for a semiaquatic species.

Huxley (1943) offers three forms of causal explanation for biological phenomenon: explaining how an adaptation functions physiologically or biochemically, showing the adaptive role of the structure or function in the life cycle of the organism, and illustrating the historical steps leading to development of the phenomenon. In this paper a brief treatment of the most obvious water deficit-related adaptive mechanisms in rice germplasm is attempted.

We begin by establishing a rather simplistic view of water deficit related adaptations. First, we assume that an observed adaptation is the response of a cause-and-effect biophysical system. The cause is the selection pressure and the effect is the presence of a particular adaptive mechanism in the germplasm. The justification for such an adaptation arising and remaining in a population will be its effect on the crop's water relations interaction with growth and yield. Single causes, such as water deficits, generally produce multiple effects. For example, water availability in the soil is not the only factor controlling the fitness of alternative root morphologies, physiologies, and system developmental patterns in a given habitat. Obviously, this simplistic view leaves much to be desired.

To establish the cause-and-effect explanation, we refer mainly to Huxley's first two propositions: illustrating the physiological adaptive value and illustrating the adaptive role in the life cycle of rice. This discussion deals first with nongrowth stage specific adaptive mechanisms, then with those relevant to specific phenological stages of the rice crop.

The scheme is presented diagrammatically in Figure 1 (A and B). Figure 1A illustrates adaptive mechanisms that are nongrowth stage specific, categorized for convenience as root or shoot related. Figure 1B illustrates adaptive mechanisms which are growth stage specific. Although evidence for some characters is meager (adaptive mechanisms followed by a question mark ?) as they have not, to my knowledge, been researched in rice, they are listed in Figure 1 on empirical evidence of occurrence and presence of genotypic variation.

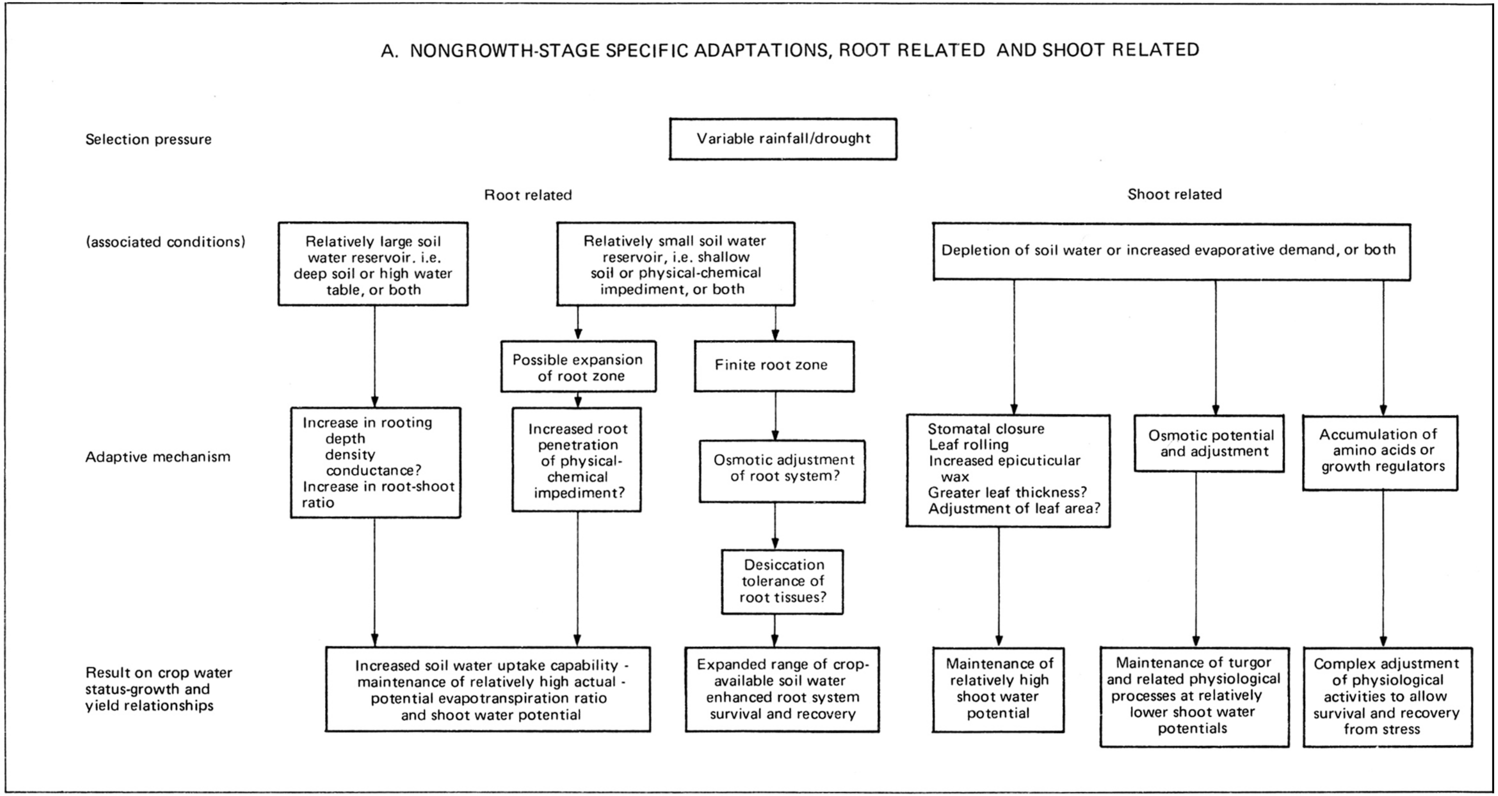
Although numerous interactions between the components — with each other and with extraneous factors — is obvious, no attempt has been made to accommodate this information in the figure. I hope this preference for simplicity is acceptable to whole plant and crop physiologists who might prefer a more functionally accurate, but greatly encumbered illustration.

## ADAPTATIONS NOT SPECIFIC TO GROWTH STAGE

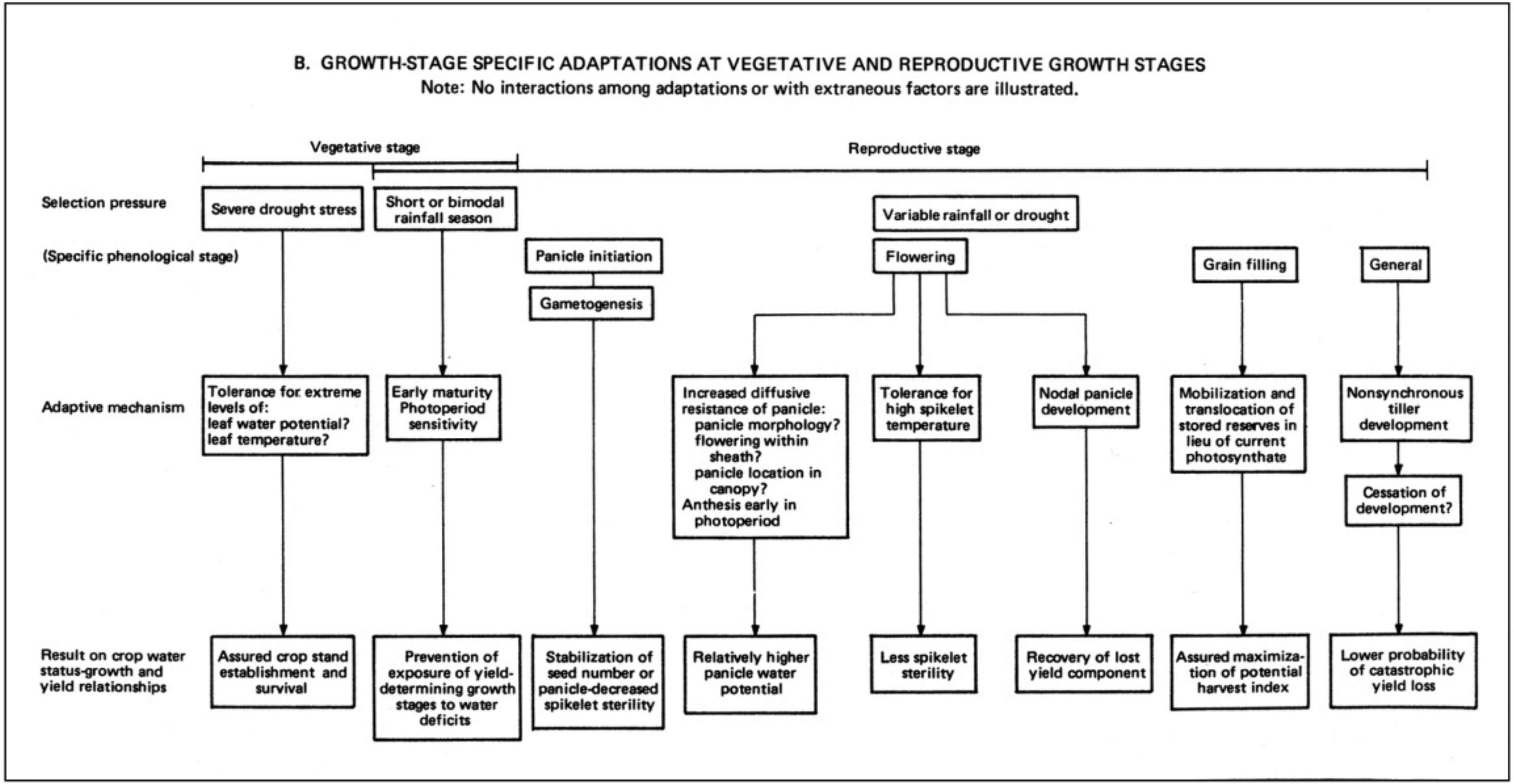
*Root-related adaptations* are discussed in relation to two general physical background conditions of rice soil. In the first condition (Fig. 1A), a large potential soil water reservoir is assumed, either in deep soil without barriers to root growth or in a water table contributing to the crop water requirement, or in both. In these conditions, cultivars with a deeper rooting habit have evolved.

---

[1] Adaptation as used here denotes both long-term phylogenetic evolution of ecotypes (constitutive) and short-term change in response to water deficit (facultative). Since the facultative is a priori a function of the constitutive, little attempt to differentiate will be made.



A. NONGROWTH-STAGE SPECIFIC ADAPTATIONS, ROOT RELATED AND SHOOT RELATED



**1.** Apparent selection pressure, adaptive mechanisms, and resultant effect on crop water relations-growth and yield relationships in rainfed rice. A question mark indicates meager evidence for the character.

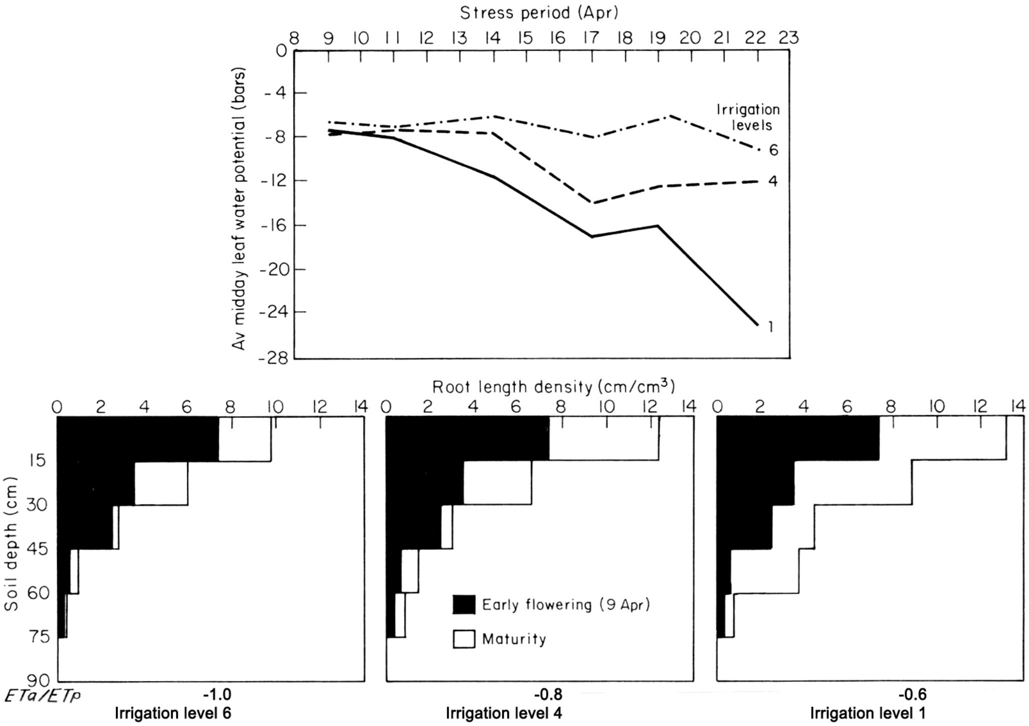
Considerable research in recent years illustrates the large range of constitutive differences in rooting depth and in density in the soil profile among rice cultivars (IRRI 1974, 1975, 1976, 1977, 1978, 1979, 1980; Reyniers et al 1976). Yoshida and Hasegawa (this volume) and Chang et al (this volume) illustrate the contribution of greater rooting depth to water uptake and its effect on plant water potential during drought. They contrast cultivars with relative differences in rooting depth, clearly illustrating genotypic variation and its effect on crop water status. In addition, Armenta (1981) and Chang et al (this volume) illustrate genotypic variation in root length and report the first estimates of heritability for root length and other root morphological traits.

Semiaquatic rice has evolved a very high root length density, 8-12 cm/cm$^3$ in the upper 15 cm of soil (Fig. 2). Yoshida (this volume) shows 22 cm/cm$^3$ in the upper 10 cm. Greater root density below this level is a constitutive adaptation associated with traditional rainfed cultivars. Recent work on the facultative nature of root length density shows that the character is more responsive to water stress than root depth. Figure 2 illustrates the large increase in root length density of IR36 grown in dryland conditions where the actual to potential evapotranspiration was manipulated to induce varying levels of plant water stress — midday leaf water potential. The responsive nature of this trait must also have important ramifications in other aspects, such as soil volume explored for limiting nutrients, and in greatly modifying crop response to succeeding droughts.

Root conductance or resistance to flow also is listed in Figure 1A, but little information is available on rice. Yoshida and Hasegawa (this volume) show evidence for axial resistance in rice roots, which presumably increases with depth. To date I am unaware of studies on radial resistance of rice roots or on genotypic variation for these characteristics in rice.

Greater rooting depth and density, whether it is a constitutive genotypic variation in nonstressed plants or a facultative expression of the trait in response to stress, will result in more available soil water during a rainless period. As a result of this greater capacity for uptake, the crop will be able to maintain relatively high shoot water potential and to continue evapotranspiring at near potential rates over a longer period. In terms of agricultural productivity, maintaining a high actual to potential evapotranspiration ratio is a strong determinant of overall crop growth and yield (Dewit 1958, Fischer and Turner 1978, Hanks 1981).

When the root zone is relatively shallow and the associated soil water reservoir is small because of soil physical or chemical impediments (Fig. lA), two adaptive schemes appear feasible. In the first, cultivars capable of penetrating the barrier will gain new soil water reservoirs. Little is known about the bulk density or penetration resistances in dryland or wetland rice fields or about how rice roots respond. Rice root penetration and proliferation decrease sharply between 0.5 and 2.0 MPa soil strength. Although experimentation with numerous genotypes is difficult because of problems in controlling soil moisture-penetration resistance interactions, we found that cultivars differ in the ability to penetrate and proliferate in soils varying in penetration resistance strength. Figure 3 illustrates the response of *Echinochloa crus-galli* L. (barnyardgrass) and two rice cultivars to

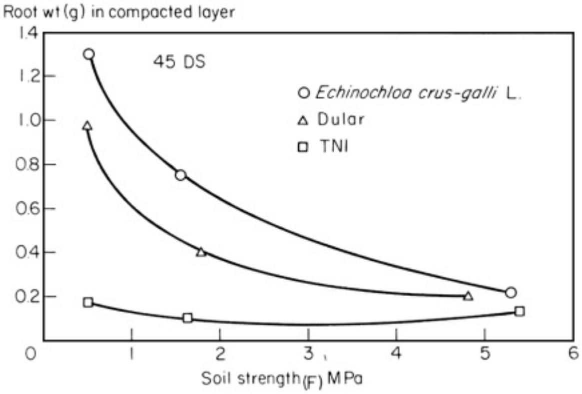


**2.** Root length density at 3 levels of irrigation and resulting plant water stress. Initial root length density was sampled 9 April 1980. The final sampling was made 7 May 1980 at crop maturity. Irrigation level 6 is non-stress or control level.
$ET_a/ET_p$ = actual-potential evapotranspiration ratio.

varying soil strength conditions. No evidence relates this adaptation to increased water uptake, but evidence from other crop species leaves little doubt of the result (Taylor 1980).

Rice cultivars exhibit ample tolerance for numerous soil chemical problems (Ikehashi and Ponnamperuma 1978). These tolerance mechanisms conceivably would lead to increased root development and water uptake potential during drought. Tolerance of rice roots for high aluminum concentrations illustrates this adaptation in cultivars grown on acid dryland rice soils of Africa and South America (Howeler and Cadavid 1976).

Where the soil water reservoir is small and expansion not possible, physiological adjustment of the root system could enhance the desiccation or dehydration tolerance of root tissues. This theoretically could expand the free energy range of water capable of being taken up by the crop. And, although this may be quantitatively small in most soils (from -18 to −30 bars), it may be significant in terms of root tissue survival. Physiological adjustment may increase tolerance for extremely low root water potentials and result in a larger functional root system when drought is terminated. This complex of traits may be an important component of



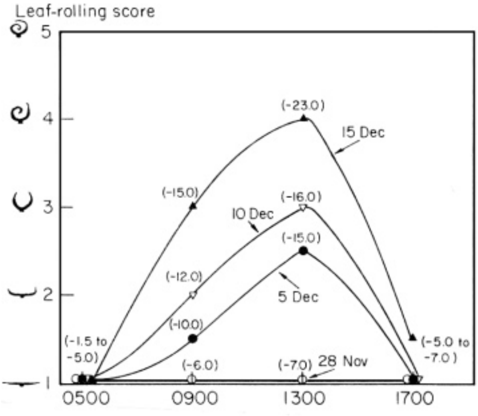
**3.** Root weight in a 14.5- × 47.5 × 3-cm compacted layer of a semi-aquatic weed species and 2 rice cultivars, Dular (rainfed upland–wetland, India) and TNl (irrigated wetland, China), 45 days after seeding (DS). The compacted layer was 3 cm deep and located 12-15 cm below the soil surface (Kandasamy and O'Toole, unpubl.).

the observed variation in survival and recovery ability among rice cultivars (Chang et al 1972, De Datta and O'Toole 1977, O'Toole et al 1978). Unfortunately, no direct measurements of rice root tissue adjustment or survival upon exposure to known water deficits are available. This adaptive mechanism and the associated potential for genotypic variation remain speculative, as is denoted by the question mark (2) in Figure 1A.

*Shoot-related adaptations* in rice germplasm, whether constitutive or facultative, may be placed in two categories: adaptations that decrease water loss from the shoot and adaptations that involve adjustment of physiological processes or of biochemical parameters such as regulatory substances.

The first type of adaptation may have a concomitant effect on carbon dioxide diffusion, since water and carbon dioxide share the same diffusion pathway in the gaseous phase. Biochemical adaptations to stress also may divert assimilates from crop growth and yield processes, reducing the economic productivity of the crop. These water deficit-induced adaptations have been reviewed with special interest focused on the cost or competitive allocation of mass and energy (Begg and Turner 1976, Hsiao et al 1976, Turner 1979). We merely enumerate the evidence for these mechanisms, since current information to speculate on this question in rice is lacking.

Rice responds to decreased tissue water status in the same manner as most other monocots, by stomatal closure and leaf rolling. Stomatal closure, demonstrated by its effect on leaf diffusive resistance, occurs at about the same leaf water potential as the initial change in leaf form (O'Toole and Cruz 1980). Because these responses occur at similar leaf water potentials, it is difficult to separate their effects in decreasing water loss from the shoot during drought. However, from the limited data available it appears that leaf rolling is effective in decreasing transpiration (O'Toole et al 1979a). Stomatal closure did not become complete even at relatively low leaf water potentials of –22 bars. Both stomatal closure and leaf rolling responses are dynamic and capable of affecting the stabilization of shoot water status. Figure 4 illustrates the diurnal response of leaf rolling in rice. As drought



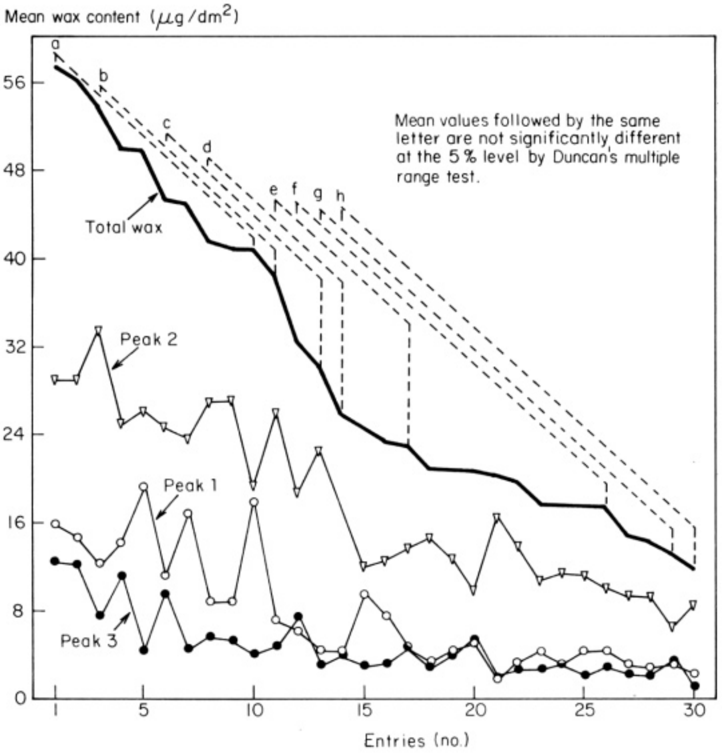
**4.** Degree of leaf-rolling is illustrated both diurnally and through a relatively long drying period. The increasing magnitude of the diurnal response illustrates the dynamic nature of this adaptation to water stress.

progresses, the degree of rolling and, presumably, associated transpirational control increases in response to leaf water stress. Leaf rolling is not a static phenomenon associated with severely stressed vegetation. It may be as distinct and finely tuned a response to water stress in rice as stomatal resistance. Dryland-adapted cultivars are noted for their plasticity in leaf rolling and may represent a greater development of that mechanism in response to short-term transient stresses.

A fundamental adaptation of species occupying terrestrial habitats is the evolution of a cuticle to prevent extrastomatal water loss from shoot tissues. Measurements of cuticular resistance in rice are 30-50% lower than in sorghum and maize (Yoshida and Reyes 1976).

The amount of epicuticular wax, a significant component of the cuticle, is related to cuticular resistance in rice and varies quantitatively per unit area between dryland- and wetland-adapted ecotypes, although the amount is much less than in other cereals (O'Toole et al 1979b). The relative amount of epicuticular wax (mg/dm$^2$) among rice cultivars may be of limited significance to the symposium objectives. However, it is perhaps the best illustration of the spectrum of water-related adaptation. Figure 5 shows the amount of epicuticular wax on the leaves of 30 diverse cultivars grown in nonstress (flooded) conditions. Of those cultivars with the greatest amounts, 3 of the 5 highest values are dryland-adapted rices from West Africa and Brazil. In comparison, barley, sorghum, and wheat have about 40 times more epicuticular wax than rice.

The last two adaptive mechanisms that act to decrease shoot water loss, denoted by a (?) in Figure 1A, are rather speculative, although there is evidence regarding genotypic variation (Ohno 1976 cited by Yoshida and Hasegawa, this volume). Greater leaf thickness is associated with dryland-adapted rice cultivars, but to my knowledge no studies exist which relate this trait to adaptation to hydrological background. Nobel (1980) has an interesting hypothesis which, briefly stated, says that greater mesophyll surface area per unit of leaf area (a possible consequence of evolving thicker leaves) should result in higher photosynthetic rates and higher



**5.** Amount of epicuticular wax per unit leaf area from diverse rice cultivars grown in flooded conditions in the 1978 dry season at IRRI. Leaves were dipped in chloroform and the extract was subjected to gas chromatography described by O'Toole et al (1979b). The weight of wax was determined for the 3 major chromatographic peaks. Peak 2 was the most discriminating qualitative difference among cultivars (O'Toole and Cruz, unpubl.).

water use efficiency. High water use efficiency would be an adaptive mechanism in rice that would greatly complement stomatal response and leaf rolling as a means of stabilizing and maintaining high leaf water potential with less adverse effects on carbon fixation.

Adjustment of transpiring leaf area through accelerated senescence of lower leaves, death of tillers, and leaf tip depth is a common response of water-stressed rice, as it is in other natural and crop species (Turner 1979). The resultant decrease in intercepted radiation and transpiring surface may result in relatively higher, more stable leaf water potential. But the effectiveness of this mechanism in an agricultural crop community is questionable and to my knowledge has not been examined.

Osmotic adjustment as an adaptive crop response to water stress has received a great deal of attention in recent years (Turner and Jones 1980). Several studies involving rice have appeared recently. These are reviewed by Steponkus (this volume). We may conclude that rice exhibits osmotic adjustment as an adaptation to water stress. But osmotic adjustment in rice appears to have a limitation of 5 to 8 bars, much like other crop species. It results in leaf elongation (perhaps the most sensitive crop response to water deficit) continuing at more negative leaf water potential. And little genotypic diversity was noted in the materials (mainly dryland cultivars) studied to date.

Larcher (1980), citing Walter (1960), illustrates the range of osmotic potentials in ecologically different types of plants. This perhaps relates more to their constitutive level of adaptation rather than to their facultative response to water stress. The range is from –2 bars in water plants to –60 bars in native shrubs. Osmotic potentials of crop plants and other mesophytes range from –5 to –22 bars. We monitored nonstress osmotic potentials in diverse rice ecotypes. Although the range (only 2.5 bars) is small, theecological origin is reflected in the ranking (Table 1). The baseline or nonstress osmotic potential of rice ecotypes may represent a long-term constitutive adaptive component.

The role of proline accumulation as an adaptation to water stress is still being debated. Stewart and Hanson (1980) review the information available on proline accumulation with emphasis on barley. Their discussion of such relevant questions as: What does adaptation to water stress or adapted to drought-prone environments mean? is quite interesting. They conclude that, although adaptive metabolic mechanisms exist, accumulation of proline is probably not one of them. Other viewpoints, generally relating proline and other amino acids as a nitrogen or energy pool to support recovery and regrowth, still require further research (Blum this volume). The degree of variation for this adaptive mechanism in rice is still unknown.

Adaptation to water stress has been proposed as the cause of variation in concentration of abscisic acid (ABA), ethylene, and cytokinins. Only ABA has been investigated in rice. Henson and Quarrie (1981) and Quarrie and Henson (1981) showed that ABA does accumulate in water stressed rice tissues. Austin et a1 (this volume) demonstrates genotypic variation in ABA accumulation and in responsiveness to applied ABA among rice cultivars. Applied ABA responsiveness was noted in terms of apparent genotypic differences in increased leaf diffusive resistance and in effect on leaf expansion.

The simplistic cause and effect basis of Figure 1A is far from adequate when we wish to assess the result of such integral plant physiological processes as osmotic adjustment and accumulation of proline and ABA.

## ADAPTATIONS SPECIFIC TO GROWTH STAGE

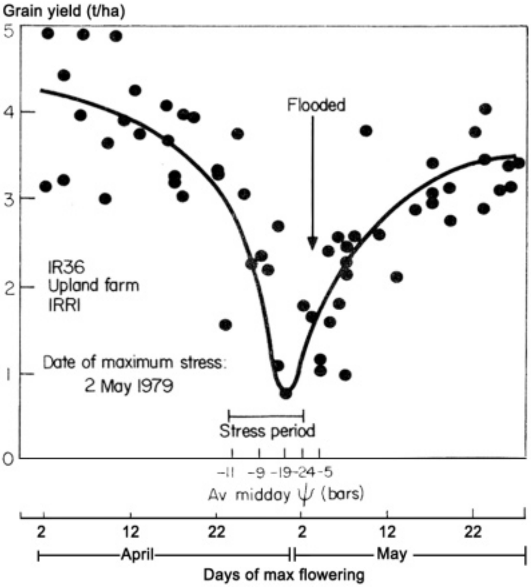
*Early vegetative stress* (Figure 1B) is highly probable in several rainfed cultural systems. No specific study has investigated rice leaf tissue tolerance for extremely low water potential. Empirical evidence from recent extensive field and greenhouse drought screening suggests that rice cultivars differ in ability to survive low tissue water status and a simultaneous increase in tissue temperature. Unfortunately, this adaptive mechanism and assumed genotypic variation must remain speculative, as is denoted by the (?) in Figure 1B.

*Reproductive stage water stress* was not studied in rice until very recently and few results have been published on which to base a discussion of the adaptive mechanisms proposed in Figure 1B. Despite this problem, the effects of stress during reproductive growth stages cannot be overemphasized.

*Short or bimodal rainfall seasons* have caused the selection of early maturing genotypes. Traditional cultivars in the chronically drought-prone areas of Bangladesh (aus crop) and North-Central India mature in less than 105 days (Krishnamurthy et al 1971). In parts of West Africa and to some extent in North Thailand, traditional cultivars appear to have been selected for photoperiod sensitivity, which assures that sensitive reproductive growth stages coincide with peaks in the rainfall distribution. Although this function of photoperiod sensitivity has not been intentionally used in breeding programs, it has been noted as an adaptation related to environmental stresses by several authors (Oka 1958, Vergara and Chang 1976). The adaptive value of early maturity and photoperiod sensitivity in rainfed rice is in preventing exposure of yield-determining growth stages, primarily the reproductive stages, to water deficit conditions.

The interaction as a selection pressure of variable rainfall or drought on individual phenological reproductive stages is less straightforward and, in the case of rice, largely unknown. Recent work at IRRI indicates that yield reduction or sensitivity to stress at reproductive stages may be ranked as FLOWERING > GAMETOGENESIS ≥ PANICLE INITIATION > GRAIN FILLING (Fig. 6).

Little is known about the actual causes of yield reduction when flowering coincides with water stress. Sterility and abortion increase and are related to decreased panicle water status (IRRI 1980). Unlike the leaves, rice panicles have no stomatal control and no change in form. similar to leaf rolling to control water loss. We have noted, however, considerable variation in the germplasm for panicle morphology, such as compactness of form, presence and length of awns on glumes,



**6.** Response of grain yield from crops planted at 16 different planting dates to a single water stress period. Crops which flowered on 2 April were near maturity during the stress period and those flowering after 22 May were near panicle initiation during the stress period (IRRI 1980).

and degree of trichome development on glumes. These variations in panicle morphology may be adaptive by acting to increase resistance to water diffusion out of the panicle, by providing alternative means of enhancing sensible heat transfer to the atmosphere, or both.

Panicle emergence from the flagleaf sheath is dependent on elongation growth at the panicle node. Failure to emerge during water stress does protect the panicle from evaporative demand. In the vast majority of cultivars observed, it unfortunately leads to complete sterility of those spikelets left inside the leaf sheath on a partially emerged panicle (Namuco and O'Toole 1980). In some cultivars, fertile and fully developed grains are found inside the sheath. The most striking example is the cultivar Sathi, which originates in the Indian State of Uttar Pradesh. In this cultivar, the panicle emerges only slightly from the flagleaf sheath. Fertile grains develop within the sheath, which partially opens as the panicle enlarges.

The location of the panicle in the crop canopy as it emerges and flowers may also be an adaptive mechanism related to observed differences in degree of spikelet sterility. The angle of the flagleaf and subtending leaves, the degree of panicle exsertion, and the panicle attitude during flowering determine the proximity of the particle to, and to some extent the magnitude of, crop boundary layer resistance. In conditions of high wind speed and evaporative demand, this characteristic, as well as the other morphological traits mentioned, may result in relatively higher panicle water status during flowering.

The sensitivity of flowering to water stress and potential water stress-induced high temperature effects on sterility lead to another adaptive mechanism. Both spikelet temperature and panicle water potential follow diurnal curves, reaching their respective peak and valley limits at 1200 to 1400 hours. Flowering early in the photoperiod, when both water and temperature factors are more favorable, would be an adaptive response. Variation in flowering time exists in rice (Nishiyama and Blanco 1980). Genotypic variation for tolerance for high temperature-induced sterility at flowering also has been illustrated by Satake and Yoshida (1978).

Although we know very little about panicle water relations and the actual causes of water stress-induced sterility at flowering, this discussion illustrates the potential for identifying adaptive mechanisms with great practical value.

In terms of individual tiller development, a water deficit at these reproductive stages causes irreparable loss of potential yield (O'Toole and Chang 1979). In 1979, we observed that plots of four cultivars severely stressed at flowering had a higher number of panicles than tillers per square meter. Further examination of the yield components revealed that several tillers had two panicles. The original panicle was completely sterile. The second panicle, originating from the penultimate leaf or flagleaf nodes, developed after the original assimilate sink became nonfunctional. My earlier statement needs modification to individual panicle rather than tiller. Another form of adaptive mechanism, activation of a secondary panicle meristem to offset catastrophic yield loss from flowering stage stress, is evident.

Other adaptive mechanisms that prevent catastrophic yield loss are the nonsynchronous development of tillers. Rarely will drought conditions prevail over the full 10 to 14 days flowering period or throughout the 18 to 35 days grain filling period of an individual crop. Cessation of development or delay of critical periods has been suggested as an adaptive mechanism in some cultivars but no definitive study is available to support this contention.

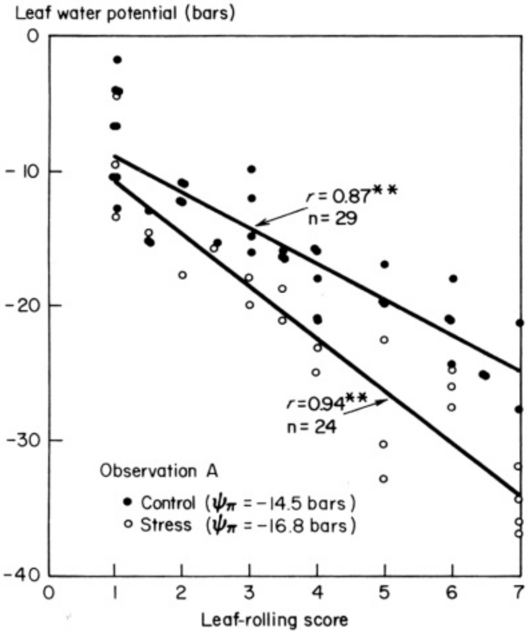
Gametogenesis and panicle initiation are considered less sensitive than flowering, although production of viable gametes and seed number per panicle is determined at these stages. Currently there is no specific adaptation which can be considered more pronounced or functional at these stages. Because of the carbohydrate requirements and the narrow time frame of these events, it appears that water stress may affect these developmental steps through limitations on current assimilate (Fischer 1973, Hsiao et al 1976) rather than through direct effects from water deficits on the tissues involved.

Water deficits in rice during grain filling (0-21 days after flowering) generally produce the expected decreased grain weight. If the current photosynthate supply is limiting, the ability to mobilize and translocate reserves would be adaptive. Reyniers and Jacquot (1978), working in Ivory Coast, showed apparent varietal differences in grain-filling ability during drought but little definitive work exists on the problem or on variation among rice cultivars for this capability.

## INTERACTION AMONG ADAPTIVE MECHANISMS

The complexity of interactions implied in Figure 1 indicates that the subject is well beyond the scope of this paper even if the information were available for rice. Scientists dealing with crops on which sufficient research has been accomplished have attempted to integrate the effects of water stress into crop growth models within which facultative adaptation is an important parameter because of its effects on allocation of dry matter (Loomis et al 1979). The nature of constitutive adaptation is recognized as variation among species in such models. Hsiao et al (1976) pooled information across crops in an effort to illustrate the dynamic interactions between water stress on crop growth, development, and yield. The information dealt with carbon dioxide assimilation and partitioning and expansive growth and with their interactions with crop developmental stages, especially the reproductive stage.

In Figure 1A, several of the adaptive mechanisms result in relatively higher plant water potential. This may be a desirable result if, for example, the increased root growth does not reduce the agricultural goal — economic yield potential. In the case of a constitutive adaptation such as greater root-shoot ratio, it may be argued that the greater allocation per plant of dry matter to the root system will reduce the yield potential by decreasing the proportion of total dry weight in economic yield. However, if, as Yoshida and Hasegawa (this volume) argue, a moderate yield of 3-4 t/ha is an adequate goal in rainfed rice systems, the number of plants per unit area can be agronomically adjusted so that this level of yield is attainable in favorable years. In drought years, the yield decrease will be minimized by the greater root-to-shoot ratio in a given cultivar, even though on a single plant basis it may appear less agronomically desirable because of the low economic-to-total dry weight ratio. In a facultative adaptation such as increased root length density in response to drought (Fig. 2), the result may be very growth



**7.** Relationship between leaf water potential and degree of leaf rolling from leaves of crops with different water stress pretreatment. The turgid osmotic potential ($\Psi\pi$) illustrates the effect of water status history before the observations (Hsiao et al, unpubl.).

stage specific. If assimilates are diverted to increased root growth at the vegetative stage when tiller number is determined, the reduction in yield may be relatively small. Modern rice cultivars produce an abundance of tillers, of which only 30-40% (depending on cultural practices) usually bear panicles. But if the partitioning of assimilates to the root system occurred at flowering, as is the case in Figure 2, the result might be very detrimental (irrigation levels 1, 4, and 6 yielded 0.9, 4.6, and 5.0 t/ha, respectively).

Had a similar stress occurred in the vegetative stage to induce a more extensive root system before the stress at flowering, the detrimental effect on flowering and yield would obviously have been alleviated. Again, we are reminded of the highly dynamic and integrative nature of crop development, especially of the importance of sensitive yield determining stages.

At any stage in crop development, shoot-related adaptive mechanisms that result in relatively higher shoot water status may be negated by their effect on carbon fixation. An interesting interaction between leafrolling (decreases transpiration — stabilizes leaf water potential) and osmotic adjustment of the bulk tissue demonstrates the complex nature of interaction among adaptive mechanisms. Figure 7 illustrates the effect of osmotic regulation of only 2.3 bars (turgid osmotic potential) on the leaf water potential-leaf rolling relationship. The shift in degree of water stress which causes a given level of leaf rolling is related to the osmotic adjustment of the bulliform cells primarily responsible for lateral leaf extension. Presumably, this osmotic regulation has a metabolic cost. But, if it lowers the leaf water potential level at which leaf form begins to change and alters the level at which an equal degree of leaf rolling and interference with carbon dioxide diffusion takes place, the integrative effects on carbon fixation may be a positive net assimilation during a period of drought.

Further appraisal of Figures 1 (A and B) leads to many important possible interactions and to numerous questions that illustrate our lack of knowledge about rice water relations, especially during the reproductive stage.

## CONCLUSION

Numerous aspects of adaptation to water stress in rice have been investigated in recent years. The work has sought to characterize and understand how dryland rice cultivars differ from the semiaquatic majority of cultivars in the rice germplasm pool. Concurrent studies have attempted to explain the growth and yield of various cultivars in response to water deficits. The results of these approaches were not easily rationalized, as they often did not agree on which traits were providing greater drought resistance to the rainfed rice crop.

Research contrasting wetland- and dryland-adapted cultivars illustrated adaptations that showed a spectrum of rice ecotypes, ranging from those with less control of internal water relations to those that appear to have been selected for a higher degree of physiological homeostasis in internal water relations. Walter (1967 cited by Larcher 1980) refers to plants hydrologically adapted in this manner as homoiohydric. Physiological homeostasis is a type of phenotypic reaction whereby organisms do not conform to changes in the external environment but instead resist changes by developing self-regulating processes that maintain the internal condition (water status) at a relatively constant level despite fluctuating external changes. The capability to regulate and stabilize shoot water status by increased water absorption and control of shoot water loss is a basic premise for terrestrial plant adaptation.

In much of the previous work it was assumed that adaptive mechanisms observed in dryland rices were the result of natural selection and thus desirable. An attendant view would be to discard those traits associated with the more primitive or less homoiohydric path of adaptation. However, this approach has been challenged on the grounds that those traits associated with traditional dryland cultivars, although sound from anecophysiological point of view, may not be compatible with the goal of agricultural productivity. This challenge stems from the impressive primary productivity and grain yield response of improved wetland cultivars grown in dryland culture. The improved wetland cultivars do not appear to exhibit the relatively high levels of physiological homeostasis for water status seen in dryland cultivars in the same conditions.

The adaptive mechanisms listed in Figure 1 may be expressed to a greater degree in the homoiohydric dryland ecotypes of rice. However, it is time to question if all adaptations associated with dryland cultivars are really adaptive, given the goals of agricultural productivity. We should also determine which characteristics of wetland-adapted ecotypes might be useful when recombined in a relatively more homoiohydric background.

We need to know enough about the functions of and interactions among these

**Table 1. Turgid osmotic potential measurements from canopy level leaves of 8 diverse rice cultivars. Plants grown during the 1979 dry season in flooded conditions on the IRRI farm and sampled at 56 days of age (n = 5-6).**

| Cultivar | Origin | Osmotic potential[a] (bars) |
|---|---|---|
| 63-83 | Africa - dryland | – 11.2 a |
| IAC 1246 | Brazil - dryland | – 11.6 ab |
| Kinandang Patong | Philippines - dryland | – 11.7 abc |
| Nam Sagui | Thailand - rainfed wetland | – 12.3 abc |
| IR36 | Philippines - irrigated wetland | – 12.5 abcd |
| TN1 | China - irrigated wetland | – 12.9 bcd |
| Mahsuri | Malaysia/India - rainfed wetland | – 12.9 cd |
| Leb Mue Nahng 111 | Thailand - deep water | – 13.7 d |

[a] Values followed by the same letter do not differ significantly at the 5% level by Duncan's Multiple Range Test.

adaptive mechanisms, regardless of ecological origin, to recombine them in such a manner as to maximize our agricultural production goals. That this recombination of traits may not be in keeping with apparent natural selection for drought-prone environments should not dissuade a knowledgeable attempt. One example of a desirable trait that may arise from wetland-adapted germplasm is lower osmotic potential. Perhaps because of a lack of adaptations for control of internal water status, wetland rice has been selected for cellular or protoplasmic types of adaptation not found in dryland cultivars. The constitutive adaptation of relatively lower osmotic potential (Table 1) may be a form of adaptive mechanism found in the wetland ecotypes that, when placed against the background of other homoiohydric mechanisms for maintenance of high water potential and continued evapotranspiration, will yield both a more stable and a more productive plant system.

As in most discussions of this nature, I end by asking, not answering, a question: How do we intelligently evaluate the relative importance of adaptive mechanisms, given the great diversity of drought conditions encountered in various rainfed rice environments?

## REFERENCES CITED

Armenta-Soto, J. L. 1981. Diallel analysis of root characteristics in rice. Unpublished Ph D thesis, University of the Philippines at Los Baños, Philippine.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217

Blum, A. 1982. Evidence for genetic variability in drought resistance and its implications in plant breeding. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Laguna, Philippines.

Chang, T. T., G. C. Loresto, and O. Tagumpay. 1972. Agronomic and growth characteristics of upland and lowland rice varieties. Pages 645-661 *in* International Rice Research Institute. Rice breeding. Los Baños, Philippines.

Chang, T. T., and B. S. Vergara. 1975. Varietal diversity and morpho-agronomic characteristics of upland rice. Pages 72-90 *in* International Rice Research Institute. Major research and upland rice. Los Baños, Philippines.

Chang, T. T., G. Loresto, J. C. O'Toole, and J. L Armenta-Soto. 1982. Strategy and methodology of breeding rice for drought-prone areas. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Laguna, Philippines.

Crawford, R. M. M. 1978. Biochemical and ecological similarities in marsh plants and diving animals. Natunvissenschaften 65:194-201.

De Datta, S. K., and J. C. O'Toole. 1977. Screening deepwater rices for drought tolerance. Pages 83-92 *in* International Rice Research Institute. Proceedings 1976 Deep-water rice workshop, 8-10 November, Bangkok, Thailand. Los Baños, Philippines.

DeWit, C. T. 1958. Transpiration and crop yields. Versl. Landbouwkd. Donderzock. 64.6. 88 p.

Fischer, R. A. 1973. The effect of water stress at various stages of development on yield processes in wheat. Page 233 *in* R. O. Slatyer, ed. Plant response to climatic factors. Proceedings of the Uppsala Symposium, 1970, UNESCO, Paris.

Fischer, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semiarid zones. Ann. Rev. Plant Physiol. 29:277-317.

Hanks, R. J. 1981. Yield and water use relationships. ASA special publication. (in press)

Henson, I. E., and S. A. Quarrie. 1981. Abscisic acid accumulation in detached cereal leaves in response to water stress. I. Effects of incubation time and severity of stress. Z. Pflanzenphysiol. 101:431-438.

Howeler, R. H., and L. F. Cadavid. 1976. Screening of rice cultivars for tolerance to Al-toxicity in nutrient solutions as compared with field screening method. Agron. J. 68:551-555.

Hsiao, T. C., E. Fereres, E. Acevedo, and D. W. Henderson. 1976. Water stress and dynamics of growth and yield of crop plants. Page 536 *in* O. L. Lange, L. Kappen, and E. -D. Schulze, eds. Water and plant life. Springer-Verlag, Berlin.

Hughes, N. F. 1973. Environment ofangiosperm origins. Pages 135-137 *in* Palynology of mesophyte. Proceedings of the 3rd International Palynological Conference (Navosibirsk). Nauka. Moscow.

Hughes, N. F. 1976. Cretaceous paleobotanical problems. Pages 11-21 *in* C. B. Beck, ed. Origin and early evolution of angiosperms. Columbia University Press, New York.

Huxley, J. S. 1963. Evolution: the modem synthesis. London, Allen and Union Publishers. 652 p.

Ikehashi, H., and F. N. Ponnamperuma. 1978. Varietal tolerance of rice for adverse soils. Pages 801-823 *in* International Rice Research Institute. Soils and rice. Los Baños, Philippines.

IRRI (International Rice Research Institute). 1974. Annual report for 1973. Los Baños, Philippines. 266 p.

IRRI (International Rice Research Institute). 1975a. Annual report for 1974. Los Baños, Philippines. 384 p.

IRRI (International Rice Research Institute). 1975b. Major research in upland rice. Los Baños, Philippines. 255 p.

IRRI (International Rice Research Institute). 1976. Annual report for 1975. Los Baños, Philippines. 479 p.

IRRI (International Rice Research Institute). 1977. Annual report for 1976. Los Baños, Philippines. 418 p.

IRRI (International Rice Research Institute). 1978. Annual report for 1977. Los Baños, Philippines. 548 p.

IRRI (International Rice Research Institute). 1979. Annual report for 1978. Los Baños, Philippines. 478 p.

IRRI (International Rice Research Institute). 1980. Annual report for 1979. Los Baños, Philippines. 538 p.

Krishnamurthy, Ch., S. V. S. Shastry, and W. H. Freeman. 1971. Breeding rice for tolerance to drought and salinity. Oryza 8(2):47-54. (suppl.)

Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, Berlin. 303 p.

Loomis, R. S., R. Rabbinge, and E. Ng. 1979. Explanatory models in crop physiology. Ann. Rev. Plant Physiol. 30:339-367.

Namuco, O. S., and J. C. O'Toole. 1980. Effect of water stress on panicle emergence in rice. Paper presented at the American Society of Agronomy meeting, Nov. 30-Dec. 5, 1980, Detroit, Michigan.

Nishiyama, I., and L. Blanco. 1980. Avoidance of high temperature sterility by flower opening in the early morning. JARQ 14:116-117.

Nobel, P. S. 1980. Leaf anatomy and water use efficiency. *In* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York.

Oka, H. 1958. Photooeriodic adaptation to latitude in rice varieties. Phyton 11(2):153-160.

O'Toole, J. C., R. S. Aquino, and K. Alluri. 1978. Seedling stage drought response in rice. Agron. J. 70:110l-1103.

O'Toole, J. C., and T. T. Chang. 1979. Drought resistance in cereals: Rice - a case study. Pages 373-406 *in* H. Mussell and R. C. Staples, eds. Stress physiology of crop plants. Wiley-Interscience, New York.

O'Toole, J. C., R. T. Cruz, and T. N. Singh. 1979a. Leaf rolling and transpiration. Plant Sci. Lett. 16:111-114.

O'Toole, J. C., R. T. Cruz, and J. N. Seiber. 1979b. Epicuticular wax and cuticular resistance in rice. Physiol. Plant. 47:239-244.

O'Toole, J. C., and R. T. Cruz. 1980. Response of leaf water potential, stomatal resistance and leaf rolling to water stress. Plant Physiol. 65:428-432.

Quarrie, S. A., and I. E. Henson. 1981. Abscisic acid accumulation in detached cereal leaves in response to water stress. II. Effects of leaf age and position. Z. Pflanzenphysiol. 101:453-460.

Reyniers, F. N., J. M. Kalms, and J. Ridders. 1976. Differences de comportement d'un riz pluvial et d'un riz irrigue; en condition d'alimentation hydrique deficitaire. 1. Etude des facteurs permettant d'esquiver la secheresse. L'Agron. Trop. 31(2):179-187.

Reyniers, F. N., and M. Jacquot. 1978. Demarche pour l'obtention de la resistance varietale a la secheresse: cas du riz pluvial. L'Agron. Trop. 33(4):314-317.

Satake, T., and S. Yoshida. 1978. High temperature-induced sterility in Indica rice at flowering. Jpn. J. Crop Sci. 47:6-17.

Steponkus, P. L., J. M. Cutler, and J. C. O'Toole. 1980. Adaptation to water stress in rice. *In* N. C. Turner and P. I. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Steponkus, P. L., K. W. Shahan, and J. M. Cutler. 1982. Osmotic adjustment in rice. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Laguna, Philippines.

Stewart, C. R., and A. D. Hanson. 1980. Proline accumulation as a metabolic response to water stress. *In* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Takhtajan, A. 1969. Flowering plants: origin and dispersal. Oliver and Boyd, Edinburgh.

Taylor, H. M. 1980. Modifying root systems of cotton and soybean to increase water absorption. In N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. Pages 343-372 *in* H. Mussel and R. C. Staples, eds. Stress physiology of crop plants. Wiley-Interscience, New York.

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustment: A review and evaluation. *In* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Vergara, B. S., and T. T. Chang. 1976. The flowering response of the rice plant to photoperiod: a review of literature. Int. Rice Res. Tech. Bull. 8. Los Baños, Philippines.

Yoshida, S. 1977. Rice. Pages 57-87 *in* Paulo de T. Alvim and T. T. Kozlowski, eds. Ecophysiology of tropical crops. Academic Press, New York.

Yoshida, S., and E. de los Reyes. 1976. Leaf cuticular resistance of rice varieties. Soil Sci. Plant Nutr. 22(1):95-98.

Yoshida, S., and S. Hasegawa. 1982. The rice root system: its development and function. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Laguna, Philippines.

# BREEDING AND SELECTION APPROACHES FOR DROUGHT-PRONE AREAS—RICE

# STRATEGY AND METHODOLOGY OF BREEDING RICE FOR DROUGHT-PRONE AREAS

T. T. CHANG, G. C. LORESTO, J. C. O'TOOLE,
AND J. L. ARMENTA-SOTO

Cultivated rices encompass enormous genetic diversity. Similarly, rice-growing environments include a wide spectrum of variation in climatic, hydrological, and edaphic conditions. Because drought is a common production constraint to different types of rice culture, rice plant responses to drought should be examined by a diagnostic approach.

The primary goals, multidisciplinary approach, and progress of IRRI's breeding program to improve and stabilize rice yields for drought-prone areas are enumerated. Performance evaluation across environments and seasons is a useful tool in assessing the progress of our breeding program.

Genetical and physiological studies are undertaken to gain a more complete understanding of the complex problem of varietal responses and environmental interactions. This knowledge will help achieve genetic improvement under a wide spectrum of water stress and related adverse environments.

Areas for future endeavor are suggested on both international and interinstitutional bases.

## IMPORTANCE OF DROUGHT TO RICE PRODUCTION

Distant progenitors of cultivated rices (*Oryza sativa* L. and *O. glaberrirna* Steud.)

---

The International Rice Research Institute, Los Baños, Philippines, and Centro de Investigaciones Agricolas de Sinaloa, Apdo. Postal Num. 356, Culiacan, Sinaloa, Mexico.

were semiaquatic. Through several millenia of eco-genetic differentiation and adaptation, both cultigens evolved into numerous ecotypes adapted to dryland, shallow-wetland, and deepwater-wetland cultures (Chang 1976a, 1976b; O'Toole and Chang 1979). This diversity in cultivated rices has lent great impetus to research on drought resistance (O'Toole and Chang 1979) as well as on other climatic stresses, biotic stresses, and adverse soil factors (IRRI 1974b, Chang et al 1975, Ikehashi and Ponnamperuma 1978, Chang 1980).

Large tracts of rainfed (nonirrigated) fields are found in South Asia, Southeast Asia, South America, and West Africa. About 73 million hectares of the world's 141 million hectares of rice land are rainfed. Rainfed rice is grown on 59 million hectares, 67% of the total rice hectarage, in South and Southeast Asia. The proportion of rainfed rice to total rice grown increases to nearly 90% in South America and Africa (Barker and Herdt 1979, Huke and Huke 1981).

Because of climatic vagaries, substantial portions of the rainfed rice areas suffer from water deficits or excesses. An earlier paper (O'Toole et al 1982) discussed the importance of drought to rice production. Hsieh and Ruttan (1967), in a case study of three countries (Philippines, Taiwan, and Thailand), showed the significance of water deficits to fluctuations in rice production.

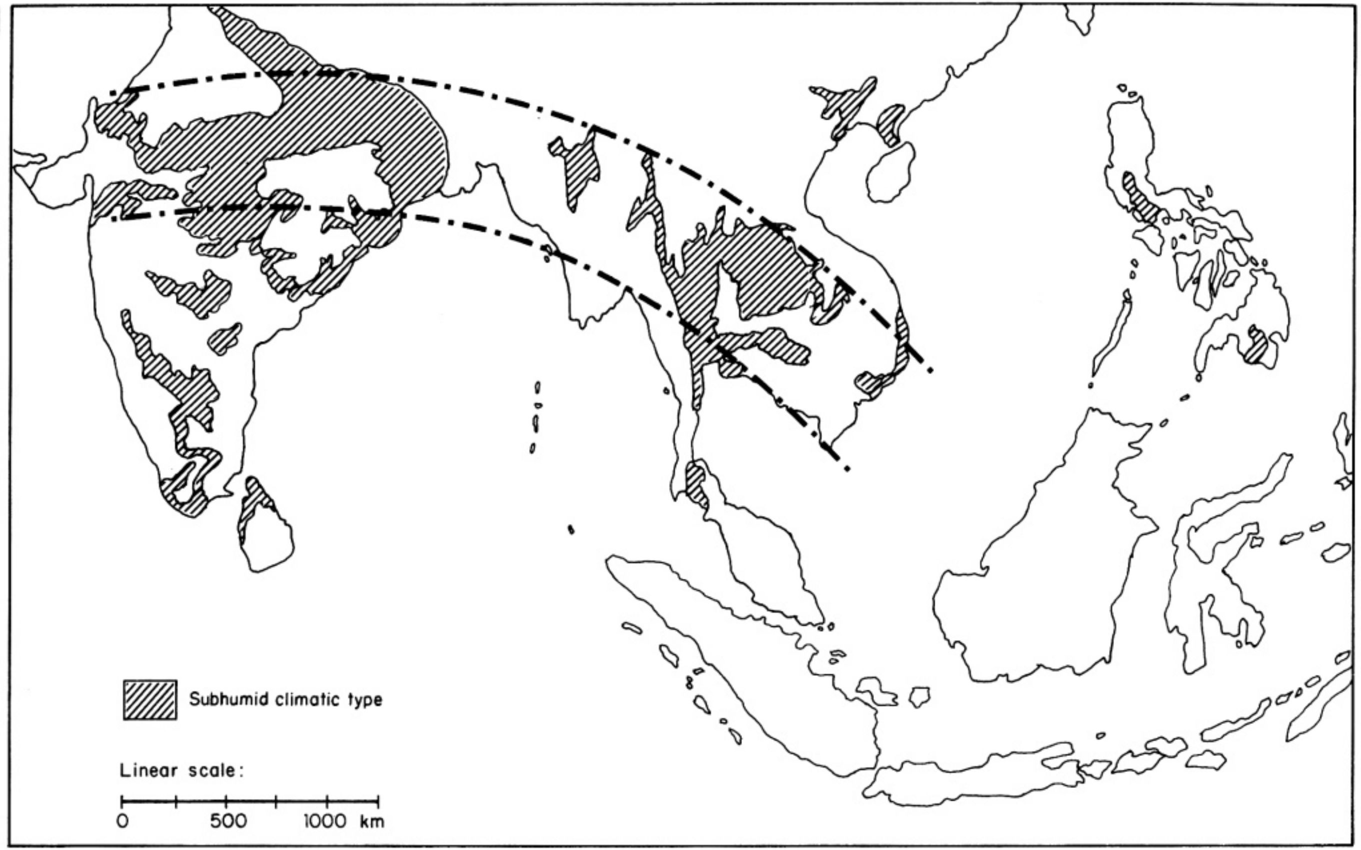
Drought and flood frequently alternate within a crop season. This cyclic incidence has confounded the interpretation of the effect of water stresses on rice yields. In many instances, the ability of a rice genotype to recover from water deficit largely determines the final grain yield (Chang et al 1974, Loresto et al 1976). This recovery aspect frequently overshadows the contribution of drought resistance to rice yield.

## DIAGNOSTIC APPROACH TO THE STUDY OF RICE RESPONSES TO DROUGHT

Much of our research has been directed toward the types of drought found in a wide belt stretching across South and Southeast Asia (Fig. 1). These drought-prone rice-growing regions correspond to the subhumid climatic type of Thornthwaite (Carter and Mather 1966). Within this geographic region, the early vegetative stage and the reproductive stages of flowering and grain filling are most commonly affected by water deficits. Water stress at the tillering stage is less significant. Direct-seeded or transplanted rice may be adversely affected by the erratic onset of monsoon rains if the crop has not yet developed a sufficiently large root system to cope with evaporative demand. Water stress in the sensitive reproductive stages —flowering and grain filling — reduces yield components for which the crop has no means of compensation or replacement.

The characterization of type of drought or drought profile requires further basic division in addition to large spatial (geographic-climatic units) and temporal (growth stages) limits.

More specific hydrological characterization of rice-growing conditions in the target areas leads to a basic separation of dryland (upland) and wetland (lowland) sites. O'Toole and Chang (1978) illustrated the array of edaphic, climatic, hydrologic, biotic, and agronomic descriptors of these contrasting rice environments. The major hydrological differences are:



**1.** Areas in South and Southeast Asia representing the subhumid climatic type of Thornthwaite. The belt across the region illustrates the target area where vast hectares of drought-prone rice are grown (adapted from Carter and Mather 1966).

- Dryland rice in Asia, generally cultivated in areas where soils are deep but light textured. The land is prepared dry and remains aerobic most of the growing season. Direct rainfall is the major source of crop water requirements.
- Wetland rice, characterized by shallow clay soils with a distinct hard pan. Soils frequently are puddled and remain primarily in anaerobic conditions during the growing season. Direct rainfall, surface and subsurface interflow, and water table are sources of the crop water requirement.

Our discussion will deal with breeding and selecting for drought resistance in dryland and wetland conditions, even though these divisions are not well-delineated because of inherent hydrological variation across locations and within as well as across years at the same location.

Directing research for such a vast region as South and Southeast Asia, as is the mandate of the International Rice Research Institute, has inherent limitations. The lack of a clear description of hydrological conditions and crop phenological stages affected by water deficits is one of the acute problems faced by national, regional, or international research centers.

We are fully aware of these limitations. Nevertheless, we feel that our program in crop improvement for drought resistance has been instrumental in developing awareness of genotypic variations of response to this physically-based environmental stress, in elucidating the underlying causes or adaptive mechanisms, in developing and testing practical breeding and selection methods, and in initiating genetic studies which will provide fundamental information upon which breeding methods, selection criteria, and screening methods eventually will be refined.

In this paper we discuss our interdisciplinary efforts toward understanding the complex problem of drought responses and improving the genetic capability of a rice plant to cope with a wide spectrum of water stresses and related adverse environments.

## GOALS AND APPROACHES IN RICE BREEDING

Resistance to drought and recovery from water deficit constitute essential links in the long, complex process of grain production. Drought resistance determines the base yield under stress while recovery prescribes the upper potential after stress. An extremely high level of drought resistance is frequently associated with low yield capacity. Outstanding recovery ability requires a vigorous vegetative growth and a prolonged maturity (Chang et al 1974, Chang and Vergara 1975, Loresto et al 1976). Moreover, drought resistance and recovery ability frequently are negatively correlated in rice cultivars (IRRI 1971; Chang et al 1972,1974; Loresto et al 1976). Breeding programs should consider incorporating resistance and recovery components in specific combinations so that both a realistic yield potential and a stable production level can be attained under a given set of environmental conditions. The environment-specific nature of rice production in various drought-prone areas presents breeders with difficulties and challenges in coping with production constraints.

## Exploratory research on drought resistance

IRRI research on drought resistance began in the early 1970s. A 20-variety set of dryland and wetland cultivars was compared under 2 water regimes (IRRI 1971, Chang et al 1972). It soon became apparent that varietal variation in morphoagronomic traits was a continuum, although several traits were genotypically correlated at the extremes.

A high level of field resistance to drought was associated with low tillering ability, tall plant stature, deep and thick roots, large plasticity in leaf rolling and unrolling, full panicle development and exsertion, and uninterrupted grain development under water stress — a complex of traits generally found in traditional Southeast Asia dryland varieties.

On the other hand, the plant's ability to recover from drought was associated with good tillering ability, low plasticity in leaf rolling and unrolling, tolerance for desiccation, delayed heading, and decreased grain size and weight under water deficit — manifestations common in traditional wetland varieties and high-yielding semidwarfs.

Another group of early-maturing varieties grown under alternately wet and dry cycles had a combination of moderate levels of drought resistance and the escape mechanism of earliness — the traits of low-yielding aus varieties and the Assam collections of South Asia.

In comparing dryland and wetland cultures, we identified a negative association between drought resistance and recovery ability, the genotype-environment interactions of root development, and the differential patterns in panicle and grain development among variety groups (IRRI 1971, 1972, 1974a; Loresto and Chang 1971; Chang et al 1972).

We developed a mass screening technique under dryland culture and devised a scoring system based on leaf rolling and unrolling and the death of lower leaves as well as of the reproductive system (IRRI 1971, 1972, 1973, 1974a; Chang et al 1972, 1974; Loresto et al 1976; Loresto and Chang 1981). The reliability of the screening technique, which largely reflects a root system consisting of deep and thick roots, has been verified by studies on leaf water potential (O'Toole and Moya 1978, O'Toole and Cruz 1980) and root characteristics of plants grown in the field, tubes, or boxes (Loresto and Chang 1971; IRRI 1971, 1972, 1975; Parao et al 1976). When the mass screening was expanded to simulated rainfed-wetland culture, where the soil is puddled and the plants transplanted, we found a high level of correlation between dryland and wetland tests (IRRI 1977, 1978; Chang et al 1979). This commonality has added scope to mass screening efforts.

Testing of young seedlings in the phytotron revealed a broad spectrum of varietal reactions to desiccation. Such reactions correlated with varietal resistance in deepwater culture where the seedlings frequently experience severe water stress shortly after emergence (De Datta and O'Toole 1977, O'Toole et al 1978). This technique has been modified and incorporated as a vital test in the breeding of deepwater rices.

## Breeding objectives for different hydrologic-edaphic regimes

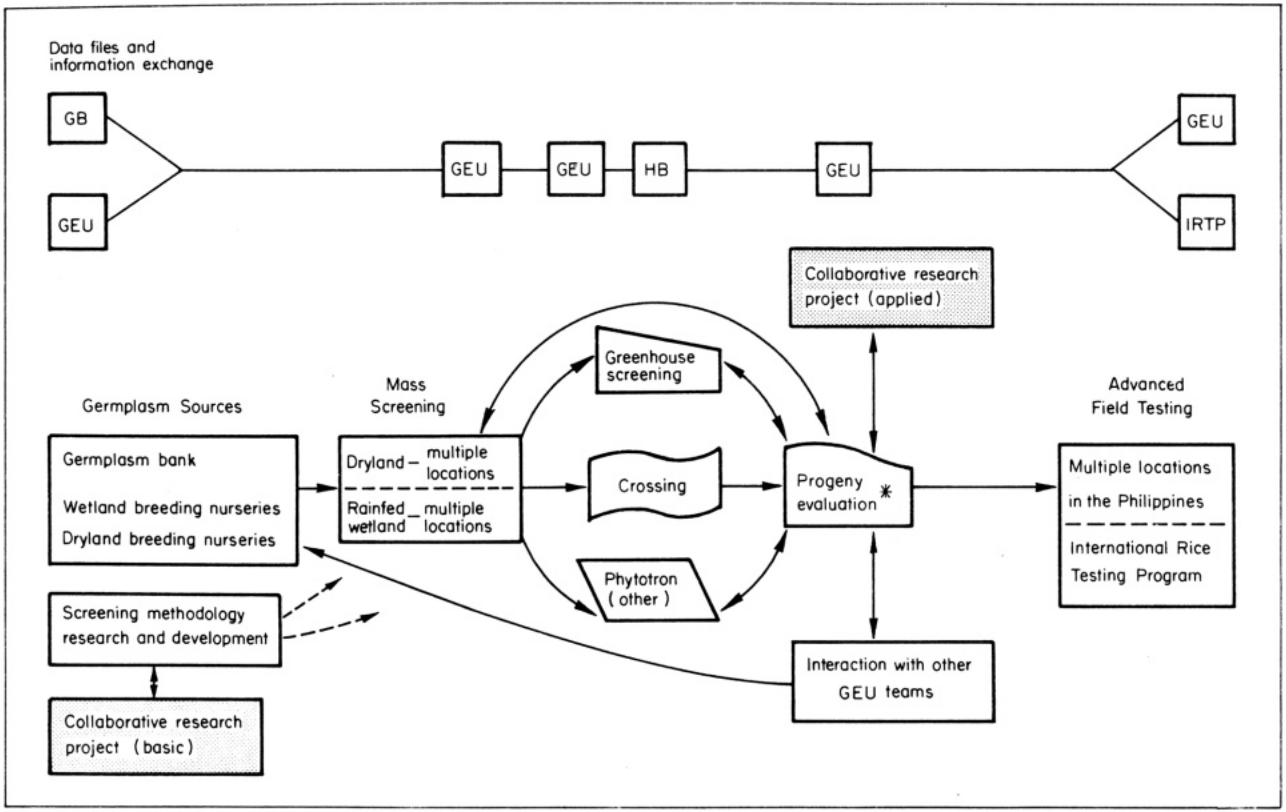
*Rainfed-dryland culture.* For the drought-prone areas where drought resistance is conferred primarily by deep and thick roots, maintenance of favorable leaf water potential and early maturity are the principal objectives. Plant stature should be moderately tall, so that height will remain 1 m or above under stressed conditions. Moderately long and droopy leaves are most plastic in leaf rolling and unrolling and may help conserve water in plant tissues. Seedling vigor is needed for good stand establishment. Leaf droopiness may help young rice plants compete with weeds. Tillering ability should be moderate and rather plastic so that plants may use the extra water and nutrients in a wet year. A moderate level of recovery ability would be helpful when rainfall distribution is erratic. High ratios of root to shoot weight and grain to straw (harvest ratio) are desirable. Since rice grown on dryland farms is largely consumed at home by subsistence farmers, popular preference for rather long and well-exserted panicles, nonshattering habit, medium-to-bold grains, and around 25% amylose content should be observed (Chang and De Datta 1975). Blast resistance is a general requirement. Many dryland soils are high in acidity and present such problems as manganese and aluminum toxicities and iron deficiency.

*Rainfed-wetland culture.* Other than in deepwater areas and areas with stagnant water, the cultural system for rainfed-wetland rice is essentially the same as for irrigated rice. Drought resistance and recovery ability are two important requisites for adaptation and yield stability. Deep and thick roots may help extract water nutrients from the subsoil, but their effectiveness is less than under dryland culture because of the prevalence of hardpan below the topsoil. Early maturity *per se* or a restricted growth duration imposed by photoperiod sensitivity also provides adaptiveness to a sharp cutoff in precipitation. Intermediate tillering ability, medium panicle size, and full panicle exsertion generally are preferred by farmers (Chang et al 1979). Weed competition generally is serious under alternating wet and dry cycles. This culture shares the same syndrome of diseases and insects as an irrigated culture. Adverse soil factors occur frequently. An intermediate plant stature (about 1.2 m) is desirable to cope with large variations in water depth and water deficit.

*Irrigated culture.* Rice fields may be completely or partially supplied with irrigation water, more likely partially in tropical areas. A substantial portion of the irrigated areas of South and Southeast Asia annually suffers from water deficits. However, stress periods are shorter than in the rainfed areas. Recovery ability may be more important than drought resistance.

## Breeding strategies at IRRI

The primary strategy of IRRI's Genetic Evaluation and Utilization (GEU) Program is to exploit full use of gene pools in diverse rice germplasm to cope with one or more production constraints. Research efforts are multidisciplinary (IRRI 1974b, Brady 1975). Our approach is to identify genotypic responses to drought which can be selectively hybridized and recombined to develop an array of genotypes adapted to various needs of drought-prone areas. In this manner, we not only use drought resistance and recovery components existing in the germplasm collection but also biotic resistances and eco-edaphic tolerances identified by GEU teams. Figure 2 shows the schematic flow of activities.



**2.** Schematic representation of activities representing the drought resistance component of IRRI Genetic Evaluation and Utilization program.

The hub of GEU activities is the germplasm collection; the operational link for various GEU traits is hybridization. Rice breeders and problem-area scientists (agronomists and plant physiologists) jointly plan the kinds of crosses that will meet breeding objectives. The breeders then choose a broad array of parents which will provide the projected inputs as well as other related inputs, such as disease resistance, insect resistance, grain quality, and tolerance for adverse soils. The physical aspects of crossing, selecting, and recrossing are handled by the breeders, but many of the tests are performed by problem-area scientists. Experimental results are periodically reviewed to provide the basis for the next planting.

Meanwhile, more critical studies are conducted to develop better techniques or to reveal the nature of varietal differences. For more academic problems, the assistance and cooperation of scientists in universities or research institutions of the developed countries is sought. For multi-location testing, we collaborate with scientists in national programs at sites where a constraint is chronic. The International Rice Testing Program (IRTP) and the collaborative research projects provide the avenue for international cooperation.

Parental materials come from these categories:

- Cultivars with high levels of drought resistance and tolerance for certain adverse soil factors, furnished by traditional dryland varieties of mainland Southeast Asia and West Africa.
- Some dryland cultivars grown at high elevations with tolerance for low night temperatures.
- Several Japanese dryland varieties with good drought resistance.
- Early-maturing cultivars of South Asia and several varieties from China with moderate levels of drought resistance and with escape mechanisms—dual-purpose types.
- Traditional rainfed-wetland varieties of Southeast Asia with excellent recovery abilities.
- Semidwarf IR varieties and lines with high-yielding backgrounds, excellent recovery abilities, and high Levels of pest resistance. Shallow root systems (IRRI 1977) may aid semidwarfs to recover quickly after light showers.

Many improved varieties released by national centers in recent years also have excellent recovery ability.

Mass screening is carried out in the dry seasons for drought resistance and recovery ability present in the germplasm collection, in breeding materials developed in both dryland and wetland nurseries, and in many IRTP entries. During the main crop season (wet season), agronomic evaluation and drought screening are made at several sites in the Philippines and in collaborative nurseries representing a series of hydrologic-edaphic environments. We can identify relatively drought-resistant lines among those produced in the wetland nurseries that can fit into rainfed-wetland situations. Selection of progenies at drought-prone sites identifies truly resistant genotypes when water deficit does occur. If no water deficit occurs, yield potential under a more favorable environment may be identified. By diagnosing environment factors prevailing in different drought-prone areas, we are in a better position to incorporate specific drought-resistant mechanisms and recovery abilities into the breeding populations.

## PROGRESS AND CONSTRAINTS IN BREEDING

### Identification of parents and hybridization

Mass screening for drought resistance under dryland culture began at IRRI in 1974 (Chang et al 1974). Hybridization started in 1972. About 16,500 accessions from the germplasm bank have been screened and data on vegetative phase responses obtained. Data for the reproductive phase have been obtained on only 6,193 entries, as early showers in April disrupt the water stress period.

Breeding lines have been tested on 10,093 entries. Moreover, about 2,500 both unimproved and improved entries have been screened under simulated rainfed-wetland culture.

Varietal reactions on 28,744 varieties and lines obtained in the dryland screening tests from 1973 to 1980 are summarized in Table 1. The data show that large numbers of highly resistant entries were readily identified at the vegetative stage, while rather few entries were found resistant at the reproductive stage. Traditional varieties which showed resistance at the reproductive phase came mostly from Brazil, India, Laos, and West Africa.

During 1972-80 we made 3,849 crosses. In single crosses made in early years, one parent was a traditional dryland variety chosen from the drought-resistant entries in the mass screening test while the other was a semidwarf with high levels of disease and insect resistance. Such small numbers of desirable progenies were obtained from traditional dryland/semidwarf crosses (IRRI 1974a, 1975, 1976) that we soon switched to 3-way and double-crosses, frequently involving a line selected from the single-crosses as one parent.

Genetic studies using *gh* (gold hull), *gl* (glabrous leaf), and *wx* (waxy) loci as gene-markers revealed that inviability of $F_1$ seeds, partial sterility of $F_1$ plants, and aberrant segregation in $F_2$ populations were involved. Homozygous recessive genotypes were deficient in $F_2$ samples of dryland/semidwarf crosses (Hung and Chang 1976). Later studies also showed that the typical 3 (tall):1 (semidwarf) segregation ratio did not show up in the $F_2$ populations of tall/semidwarf crosses (Lin and Chang 1981). While different kinds of chromosomal aberrations were detected at meiosis, the frequencies were not high enough to account for the partial $F_1$ sterility and the atypical $F_2$ segregation (Barrios 1981). However, as more crosses were made on derivatives of the single-crosses, we gradually overcame the problems of $F_1$ inviability, partial sterility, and atypical segregation.

### Heritability of drought resistance

One question frequently is asked: Is the complex trait of drought resistance heritable? Because drought scores obtained in field experiments varied by 1 or 2 decimal codes in different seasons and because control conditions were difficult to maintain over seasons, genetic studies were difficult to implement. Partial sterility and aberrant segregation also made genetic studies on wide crosses impractical.

However, from hundreds of crosses we were able to establish that drought-resistant progenies would appear at higher frequencies in crosses having one resistant dryland parent than in semidwarf/semidwarf crosses within the wetland group (IRRI 1976). Table 2 compares 11 groups of crosses.

**Table 1. Summary of field scores on drought resistance of 28,744 varieties and lines, IRRI Plant Breeding Department, 1973-80 dry seasons.**

Part A

| Groups | Entries (no.) | Entries (no.) with given vegetative score | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Germplasm bank accessions[a] | 16,509 | 68 | 428 | 1038 | 3003 | 6337 | 4689 | 900 | 43 | 3 |
| Dryland breeding lines | 6,548 | 155 | 286 | 682 | 1593 | 2545 | 1174 | 104 | 9 | |
| Wetland breeding lines | 3,545 | | 1 | 46 | 325 | 1321 | 1469 | 322 | 54 | 7 |
| Breeding lines from other countries | 886 | | 3 | 40 | 152 | 323 | 291 | 60 | 11 | 6 |
| Entries in international nurseries | 459 | | 1 | 3 | 32 | 138 | 166 | 80 | 4 | 35 |
| *Oryza glaberrima* strains | 797 | 5 | 265 | 63 | 73 | 237 | 136 | 17 | 1 | |

| | | Entries (no.) with given reproductive score | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Germplasm bank accessions | 6,193 | 10 | 24 | 186 | 183 | 517 | 319 | 1571 | 713 | 2670 |
| Dryland breeding lines | 2,855 | | | 14 | 15 | 147 | 149 | 1111 | 633 | 786 |
| Wetland breeding lines | 2,058 | | | 1 | 2 | 49 | 52 | 674 | 348 | 932 |
| Breeding lines from other countries | 417 | | | 12 | 11 | 37 | 13 | 87 | 23 | 234 |
| Entries in international nurseries | 144 | | 1 | 2 | 3 | 8 | 7 | 55 | 9 | 59 |
| *Oryza glaberrima* strains | 350 | | | 121 | 46 | 28 | 15 | 54 | | 86 |

[a] 13,494 accessions have field drought scores and recovery data in the GB file. About 3,000 accessions were either duplicates or were retested 2 to 3 times.

**Table 2. Distribution of $F_4$-$F_8$ dryland and breeding lines by field reaction to drought. IRRI, 1975 dry season.**

| Type of cross | Lines (no.) | Frequency of reaction[a] | | | | | |
|---|---|---|---|---|---|---|---|
| | | R | MR | I | MS | S | X[b] |
| Dryland/wetland | 138 | 9 | 64 | 50 | 10 | | 5 |
| Dryland/wetland//dryland | 2 | | 2 | | | | |
| Dryland/wetland//wetland | 14 | | 11 | 3 | | | |
| Wetland/dryland//dryland/wetland | 4 | | 3 | 1 | | | |
| Dual-purpose/dryland//wetland/dryland | 10 | | 7 | 2 | | | 1 |
| Dual-purpose/dryland///wetland/dryland//dryland | 3 | | 1 | | 2 | | |
| Dual-purpose/wetland//dual-purpose/dryland | 2 | | | 2 | | | |
| Dual-purpose/wetland//wetland/dryland | 71 | | 24 | 12 | | | 35 |
| Wetland/wetland//dryland/wetland | 24 | | 7 | 9 | | | 8 |
| Wetland/wetland//wetland/wetland | 8 | | | 2 | | | 6 |
| Wetland/wetland | 46 | | 17 | 29 | | | |

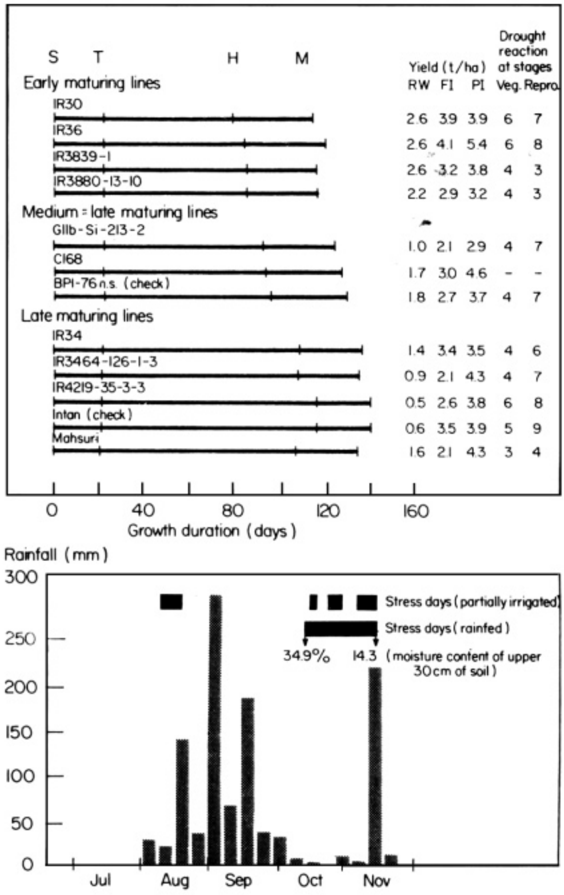
[a] R = resistant, MR = moderately resistant, I = intermediate, MS = moderately susceptible, S = susceptible.
[b] Questionable reaction due to unevenness in soil moisture distribution as indicated by the control varieties.

Multilocation dryland tests in several national programs under the International Rice Testing Program reported breeding lines such as IR1746-226-1 (OS4/IR8), IR1750-F5B-5 (E425/IR22), IR3839-1 (Pelita 1-2/1R1529-680-3//IR442-2-58/Rikuto Norin 21), and IR5178-1-1-4 (IR1746-194-1/IR1487-372-4) outstanding in drought resistance (IRRI 1980, 1981b; Singh and Singh 1980). These lines can be traced back to one of the drought-resistant parents identified at IRRI: OS4, E425, and Rikuto Norin 21 (IRRI 1976, 1979). Similarly, IR52 (IR5853-118-5) has been identified as adapted to rainfed-wetland areas where drought may be a factor. This line was repeatedly given a relatively high score in different drought tests. One of its parents is Nam Sagui 19, a popular variety grown in drought-prone northeast Thailand (IRRI 1980). The group of drought-resistant IR3880 lines also can be traced to Khao Dawk Mali 105, another major variety in northeast Thailand.

## Drought resistance and agronomic performance

Drought resistance and recovery ability are evaluated in the dry season, when environmental conditions do not permit a realistic assessment of yielding ability. While agronomic performance is evaluated in the wet season, the total precipitation and rainfall distribution are so variable from year to year that agronomic performance cannot be equated with drought resistance. When we deal with a relatively small number of entries, we grow one set of genotypes at a well-drained site at IRRI where water stress frequently occurs during the wet season. Another set is grown in an irrigated field or in a dryland field with a high water table. The relative reduction in yield due to water stress is used to assess the relationship between drought resistance and yield performance.

In recent years we have conducted multilocation tests of wetland and dryland culture. Precipitation and stress days are monitored, along with the routine agronomic counts and measurements. We use a combination of three factors to compare genotypes: 1) the timing and length of water stress in relation to the reproductive stages, 2) grain yield obtained under different water regimes or at different sites, and 3) drought reactions scored at vegetative and reproductive stages during the dry season. Figure 3 illustrates this approach in an experiment involving three regimes under rainfed-wetland culture (Chang et al 1979). This form of multicriteria comparison has provided more meaningful interpretations of varietal differences in agronomic performance related to drought than comparison of absolute yields. The method also takes into consideration the recovery factor as an important determinant of grain yield.



**3.** Rainfall distribution, stress days, growth duration, drought reactions, and yields of 12 rices tested at Gapan, Nueva Ecija Province, Philippines, 1977 wet season. S = seeding, T = tillering, H = heading, M = maturity, R = rainfed wetland, FI = fully irrigated, PI = partially irrigated.

## Overall progress and constraints in breeding

During the last 5 years we have upgraded the yield potential in drought-resistant dryland lines from the 2 t/ha upper limit of traditional varieties to nearly 3.5 t/ha in lines having an intermediate plant height and moderate blast resistance. These lines have intermediate (20-25%) amylose content. Some lines are resistant to brown planthopper biotype 1 and moderately resistant to bacterial blight and sheath blight. IR3880-29 (IR841-67/C22//Pelita 1-2/IR1541-76), IR5931-110 (Monolaya/IR1487-372-4//MRC 172-9), and IR6023-10-1 (BPI-76*9/Dawn //LAC23) have ranked among the top 5 in performance at IRTP dryland nurseries in Bangladesh, India, Philippines, and Thailand (IRRI 1981b). IR5178-1-1-4 (IR1746-194-1-1-1/IR1487-372-4) has demonstrated outstanding levels of drought resistance but its yield potential is slightly under 2 t/ha because of its low tillering ability (Singh and Singh 1980, IRRI 1980).

Among lines which combine a moderate level of drought resistance and good recovery ability, yield potential is around 4 t/ha — comparable to semidwarf IR43 and IR45. These lines include IR3839-1 (Pelita I-2/IR1529-680-3//IR442-2-58/RN21), IR3880-13 (IR841-67/C22//Pelita I-1/IR1541-76), IR3880-29, and IR6115-1-1-1 (IR1529-680/Moroberekan). The lines are still deficient in resistance to green leafhopper, whitebacked planthopper, and some diseases prevalent in wetland culture.

IR1754F5B-23 (E425AR8) has been shown highly tolerant of manganese and aluminum toxicities. IR7760-4-8 (Aus 81/IR1750-F5B-3//IR2035-290-2-1-1) has been reported tolerant of iron deficiency (IRRI 1977, 1979).

Only a few experiment stations in South and Southeast Asia conduct breeding programs designed to develop drought-resistant rices. Among dryland testing sites under the IRTP, many locations have annual precipitations above 1,000 mm or a protracted wet season. Top performers in the yield trials were dominated by high-yielding semidwarfs such as IR43 and IR45, which were bred under wetland nurseries, or by a number of improved varieties with intermediate plant stature and excellent recovery ability, such as C22 and BPI-76 (n.s.). The yield performance of such lines was discussed by De Datta and Seshu (this volume). However, farmers in drought-prone areas have not shown interest in semidwarf lines because severe water stress greatly reduces plant stature, delays maturity, and results in small, shriveled grains (Janaand De Datta 1971, IRRI 1973, Chang et al 1974).

In our collaborative ventures we also find that competently trained workers who can characterize drought responses and provide environment-based interpretations are scarce. Resources at the small number of experiment stations in drought-prone areas are inadequate to make crosses and conduct breeding operations.

To augment the breeding activities at national centers and at other international centers, we have made hundreds of crosses for Brazil, India, Liberia, Thailand, and the International Institute of Tropical Agriculture (IITA). We also have provided seeds for drought screening nurseries. Again, high sterility in the traditional/semidwarf crosses was found.

## Yield performance across environments

Yield stability indexes (*b*) using simple linear regression were computed for 21

**Table 3. Stability index (*b*), coefficient of determination ($R^2$), mean grain yield, and mean maturity days of 21 varieties tested in 12 environments (4 years × 3 sites), 1977-80.**

| Variety or line name | *b* | $R^2$ | Mean yield (t/ha) | Days to maturity (mean) |
|---|---|---|---|---|
| IR36 | 0.9884** | .81 | 1.9 | 118 |
| IR43 | 1.4028** | .83 | 2.8 | 132 |
| IR45 | 1.1679** | .87 | 2.4 | 135 |
| IR3646-9-3-1 | 1.023** | .93 | 2.1 | 129 |
| IR3839-1 | 1.346** | .82 | 2.4 | 118 |
| IR3858-6 | 0.8896** | .77 | 2.0 | 131 |
| IR3880-10 | 1.0771** | .93 | 2.4 | 129 |
| IR3880-17 | 0.9921** | .77 | 2.2 | 128 |
| IR3880-29 | 1.135** | .89 | 2.0 | 116 |
| IR5178-1-14 | 0.7884** | .57 | 1.6 | 116 |
| IR5179-2 | 1.006** | .94 | 1.9 | 118 |
| IR5260-1 | 0.9248** | .86 | 1.9 | 117 |
| IR5716-18-1 | 1.0656** | .93 | 2.0 | 124 |
| IR5982-7-6-1 | 1.1410** | .88 | 2.2 | 130 |
| IR6115-1-1-1 | 1.4198** | .93 | 3.0 | 130 |
| IR7805-22-3-1 | 0.7716** | .86 | 1.8 | 131 |
| IR7805-22-3-2 | 0.7086** | .82 | 1.7 | 130 |
| IR9669 selection | 1.3408** | .87 | 2.9 | 132 |
| MRC438 (BPI-Ri-6) | 0.9272** | .86 | 2.2 | 132 |
| UPL-Ri-5 (C171-136) | 1.012** | .93 | 2.3 | 134 |
| Kinandang Patong | 0.6743** | .76 | 1.4 | 126 |

varieties tested in 12 environments (4 years × 3 sites) from 1977 to 1980 in a farmer's field at Batangas Province and at 2 sites on the IRRI farm. The coefficient of determination was computed. Table 3 shows the stability index, mean yield, and mean days to maturity.

Among the high yielding varieties, IR6115-1-1-1 had the highest mean (3 t/ha). It was followed by an IR9669 selection (2.9 t/ha) and IR43 (2.8 t/ha). All three lines had high regression values (1.3408** to 1.4198**), indicating that they performed well under favorable environments. These lines had an average maturity of 130-132 days from seeding during the drier seasons of 1977 and 1979. However, under favorable conditions maturity shortened to only 120 days. The prolonged maturity during water stress enabled the plants to utilize the abundant rainfall which usually occurred later in the crop season.

During severe stress at the railroad site on the IRRI farm in 1977 and 1979, IR6115-1-1-1 still gave higher yields than IR43 and the IR9669 selection.

Among the early-maturing entries, IR3839-1 showed the highest mean yield (2.4 t/ha) and a high *b* value (1.346**). It performed well under relatively low but evenly distributed rainfall.

Lines that produced moderately high yields at even more stable levels were IR3880-10 (2.4 t/ha), IR3880-17 (2.2 t/ha), and C171-136 (2.3 t/ha). A delay in maturity of 10-14 days was also observed when these entries were subjected to moisture stress.

Another set of 22 lines was tested for 3 years (1978–80) at 3 locations. IR5931-110-1 showed a high mean yield (2.5 t/ha) and a high b value (1.3665**). It matured in 120 days and moisture stress did not prolong its maturity. Its yields under unfavorable conditions in 1980 at the railroad site were still higher (1.7 t/ha) than those of the local check Kinandang Patong (1.1 t/ha).

IR6023-10-1-1 and IR52 were stable in all environments but yields were only 2.1 and 2.2 t/ha. IR5929-12-3, an early-maturing line, showed a stability index of 1.0366 and a mean yield of 2 t/ha, indicating very low yield fluctuations during drought years. IR7790-18-1-2, which had an average yield of 2 t/ha, had a *b* value of 0.9028**. These lines appeared to perform well under unfavorable conditions.

From these findings, we infer that in drought-prone areas with low precipitation and a short crop season, early-maturing lines with moderately high and stable yields are needed. IR3880-29, IR5178-1-1-4, and IR7790-18-1-2 are generally early maturing, but their average yields were 1.97, 1.56, and 1.95 t/ha, respectively. However, these levels were still higher than the yield of Kinandang Patong (1.4 t/ha) which also matures in 120 days IR5178-1-1-4 had the lowest regression value (0.7884**) of the 3 early lines, indicating that it performed well under unfavorable conditions. Singh and Singh (1980) also reported that IR5178-1-1-4 was the only test variety of the 1979 IURYN that produced grain (1.4 t/ha) during the severe drought of 1979, when only 337.5 mm of rain fell at Nagina, U.P., India. Local check Nagina 22 produced only 0.3 t/ha.

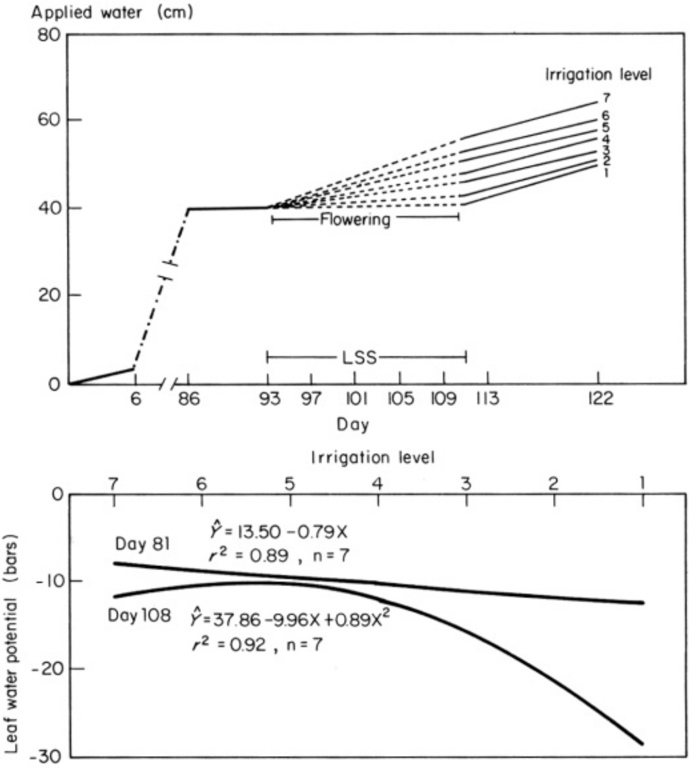
In areas with abundant rainfall or with low but evenly distributed precipitation, high yielding semidwarfs with moderate levels of drought resistance and good recovery ability, such as IR43, IR5931-110-1, IR6115-1-1-1, and IR9669 selection, are suitable. However, varieties with both drought resistance and good recovery ability are needed for stable yields in areas with a longer rainy season or with a bimodal rainfall pattern which are also prone to occasional prolonged drought periods. Lines such as IR3880-10, IR5929-12-3, and IR6023-10-1-1 were found to perform well even in drought years.

## INTERDISCIPLINARY STUDIES OS THE RELATIONSHIP BETWEEN DROUGHT RESISTANCE AND YIELD PERFORMANCE

### Yield stability under different irrigation levels

Several papers in this symposium (Blum, Garrity et al, Seetharama et al, Bidinger et al) have proposed the use of some form of stability analysis of yield across environments in which variation in water supply or adequacy is the major determinant of yield. Recently we tested the efficacy of the line source sprinkler system (Hanks et al 1976) in creating a continuously variable water supply (Puckridge and O'Toole 1981). By sampling at several locations across the water supply gradient, we can evaluate growth and yield of varieties or lines in terms of stability, with the assurance that the influence of other variables — soil and climate — is minimized.

During the 1980 dry season at IRRI we tested 10 varieties and lines for yield response on the line source sprinkler gradient. Rices were planted at five dates corresponding to maturity groups. Water stress at flowering gives the maximum degree of yield response to the continuously variable water treatment. The irrigation gradient was implemented for 18 days to coincide with the expected flowering dates of all varieties. Before and after treatment the field was irrigated by a



**4.** Upper graph illustrates the application of irrigation water at 7 locations using a line source sprinkler (LSS), and the crop age and flowering period for 9 cultivars. Lower graph illustrates the crop water status at each of 7 irrigation levels before the LSS treatment began (day 81) and just before return to full irrigation (day 108) in the entire area.

sprinkler set which supplied 1.2 pan evaporation evenly over the field. Figure 4 illustrates the application of the irrigation gradient and crop response to it. Nine entries which flowered at the same time as IR36, the check variety, are used to discuss different ways of analyzing this test in relation to the objective of the experiment.

The simplest approach is regression of individual entry mean yield on the mean of all entries at each water supply level or environment. Interpretation of the slope parameter and associated statistics have been the subject of a number of papers. The interpretation presented by Finlay and Wilkinson (1963), in which the slope parameter or stability index is used as a relative comparison among entries, is straightforward and intuitively compelling. However, Fischer and Maurer (1978) recognized the correlation between yield potential and slope. To alleviate this problem in selecting for yield response to drought, they utilized an approach in which yield as influenced by drought ($Y$) was expressed as a function of yield potential ($Y_p$), an estimate of drought intensity ($D$), and a susceptibility index ($S$).

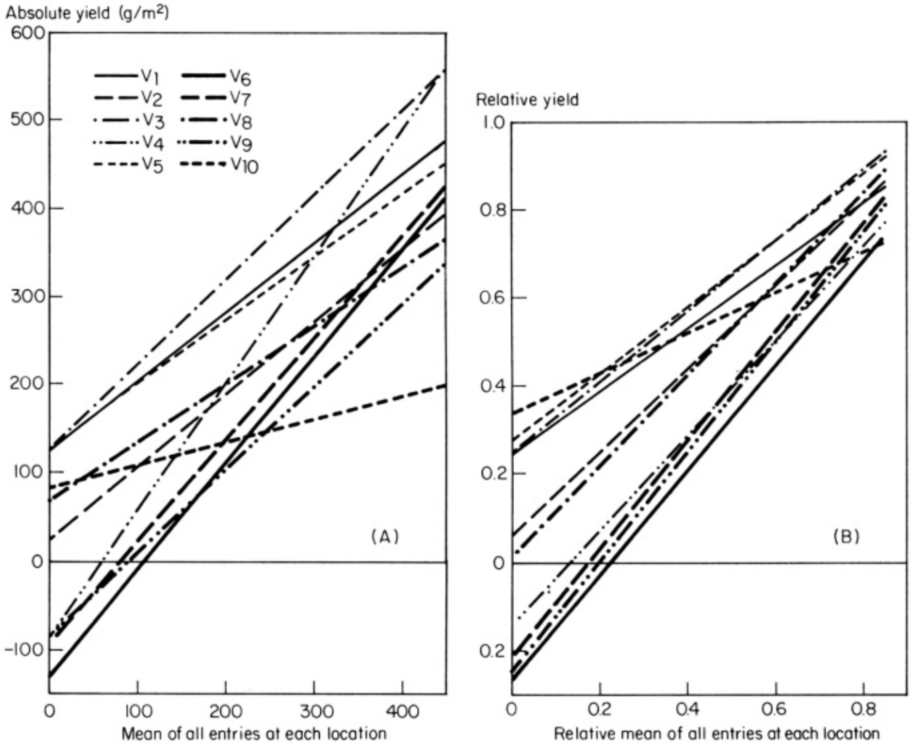
$$Y = Y_p(1-SD) \tag{1}$$

In a slight modification, we elected to use relative yield instead of absolute yield to carry out a stability index analysis. In this case, $Y_p$ is the highest yielding location sampled on the line source sprinkler gradient. All other locations are expressed as a proportion of $Y_p$,

$$Y_r = \frac{Y_i}{Y_p} \tag{2}$$

where $Y_r$ is the relative yield and $Y_i$ is absolute yield at each location. The relative values are utilized in the stability analysis in the same manner as absolute values. The relative values also are found to exhibit a high degree of linearity, enhancing the interpretative value of the regression analysis. Figure 5A and B compares results using absolute and relative yields from the same set of nine entries.

The use of the slope and intercept statistics from the absolute yield data illustrates the problem of interpreting mean yield. Variety 4, which has the second



**5.** (A) illustrates the relationship between absolute yield of 9 rices and one hypothetical cultivar and the mean yield of all cultivars at each of 7 irrigation levels (locations).

(B) illustrates the relationship of relative yield of each cultivar and the mean relative yield at each of 7 irrigation levels.

highest mean yield, shows the greatest slope or least desirable response across the water gradient. The intercept and slope can be used to separate the three selections showing highest yield in the worst environment ($V_1$, $V_3$, and $V_5$). In this case, they also have slopes $\leqslant 1.0$. The intercept and slope illustrate equally well the three selections which appear least desirable (low intercept and high slope, $V_4$, $V_6$, and $V_7$). In this particular experiment, $V_1$ and $V_5$ appear to combine the desirable features of high intercept, relatively low slope, and yield potential.

If the objectives of this experiment were modified in such a way that yield stability was the primary criteria, then the information on relative yields (Fig. 5B) would become ofgreatest interest. Varieties $V_1$ and $V_5$ would again show desirable intercept and slope characteristics. However, adding hypothetical variety $V_{10}$, which illustrates the low but stable yield response of many traditional varieties, to Figure 5 demonstrates the usefulness of the relative yield slope parameter as an estimate of relative drought resistance. But $V_{10}$, although very stable, is not agronomically desirable (Fig. 5A). The recombination of yield potential and stability is the eventual goal of drought-resistance breeding programs.

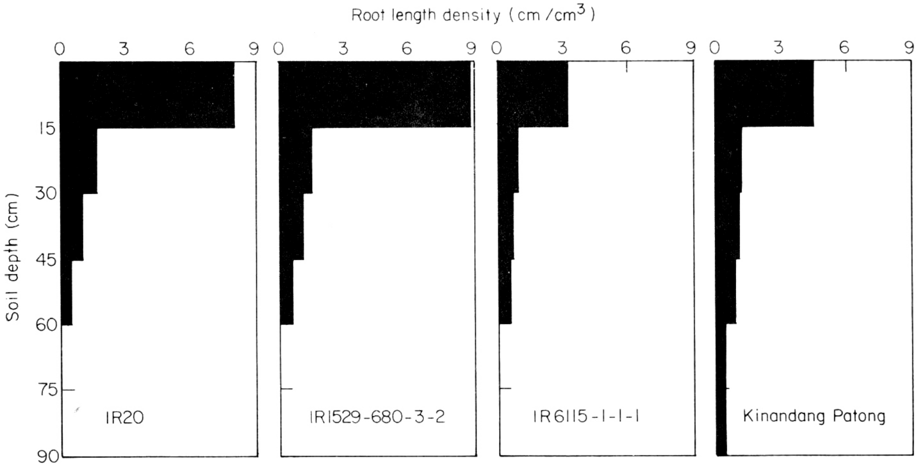
Using relative yield appears to solve the problem of yield potential and to allow interpretation of the slope as an estimate of relative stability of yield across a set of production locations or environments where water supply is definitely the major variable.

In this example experiment, we attempted to synchronize flowering across entries by planting at five different dates. However, of the 32 varieties tested, only 9 actually flowered simultaneously. Fischer and Maurer (1978) proposed a means of adjusting yields for the problem of drought escape. However, their trials were characterized by a terminal drought whereas our method is characterized by a severe stress coinciding with flowering, then relief of stress. We currently are investigating practical means of adjusting relative yields to compensate for differences in flowering date during the line source sprinkler treatment.

These methods show promise for enabling the screening of varieties for yield response to drought while exercising control on the degree of stress and the growth stage affected. The use of the line source sprinkler in the dry season will enable breeders to accurately simulate desired levels of water stress and deal selectively with growth stage, two problems previously thought insurmountable. Results from this more precise experimental method will lend themselves to refined analytical techniques and, because it is a yield function, will change the attitude that selection for drought resistance is based inextricably on chance occurrence of random drought events and is subject to empirical non-yield related selection methods.

## Root system and water extraction

It is obvious that a deeper root system provides more soil-stored water for a dryland rice crop during drought. However, little information quantifies this relationship or illustrates varietal differences. We compared the water extraction of 4 cultivars during the 1979 dry season over a 20-day period, when the crop was 72 days old and the leaf area indices of all plots were >6.0. Pan evaporation during the period was 6-8 mm/day and no rainfall occurred.



**6.** Root distribution at maturity, obtained from previously stressed plots.

All varieties kept midday leaf water potential above –23 bars during the first 8 to 10 days of the stress period. The well-watered control plots were about –10 bars (Fig. 6). Kinandang Patong (KP), a traditional dryland cultivar, extracted somewhat more water than the three others during this part of the stress treatment.

From days 10 to 20, stressed plants showed severely low midday leaf water potentials, from –25 to –40 bars by the end of the stress period. Figure 6 illustrates the relatively high leaf water potential of KP and its higher soil moisture extraction rate below 60-cm depth. The root length density of each cultivar (Fig. 7) agreed with the leaf water potential and water extraction pattern of the cultivars.

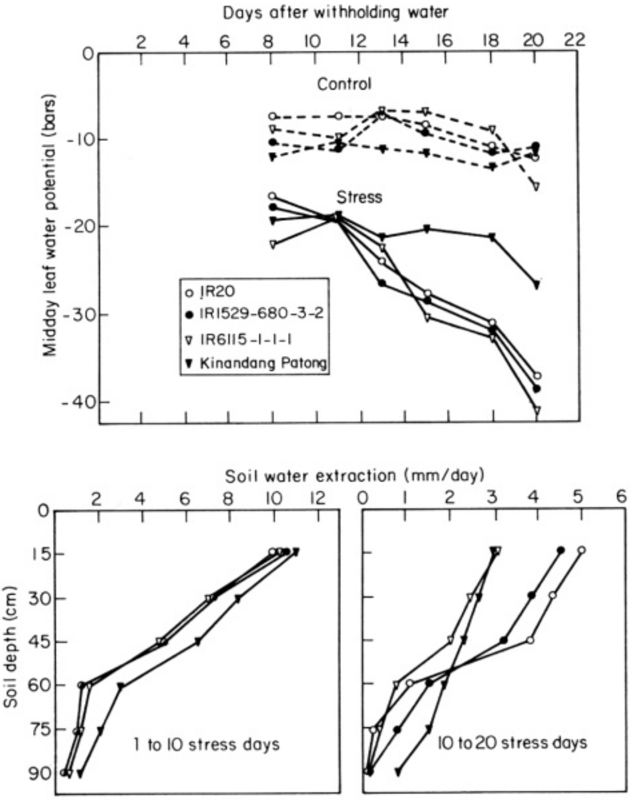
The two wetland cultivars, IR20 and IR1529-680-3, had very high root length densities, 8 to 9 cm/cm$^3$, in the upper soil profile. This corresponds to high extraction rates at this soil depth. The root length density of KP also reflected its extraction pattern and leaf water potential response during the last 10 days of the stress period. However, total rates of soil water extraction in that period were quite low. Maintenance of a relatively high leaf water potential was not achieved by maintaining high flux or evapotranspiration rates. Other shoot characteristics also must have been involved.

These results illustrate the interrelationships among depth and density of roots, soil moisture extraction, plant water status, and cultivars exposed to the same soil and climatic drought conditions.

## Varietal differences in root pulling force

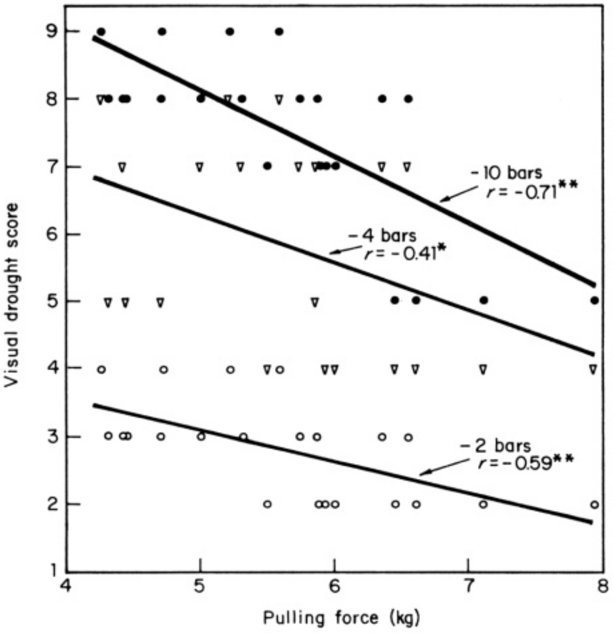
Although genotypic variation for root system characteristics is well documented in semiaquatic rice, breeding and selection based on root system evaluation has not been attempted. Simple methods to evaluate root systems have yet to be developed.

Recently O'Toole and Soemartono (1981) reported the development and testing of a simple device to measure the pulling force required to uproot rice seedlings.



**7.** Midday leaf water potential and soil water extraction rate during drought stress.

**8.** Relationship between root pulling force and visual drought score of several varieties at 3 progressive levels of soil water potential.



The force required to pull rice seedlings from wet paddy soil correlated with root weight, root branching, and thick root number. Pulling force showed a significant negative correlation with drought stress score (Fig. 8). The capability to separate rice cultivars by this technique and the relationship of root pulling force to other drought screening methods have been demonstrated.

This agrees with surveys of Philippine rice farmers, who said drought-resistant traditional cultivars were noted for the physical difficulty of pulling seedlings from the seedbed before transplanting.

The greatly divergent physical and chemical conditions in which rice is cultivated pose difficulties in evaluating the phenotypic acceptability of the root system as opposed to visual evaluation of the shoot in response to a new environment. This technique can be used as a drought resistance screening tool in irrigated fields when special field or greenhouse facilities are not available. It is also thought that this technique may find application as an indication of cultivar suitability to other problems affecting root development, such as tolerance for problem soils, insect or nematode resistance, or the effect of agronomic practices like direct seeding or root-zone application of chemicals.

## Other studies on the root system

We recently initiated studies on varietal differences in root penetration when soils have different bulk densities. Penetration strength is related to the ability of the rice plant to extract water and nutrients in the subsoil below the hard pan. This fact is of significance in rainfed wetland culture where the soil is prepared by puddling and hardpan prevails.

IRRI plant physiologists are studying root growth in relation to aluminum toxicity. Aluminum toxicity is common in highly acidic dryland soils (IRRI 1980).

## Inheritance of root characteristics

An aeroponics system (Carter 1942, Zobel et al 1976) set up in late 1979 enabled us to study the genetic behavior of root components in $F_1$ and $F_2$ populations. A diallel set of 8 tall dryland/semidwarf crosses was investigated.

Parental and $F_1$ arrays indicated overdominance for maximum root length, root thickness at three sampling sites, root number, and dry root weight. In the dryland varieties, an excess of dominant alleles controlled deep roots. In IR8 and IR20, an excess of dominant alleles controlled shallow roots. An excess of dominant alleles conferred thin roots in most crosses. The genic control of thick roots varied from parent to parent. An excess of recessive alleles controlled low root number while dominant alleles conferred high root number in two parents. Either dominant or recessive alleles controlled high root weights. Additive gene action was indicated for maximum root length, root thickness, root number, and root-to-shoot weight ratio. Plant height and tiller number showed a combination of additive effects and dominance, while root weight and shoot weight showed only dominant gene action.

Root length was positively correlated with plant height, root and shoot weight, root-to-shoot ratio, and root thickness in the $F_1$ plants. Root thickness was positively correlated with plant height, root weight, and root-to-shoot weight ratio. Root number was positively correlated with tiller number and the dry weight of roots and shoots. However, there was no correlation between root number and root length, plant height, or root thickness.

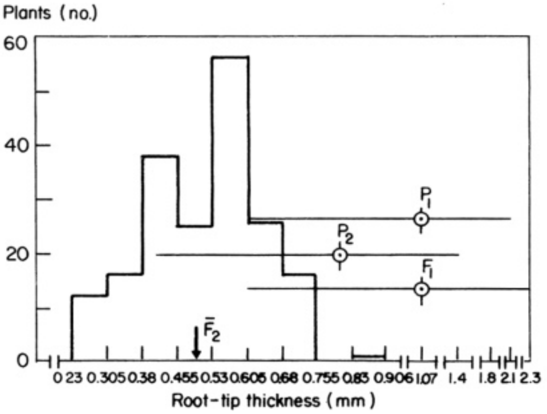
Heritability estimates (narrow sense) based on parental and $F_1$ data were moderately high for maximum root length (61%), moderately high for root-tip and root-base diameters (62%), moderately high for root-base thickness (58%), moderately low for root-middle thickness (50%), moderately low for root number (44%), and moderately low for root weight (43%). On the other hand, estimates were high for plant height at 50 days after seeding (75%) and moderately high for root-to-shoot weight ratio (53%) and tiller number (63%).

We also studied three $F_2$ populations representing dryland/dryland, dryland/wetland, and wetland/wetland crosses. The $F_2$ distributions were continuous and slightly skewed, indicating the presence of dominance or recessiveness in different pairs of alleles. The $F_2$ data support the $F_1$ data.

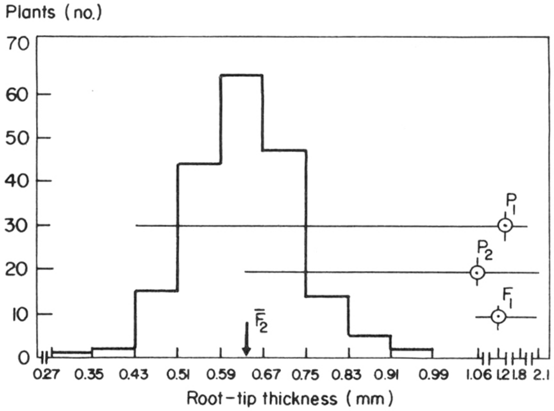
The $F_2$ distribution among the three crosses also indicated that recovery of the progenies with long roots, even in the cross of wetland/wetland crosses, is readily obtainable. This also is true for high root number. There appears to be no difficulty in recovering $F_2$ plants with heavy roots or heavy shoots. However, it would be very difficult to recover $F_2$ progenies with thick roots in a cross such as OS4/IR8 (Fig. 9). Even in a cross involving two parents having thick roots (Moroberekan/OS4), most $F_2$ plants had thin roots. (Fig. 10). This trend also was obvious in the root-to-shoot ratios. On the other hand, progeny with many roots can be more readily recovered.

Among three $F_2$ populations, correlation analysis of six traits indicated the same positive association existed as in $F_1$ analysis: between root length and root-tip thickness, root number, dry-root weight, plant height, and tiller number. Root-tip thickness was positively correlated with plant height and dry weight of roots, root thickness was negatively correlated with tiller number and root number (Armenta-Soto 1981).

Our genetic studies indicate that rice varieties differ greatly in genotypic composition for different root characteristics. Deep roots are controlled by domi-



**9.** Distribution and means of parents and $F_1$ and $F_2$ plants by root-tip thickness classes in the cross OS4 ($P_1$)/IR8 ($P_2$). Solid horizontal lines show the range of the parents and $F_1$ plants about the mean (dotted circles) while the arrow shows the mean of the $F_2$ population.



**10.** Distribution and means of parents and $F_1$ and $F_2$ plants by root-tip thickness classes in the cross Moroberekan ($P_1$)/OS4 ($P_2$). Solid horizontal lines show the range of parents and $F_1$ plants about the means (dotted circles) while the arrow shows the mean of the $F_2$ population.

nant alleles in some parents, by recessive alleles in others. The important trait of thick roots is largely conferred by recessive alleles. The low recovery of $F_2$ plants with thick roots prevails in two crosses. These findings may explain our difficulty in finding deep and thick-rooted progeny in our crosses. The bulk method of selection among large $F_2$ populations may have some advantage over the pedigree method.

## ENDEAVORS FOR THE FUTURE: STRATEGIES, RESOURCES, AND INSTITUTIONS

We do not foresee major changes in the overall strategy of rice breeders — to recombine the drought resistance, local adaptation, and stable yielding characters of traditional varieties with the improved resistance to diseases and insects and the yield potential of modern varieties. However, the speed and degree of efficacy with which we progress toward that goal could be much enhanced with a greater degree of interdisciplinary and interinstitutional collaboration. We recognize that breeding programs and institutions concerned with rainfed rice improvement vary greatly in both the physical and human resources available. Most institutions have physical, financial, and manpower constraints. But regardless of the resource base, we feel that these steps should be incorporated into any overall strategy.

- *Diagnosis.* A plant breeder who recognizes drought as a principal yield constraint in a target area may benefit from interactions with climatologists, crop physiologists, and soil scientists before embarking on a course of action. Breeders and their associates should have a good knowledge of the frequency of drought occurrence and how this relates to crop growth stages. Increased awareness of the dynamic interaction between soil, plant, and weather during a drought period (Hsiao et al 1980), especially during the reproductive phase, may greatly aid in choosing a sound course of action (Hsiao et al 1980).
- *Characterizing major drought-prone areas.* The immense diversity of environment components in major drought-prone areas of the world poses difficulties in planning specific crosses and in selecting breeding materials that

will suit the specific ecological conditions peculiar to a site. A systematic and uniform characterization of the pertinent environment factors for the important drought-affected areas would guide researchers in formulating breeding objectives and procedures and greatly accelerate the impact of varietal programs. Only the Centro Internacional de Agricultura Tropical (CIAT) and collaborating countries in Latin America have recently initiated such a systematic effort.

- *Adopting appropriate selection criteria.* The literature is replete with suggested criteria, but in practice very few meet plant breeders' requirements: rapid, inexpensive, simple, and based on the physiological interaction of drought with crop growth and yield. Unimpaired plant growth and yield during a rainless period are inextricably correlated with water use by a crop. We think that criteria based on a variety's ability to maintain high water status and efficient water use may relate most soundly to productivity in an agricultural sense. In the absence of overt symptoms, visual scoring based on leaf rolling, leaf death, and panicle development will serve as a useful tool (Loresto and Chang 1981).

  Further investigations are needed to identify the most effective combination of physiological mechanisms — escape (by early maturity or photoperiod sensitivity), avoidance (by deep roots), tolerance, and recovery (plasticity in vegetative growth) — that may suit a particular climatic-hydrological-edaphic environment, thus providing a balanced approach. Continued assistance from research institutions in developed countries would help achieve such goals.

- *Collaborative sharing of germplasm.* Research at IRRI has demonstrated some of the commonalities in drought-resistance mechanisms between dryland and rainfed-wetland culture (Chang et al 1979). Several outstanding drought-resistant parents have shown merit across West Africa, South and Southeast Asia, and Brazil. Promising parents should be identified and pooled in a coordinated hybridization and $F_2$ seed distribution program so that useful genes can be fully utilized by breeders in national and international programs. IRRI initiated such a germplasm-sharing scheme with Indian breeders in 1980 and will expand this collaboration.

  IRRI staff will continue monitoring drought resistance in breeding materials for the wetter regions, collaborative testing of materials in the drier regions outside Los Baños, and assembling genotypes having appropriate physiological mechanisms in order to meet specific needs. We also visualize a modification in the improved plant type for the drought-prone areas — intermediate plant height, moderate tillering ability, medium panicle size, and full panicle exsertion. Adequate disease and insect resistance, along with desired grain characteristics, should be incorporated into the final product. Adverse soil factors should be included in the testing program. More extensive testing should be carried out in farmers' fields within the drought-prone areas.

- *Measuring progress.* Although we have no ready answer for this critical concern, we suggest that, even though yield is of primary concern, it may be advisable to exercise caution in the initial stage. On the other hand, stability of yield or its components across crop years (as opposed to high mean yield) may be more meaningful if breeding lines are selected and evaluated in situ where high yield potential would not be realized except in unusually wet years.

- *Pooling of human and natural resources.* The problems associated with resources are particularly relevant to research on rainfed rice. Very few rainfed or nonirrigated rice experiment stations exist. Additionally, rainfed stations have been long neglected. While high-yielding varieties and associated technology in irrigated regions have received national, institutional, and individual attention, research on rainfed rices has not been adequately supported.

  IRRI is ideally located for irrigated rice research but is poorly situated for rainfed rice research because of the high rainfall and protracted wet season in most years. It is more advantageous for IRRI to make use of its physical and human resources to develop research of fundamental significance and to generate germplasm through coordinated hybridization than to pursue the whole course of progeny evaluation and variety development.

## Prospects for collaboration on water deficit research

It is most encouraging that a number of national programs are reassessing the problems of rainfed rice. CRRI in India held a symposium on rainfed rice during 1978 (ICAR 1978). Several institutions in India and Indonesia have launched research programs on rainfed rice. Initial steps have involved environmental description and subdivision of rice-growing areas by cultural type. Thailand's rainfed rice program in the northeast has received World Bank funding and the infusion of trained rice scientists from the irrigated rice program. IRRI also will collaborate with other international and regional centers that have research programs related to drought.

Even so, these programs vary greatly in the availability of governmental, institutional, and human resources. A plant breeder at any one station faces a set of factors related to technology and resources that will eventually determine the choice of tactics and the soundness of that decision. IRRI's main role in the next decade is to provide technology and training that will complement and supplement national efforts in developing a greater total impact on rice production in drought-prone areas.

Extensive testing in farmers' fields at representative sites will complement and supplement testing at experiment stations. Varietal performance on farms will provide the final measure of the success of the breeding efforts.

## REFERENCES CITED

Armenta-Soto, J. L. 1981. Diallel analysis of root characteristics in rice (*Oryza sativa* L.). PhD dissertation, University of the Philippines at Los Baños, Philippines. 176 p.

Barker, R., and R. W. Herdt. 1979. Rainfed lowland rice as a research priority — an economist's view. IRRI Res. Pap. Ser. 26. 50 p.

Barrios, L. 1981. A cytogenetic study on $F_1$ hybrids between upland and lowland varieties of rice

(*Oryza sativa* L.). BS thesis, University of the Philippines at Los Baños, Philippines.

Bidinger, F. R., V. Mahalakshmi, B. S. Talukdar, and G. Alagarswamy. 1982. Improvement of drought resistance in pearl millet. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Blum, A. 1982. Evidence for genetic variability in drought resistance and its implications for breeding. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Brady, N. C. 1975. Rice responds to science. Pages 62-96 *in* A. W. A. Brown, T. C. Byerly, M. Gibbs, and A. San Pietro, eds. Crop productivity — research imperatives. Charles F. Kettering Foundation, Ohio.

Carter, W. A. 1942. A method of growing plant in water vapor to facilitate examination of roots. Phytopathology 32:623-625.

Carter, D. B., and J. R. Mather. 1966. Climatic classification for environmental biology. Publ. Climatol. 19(4):396. C. W. Thornthwaite Associates Laboratory of Climatology, Elmer, New Jersey.

Chang, T. T. 1976a. The rice cultures. Philos. Trans. Roy. Soc. London, B, 275:143-157.

Chang, T. T. 1976b. The origin, evolution, cultivation, dissemination, and diversification of Asian and African rices. Euphytica 25:425-441.

Chang, T. T. 1980. The rice genetic resources program of IRRI and its impact on rice improvement. Pages 85-105 in International Rice Research Institute. Rice improvement in China and other Asian countries. Los Baños, Philippines.

Chang, T. T., G. C. Loresto, and O. Tagumpay. 1972. Agronomic and growth characteristics of upland and lowland rices. Pages 645-661 *in* International Rice Research Institute. Rice breeding. Los Baños, Philippines.

Chang, T. T., G. C. Loresto, and O. Tagumpay. 1974. Screening rice germplasm for drought resistance. SABRAO J. 6(1):9-16.

Chang, T. T., S. H. Ou, M. D. Pathak, K. C. Ling, and H. E. Kauffman. 1975. The search for disease and insect resistance in rice germplasm. Pages 183-200 *in* O. H. Frankel and J. G. Hawkes, eds. Crop genetic resources for today and tomorrow. Cambridge University Press, Cambridge.

Chang, T. T., B. Somrith, and J. C. O'Toole. 1979. Potential for improving drought resistance in rainfed lowland rice. Pages 149-164 *in* International Rice Research Institute. Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. Los Baños, Philippines.

Chang, T. T., and S. K. De Datta. 1975. Agronomic traits needed in upland rice varieties. Pages 93-100 *in* International Rice Research Institute. Major research in upland rice. Los Baños, Philippines.

Chang, T. T., and B. S. Vergara. 1975. Varietal diversity and morpho-agronomical characteristics of upland rice. Pages 82-90 *in* International Rice Research Institute. Major research in upland rice. Los Baños, Philippines.

Cruz, R. T., and J. C. O'Toole. 1980. Water stress and aspects of unproductive growth in rice. Paper presented at the 11th Annual Convention of the Crop Science Society of the Philippines, April 27-29, 1980. Visayas State College of Agriculture, Baybay, Leyte. 23 p.

De Datta, S. K., and J. C. O'Toole. 1977. Screening deepwater rices for drought tolerance. Pages 83-92 *in* International Rice Research Institute. Proceedings 1976 deepwater rice workshop, 8-10 November, Bangkok, Thailand. Los Baños, Philippines.

De Datta, S. K., and D. V. Seshu. 1982. Evaluating rices for drought tolerance, using field screening and multilocation testing. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Finlay, K. N., and E. N. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14:742-754.

Fischer, R. A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:897-912.

Garrity, D. P., C. Y. Sullivan, and W. M. Ross. 1982. Alternative approaches to improving grain sorghum productivity under drought stress. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Hanks, R. J., J. Keller, V. P. Rasmussen, and C. D. Wilson. 1976. Line source sprinkler for continuous variable irrigation - crop production studies. Soil Sci. Soc. Am. J. 40:426-429.

Hsiao, T. C., J. C. O'Toole, and V. S. Tomar. 1980. Water stress as a constraint to crop production in the tropics. Pages 339-370 *in* International Rice Research Institute and New York State College of Agriculture and Life Sciences, Cornell University. Priorities for alleviating soil-related constraints to food production in the tropics. International Rice Research Institute, Los Baños, Philippines.

Hsieh, S. C., and V. W. Ruttan. 1967. Environmental, technological, and institutional factors in the growth of rice production: Philippines, Thailand, and Taiwan. Food Res. Inst. Stud. (Stanford University) 7(3):307-341.

Huke, R. E., and E. H. Huke. 1981. Rice area by culture type: maps and tables. International Rice Research Institute, Los Baños, Philippines.

Hung, H. H., and T. T. Chang. 1976. Aberrant segregation of three-marker genes in crosses between upland and semidwarf-lowland varieties of rice. SABRAO J. 8(2):127-134.

ICAR (Indian Council of Agricultural Research). 1979. National symposium on yield in Kharif (February 8-11, 1978). Central Rice Research Institute, Cuttack, India. 600 p.

Ikehashi, H., and F. N. Ponnamperuma. 1978. Varietal tolerance of rice for adverse soils. Pages 801-823 *in* International Rice Research Institute. Soils and rice. Los Baños, Philippines.

IRRI (International Rice Research Institute). 1971. Annual report for 1970. Los Baños, Philippines. 265 p.

IRRI (International Rice Research Institute). 1972. Annual report for 1971. Los Baños, Philippines. 238 p.

IRRI (International Rice Research Institute). 1973. Annual report for 1972. Los Baños, Philippines. 246 p.

IRRI (International Rice Research Institute). 1974a. Annual report for 1973. Los Baños, Philippines. 266 p.

IRRI (International Rice Research Institute). 1974b. IRRI's GEU Program: tapping the genetic reservoir of rice. IRRI Rep. 2/74. 4 p.

IRRI (International Rice Research Institute). 1975. Annual report for 1974. Los Baños, Philippines. 384 p.

IRRI (International Rice Research Institute). 1976. Annual report for 1975. Los Baños, Philippines. 479 p.

IRRI (International Rice Research Institute). 1977. Annual report for 1976. Los Baños, Philippines. 418 p.

IRRI (International Rice Research Institute). 1978. Annual report for 1977. Los Baños, Philippines. 548 p.

IRRI (International Rice Research Institute). 1979. Annual report for 1978. Los Baños, Philippines. 478 p.

IRRI (International Rice Research Institute). 1980. Annual report for 1979. Los Baños, Philippines. 538 p.

IRRI (International Rice Research Institute), 1981a. Annual report for 1980. Los Baños, Philippines. 467 p.

IRRI (International Rice Research Institute). 1981b. Preliminary report of 1980 IRTP nurseries. Los Baños, Philippines.

Jana, R. K., and S. K. De Datta. 1971. Effects of solar energy and soil moisture tension on the nitrogen response of upland rice. Proc. Int. Symp. Soil Fert. Eval. (New Delhi) 1:487-497.

Lin, M. H., and T. T. Chang. 1981. Genetic study of the relationship between the lowland rice varieties and the traditional upland rice varieties. SABRAO J. (in press)

Loresto, G. C., and T. T. Chang. 1971. Root development of rice varieties under different soil moisture conditions. Pages 412-416 *in* Crop Science Society of the Philippines. Second annual scientific meeting, May 4-6, 1971. Los Baños, Philippines.

Loresto, G. C., T. T. Chang, and O. Tagumpay. 1976. Field evaluation and breeding for drought resistance. Philipp. J. Crop Sci. 1(1):36-39.

Loresto, G. C., and T. T. Chang. 1981. Decimal scoring systems for drought reactions and recovery ability in screening nurseries of rice. Int. Rice Res. Newsl. 6(2):9-10.

O'Toole, J. C., and T. T. Chang. 1978. Drought and rice improvement in perspective. IRRI Res. Pap. Ser. 14. 27 p.

O'Toole, J. C., and T. B. Moya. 1978. Genotypic variation in maintenance of leaf water potential in rice. Crop Sci. 18:871-876.

O'Toole, J. C., R. S. Aquino, and K. Alluri. 1978. Seedling stage drought response in rice. Agron. J. 70:1101-1103.

O'Toole, J. C., and T. T. Chang. 1979. Drought resistance in cereals — rice: a case study. Pages 373-406 *in* H Mussell and R. C. Staples, eds. Stress physiology of crop plants. Wiley Interscience, New York.

O'Toole, J. C., and R. T. Cruz. 1980. Response of leaf water potenrial, stomatal resistance, and leaf rolling to water stress. Plant Physiol. 65:428-432.

O'Toole. J. C., and Soemartono. 1981. Evaluation of a simple technique for characterizing rice root systems in relation to drought resistance. Euphytica (in press)

O'Toole, J. C., T. T. Chang, and B. Somrith. 1982. Research strategies for improvement of drought resistance in rainfed rices. Pages 201-222 *in* International Rice Research Institute. Rice research strategies for the future. Los Baños, Philippines.

Parao, F. T., E. Paningbatan, and S. Yoshida. 1976. Drought resistance of rice varieties in relation to their root growth. Philipp. J. Crop Sci. 1(1):50-55.

Puckridge, D. W., and J. C. O'Toole. 1981. Dry matter and grain production of rice using a line source sprinkler in drought studies. Field Crops Res. 3:303-319.

Seetharama, N., B. V. Subba Reddy, J. M. Peacock, and F. R. Bidinger. 1982. Sorghum improvement for drought resistance. In International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Singh, U. P., and K. Singh. 1980. IR5178-1-1-4, an outstanding drought-tolerant line. Int. Rice Res. Newsl. 5(6):9.

Zobel, R. W., P. D. Tredici, and J. C. Torrey. 1976. Method for growing plants aeroponically. Plant Physiol. 57:344-346.

# EVALUATING RICES FOR DROUGHT TOLERANCE USING FIELD SCREENING AND MULTILOCATION TESTING

S. K. DE DATTA AND D. V. SESHU

Drought stress causes yield reductions and sometimes total crop failures in rainfed rice areas of Asia, Africa, and Latin America. To develop rices with stable yields for drought-prone areas, screening for drought tolerance and assessing yield stability in clearly defined targeted testing sites is one appropriate and effective strategy.

Field screening of rices should evaluate separately for drought tolerance and recovery ability upon rewatering. At IRRI, we developed a field screening technique by manipulating and monitoring soil moisture tension during the dry seasons. Results show some interdependence of modern and traditional varieties in developing high-yielding rices with moderate to high levels of drought tolerance.

Results from multilocation evaluation of the International Rice Testing Program suggest that the traits tolerance for and recovery from drought do not appear to be associated with plant height or growth duration. Despite climatic, physiographic, and edaphic variations in test sites, entries such as Salumpikit showed a high level of consistent performance under drought conditions.

Multilocation testing suggests no apparent association between plant height or growth duration and yielding ability. Many semidwarfs developed for wetland culture, such as IR43, IR45, and IET1444, appear to beconsistently high yielders under moderate drought condition.

As we continue to identify donors for breeding high levels of

---

Agronomist and plant breeder, International Rice Research Institute, Los Baños, Philippines.

drought tolerance, we should utilize modern rices that combine high levels of drought tolerance and recovery on relief of moisture stress with high yield potential in addition to the traditional varieties which produce low but stable yields. Evaluation of modern rices for drought tolerance and yield stability under both assured and unassured water regimes provides relatively greater success in identifying rices that are resistant or tolerant of other associated stresses as well.

Drought stress is of serious concern for rainfed dryland, wetland, and deepwater rice areas in South and Southeast Asia and dryland rice areas in Africa and Latin America. These rainfed areas are exposed to erratic distribution and quantity of rainfall. Drought can occur during any growth stage. In South and Southeast Asia, rainfed rice (which includes transplanting or direct seeding in puddled soil, dry seeding in aerobic soil for dryland, dryland seeding in bunded fields, and seeding in deep water) is grown in large areas that suffer some degree of moisture stress regularly. In West Africa, 65% of the total rice area is in drylands that suffer frequently from drought stress (Choudhury and Abifarin 1981). In Latin America, Brazil has the largest drought-prone area, with nearly 4.7 million ha of land under dryland rice culture. In cerrado areas of Brazil, dry spells of 10–21 days (locally known as veranico) cause significant yield reductions, resulting in a low national average of about 1.2 t/ha for dryland rice.

Drought stress in rainfed rice areas affects practically every aspect of plant growth, modifying the anatomy, morphology, physiology, and biochemistry. Water stress usually has multiple effects on plant growth and development and ultimately affects yield.

Progress in drought tolerance research has lagged because much of the early research on plant response to drought stress was on soil moisture rather than on plant-water status (Sullivan 1971). Lack of proper screening methods acts as a constraint and often delays the attainment of breeding objectives. However, because drought-tolerant rices especially are expected to produce stable yields in rainfed culture, interest in identifying suitable methods for screening rices for drought tolerance has been generated recently. Several approaches and techniques have been suggested (De Datta et al 1975), but any single technique does not cover all aspects of drought tolerance.

Results of investigations on varietal differences for drought tolerance and recovery and yielding ability under droughty conditions using special field screening techniques at the International Rice Research Institute (IRRI) and natural growing conditions at several sites in Asia, Africa, and Latin America are presented here. These findings should help determine breeding approaches toward varietal improvement for rainfed areas.

## FIELD SCREENING OF RICES FOR DROUGHT TOLERANCE

Recently, different criteria have been used to select rices for drought tolerance.

One approach in field screening is to plant rice at short intervals from the beginning of the wet season. The assumptions are that the crop of each seeding date would receive a different amount of rainfall and that sunlight is relatively constant throughout the wet season (Jana and De Datta 1971, De Datta and Beachell 1972).

Chang et a1 (1974) developed a mass screening technique to evaluate drought tolerance under field conditions in the dry season. The technique subjects plants to alternate periods of moisture deficiency and moisture sufficiency at three growth stages. Similar dry season field screening at Cuttack, India, of a number of semidwarf mutants of Mtu 17 led to the identification of mutant No. 4. This raised the possibility of some grain production under extreme drought stress (Gangadharan and Misra 1979).

In West Africa, persistent drought damage in rice led the Institut de Recherches Agronomiques Tropicales et des Cultures Vivrieres (IRAT) to focus its attention on identification of genotypes most tolerant of drought stress, particularly at the reproductive stage. Varieties that appeared promising for drought tolerance, such as IRAT 13, IRAT 104, and Palawan, were identified (Reyniers and Jacquot 1978, Jacquot 1981). Choudhury and Abifarin (1981) suggest that incorporating drought tolerance into otherwise suitable genotypes is essential for varieties to be adapted to drought-prone areas in West Africa.

For unfavored mechanized dryland rice areas in Latin America, Jennings et al (1981) suggest evaluation of dryland varieties and breeding lines from diverse sources under four clearly defined environmental regimes:

1. Colombian Llanos, high rainfall, alluvial soils;
2. Colombian Llanos, high rainfall, infertile savanna;
3. Goiania, Brazil, low rainfall, moderately acid soil;
4. Peru, high rainfall, acid soils, rain forest.

Results from these test sites would provide information on combinations of stress to identify donors for specific traits. Jennings et al (1981) also suggest that, despite low genetic variability, the search to identify suitable donors for drought tolerance in the unfavored dryland areas should continue.

## Field screening technique

A field screening technique that carefully manipulates and monitors soil moisture tension was developed at IRRI (De Datta and Vicencio 1976, De Datta et al 1979). Tests were conducted during the dry seasons to avoid unwanted moisture during imposition of simulated drought. Results of these tests may not be directly applicable to wet season conditions due to differences in sunlight intensity (De Datta and Beachell 1972). But first approximations of drought reaction are needed for as many rices as possible as a basis for selection. The selections from these tests can be tested for yield and other agronomic performances in succeeding seasons. The actual field drought reactions ultimately would be observed during a wet season when dry spells of varying degrees of severity occur.

Entries for dry season field drought screening were obtained for 6 years from Genetic Evaluation and Utilization Program (GEU) materials in pedigree nurseries and observational and replicated yield trials for rainfed wetland and dryland rices; from International Rice Testing Program (IRTP) entries in international observational and yield nurseries for dryland, rainfed wetland, and deepwater rices; and from recent germplasm bank accessions of deepwater, dryland, and hill rices.

Entries were planted in dry granular soil (Tropudalf; pH 5.8; organic matter 2.6%; total N 0.14%; CEC 37 meq/100 g; soil texture, clay) in late January to early February. Ten grams of seed of each entry were manually drilled 25 cm apart in 2-row plots with 2.5-m-long rows. Seeds were covered by harrowing the direction of the furrows. After seed was covered, the field was sprinkler-irrigated to allow for germination. Every 5-7 days during the early growth stages, or when soil moisture tension (SMT) was recorded beyond 30 cb at 10 cm depth, the field was sprinkler-irrigated to ensure good stand establishment. Two equal split doses of 30 kg N/ha were applied at 10 and 20 days after seedling emergence.

At 30 days after seedling emergence, irrigation was stopped and the soil was allowed to dry. Soil moisture tension (SMT) was monitored at 20-cm depth with tensiometers. When SMT beyond 80 cb was recorded, gypsum blocks were used. As a countercheck of daily tensiometer and gypsum block readings, soil samples were collected once a week from 20-cm depth for gravimetric analyses.

Drought reactions were scored three times. The first was at 1-2 bars SMT. (No scoring was done at 1-2 bars in 1975.) At 4-5 bars SMT (3-4 bars SMT from 1975 to 1977), the second scoring was done. At 8-10 bars SMT, drought reactions were recorded for the last time. The Standard Evaluation System (SES) for Rice 1-9 scale (IRRI 1975a) was used to score entries:

1 – No to slight effects of stress,
5 – One-quarter to one-half of total number of leaves fully dried,
9 – All plants apparently dead.

After scoring for drought reactions at 8-10 bars SMT, the field was sprinkler-irrigated to relieve soil moisture stress. Drought recovery of individual entries after 10 days was scored using the SES 1-9 scale:

1 – At least 90% of plants fully recovered,
5 – 40 to 50% of plants fully recovered,
9 – No plants fully recovered.

*Check varieties and lines.* In 1975, IR442-2-58 was used as the tolerant check and IR20 as the susceptible check. Starting in 1977, Salumpikit was used as the tolerant check, IR442-2-58 as the moderately tolerant check, IR20 as the moderately susceptible check, and IRAT 9 as the susceptible check.

IR20's drought susceptibility was based on low heat tolerance and slow stomatal closure (IRRI 1974). It had the highest percentage plant height reduction in a field test of 20 varieties and lines placed under soil moisture stress (Yoshidaet a1 1974).

Salumpikit, a traditional Philippine dryland variety, was identified in 1975 as a tolerant check. IRAT 9, an accession from Ivory Coast, was identified in 1976 as a susceptible check.

Four checks were included for every 50 entries. The susceptible check IR20 was placed in every 1st plot and IRAT 9 in every 26th plot. The tolerant checks IR442-2-58 and Salumpikit were placed at random. Details on this methodology were reported earlier (Malabuyoc et al 1980).

**Table 1. Number of entries and outstanding rice selections in field screening for drought tolerance at vegetative stage. IRRI, 1975-80 dry seasons.**

| Year | Entries (no.) | Outstanding selections[a] | |
|---|---|---|---|
| | | No. | % |
| 1975 | 1003 | 32 | 3.19 |
| 1976 | 1016 | 6 | 0.59 |
| 1977 | 4119 | 51 | 1.24 |
| 1978 | 4757 | 42 | 0.90 |
| 1979 | 3897 | 145 | 3.72 |
| 1980 | 4530 | 169 | 3.73 |

[a] Drought tolerance score comparable to or better than that of IR442-2-58 and Salumpikit at 10 bars SMT (soil moisture tension). 1979 test at 5 bars SMT.

## Results of field screening

The number of varieties screened increased from 1,003 entries in 1975 to about 4,000/year in 1977, peaking at 4,757 in 1978 (Table 1). Rices with drought reactions at 5 and 10 bars SMT similar to or better than the tolerant checks were considered outstanding. The percentage of drought-tolerant selections was high in the screening tests of 1975, 1979, and 1980. In 1975, 950 out of 1,003 entries screened were traditional varieties from several countries. In 1979, entries were evaluated for drought at 1 and 5 bars SMT only. Early rains and 2 typhoons prevented the soil from reaching 10 bars SMT. In 1980, when more modern rices were tested, it took only a short time to reach 10 bars SMT. This somewhat explains the high percentage of drought-tolerant entries.

In other years, most test entries were progenies of crosses made at IRRI involving varieties and lines identified under irrigated wetland conditions for such characters as grain yield or insect and disease resistance, or both. This resulted in low percentages of entries showing drought tolerance during 1976-78. Over the years, more traditional varieties than modern breeding lines were identified as drought tolerant.

Drought susceptibility of IR20 and moderate drought tolerance of IR442-2-58 were confirmed (Table 2). IR442-2-58 combines drought tolerance and a moderate degree of flood tolerance. It is being popularized as a dryland variety in Benin, Gambia, Ghana, Guinea, and Togo (Choudhury and Abifarin 1981); as a wetland variety in Ghana and Brazil (BR-2), and as a deepwater variety in Bihar and West Bengal, India. This suggests the reproducibility of our findings in tests in other countries.

The selection of Salumpikit as a tolerant check and IRAT 9 as a susceptible check was justified by their relatively consistent drought scores, appropriate to their classification, in later years. The drought-tolerant check variety Salumpikit is a product of natural selection for drought tolerance under farmers' field conditions and dryland rice culture. It maintained consistently favorable reactions to imposed drought in all 6 years of testing.

*Rices outstanding for drought tolerance.* The experimental lines selected for drought tolerance from the several thousands planted at IRRI in pedigree nurser-

**Table 2. Outstanding selections for drought tolerance at vegetative stage in field screening and possible source of tolerance. IRRI, 1978-80.**

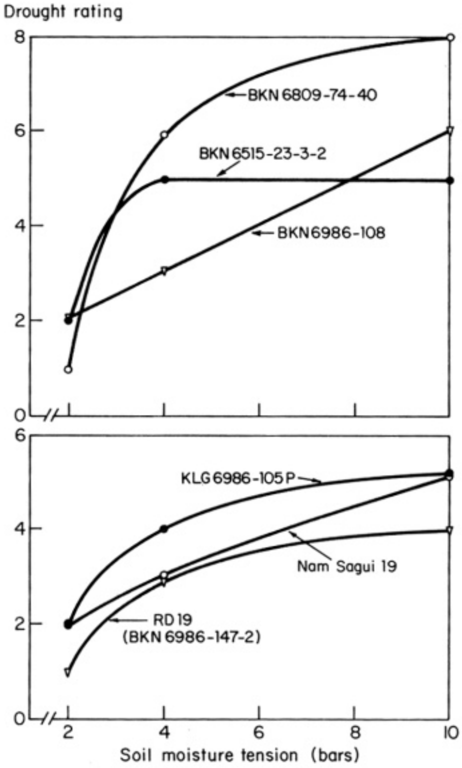
| Designation | Possible source of tolerance | Origin | Drought scores[a] | | | | |
|---|---|---|---|---|---|---|---|
| | | | 1978 | | 1979 | 1980 | |
| | | | 5 bars | 10 bars | 5 bars | 5 bars | 10 bars |
| IR52 | NS19 | | 1 | 3 | 3 | 5 | 6 |
| IR8098-194-2 | Aus 12, Tetep | | 3 | 7 | 3 | 2 | 3 |
| IR8103-120-3 | Aus 197, Tetep | | 1 | 1 | 3 | 3 | 3 |
| IR9669 Sel | Carreon | | 1 | 3 | 1 | 3 | 3 |
| IR5624-110-2 | KDML 105, Tetep | | 1 | 3 | 3 | 3 | 3 |
| IR8234-174-3 | NS19 | | 2 | 3 | 3 | 4 | 5 |
| IR9995-96-2 | NS19 | | 1 | 3 | 3 | 4 | 5 |
| Nam Sagui 19 | | Thailand | 3 | 7 | 3 | 5 | 7 |
| Carreon | | Philippines | 3 | 5 | 3 | – | – |
| Leb Mue Nahng 111 | | Thailand | 2 | 4 | 3 | 4 | 6 |
| Khao Dawk Mali 105 | | Thailand | 3 | 6 | 3 | 5 | 7 |
| IR442-2-58 (tolerant check) | | | 1 | 5 | 3 | 4 | 6 |
| Salumpikit (tolerant check) | | Philippines | 1 | 4 | 3 | 4 | 5 |
| IRAT 9 (Susceptible check) | | Ivory Coast | 6 | 9 | 7 | 7 | 8 |
| IR20 (susceptible check) | | | 5 | 8 | 5 | 6 | 8 |

[a] Standard Evaluation System for Rice (SES) 1-9 scale: 1 = no to negligible effects of soil moisture stress, 9 = all plants apparently dead.

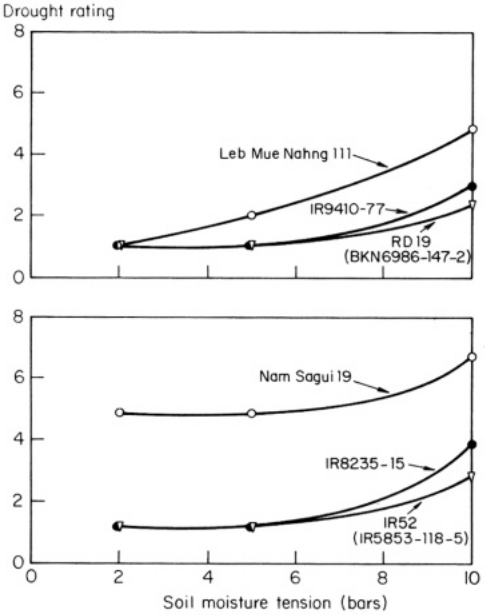
ies and from observations and replicated yield trials in 1978, 1979, and 1980 are listed in Table 2. Also shown are varieties tagged as probable sources of drought tolerance.

At 5 bars SMT several rices, such as IR52, IR8103-120-3, IR9669 selection, and IR5624-110-2, scored ratings of 1, which is considered outstanding. At 10 bars SMT, IR8103-120-3, which was derived from a cross involving Aus 197, a dryland rice from Bangladesh, received a rating of 1, which was considerably superior to the reactions of the drought-tolerant checks (Table 2).

It is interesting to note that a number of the rices identified for drought tolerance were deepwater rices from Thailand — Leb Mue Nahng 111 (one of the parents of IR442-2-58), Khao Dawk Mali 105, BKN6986-108-2, and KLG6986-143-2-P. BKN6986-108-2 is a cross between the semidwarf IR262 and the traditional Thai deepwater variety Pin Gaew. De Datta and O'Toole (1977) pointed out that deepwater rices generally encounter drought problems at the seedling stage, thus experiencing natural selection for drought tolerance at the vegetative stage. In Thailand, drought occurred in 60 years of the 126-year period, 1831-1957 (Chang et a1 1979). In 1980, BKN6986-66-2 was named as RD17 and BKN6986-147-2 as RD19, drought-tolerant deepwater rices for Thailand. Figure 1 shows drought tolerance of RD19 (BKN6986-147-2), first reported from a 1976 test (De Datta and O'Toole 1977), and Figure 2 shows drought tolerance of IR52 and



**1.** Effects of levels of soil moisture tension on reaction to drought stress during seedling and vegetative stages of field-screened rices. IRRI, 1976 dry season. 1 to 9 scale: 1 = no stress symptoms, 9 = completely dead (adapted from De Datta and O'Toole 1977).



**2.** Effects of levels of soil moisture tension on reaction to drought stress of field-screened rice during the vegetative stage. IRRI, 1978 dry season. 1 to 9 scale: 1 = no effect of stress, 9 = all plants apparently dead (adapted from De Datta et al 1979).

RD19 in the 1978 test (De Datta et al 1979). RD19 continued to show excellent drought tolerance in the 1980 test (Table 3).

Nam Sagui 19 was involved in three of the seven crosses, progenies of which exhibited consistently tolerant reactions to drought in the 1977-79 tests. Nam Sagui 19 was involved in five of only six crosses that had drought-tolerant progenies in the 1978 drought screening (De Datta et al 1979). Nam Sagui 19 itself at 10 bars SMT has shown a moderately susceptible reaction to drought (Table 2). Possibly the gene for tolerance in this variety is in a hypostatic condition and the inhibitor was triggered in the recombination resulting from crosses with the other parents involved in the study. Alternately, the tolerance at higher levels of stress (10 bars) in the progenies might be a result of a complementary interaction. Among the promising crosses was IR52 (Nam Sagui 19/IR2071-88//IR2061-214-3-6-20), which recently gained considerable attention because of its high yielding performance in IRTP trials (IRRI 1979a).

Other varieties frequently involved in the parentage of several promising lines include the traditional tall, blast-resistant varieties Carreon and Tetep, the semidwarf variety IR24, and the wild rice *O. nivara.* These results show some interdependence of modern and traditional varieties in developing high yielding rices with moderate to high levels of drought resistance.

## Recovery from drought stress

High level of recovery from drought stress is often more important for high yields in a moderate drought stress condition than high level of drought tolerance but poor recovery when drought stress is relieved. Most tolerant lines and varieties in

**Table 3. Some promising rices for drought tolerance. 4,530 lines screened in IRRI field, 1980 dry season.**

| Designation | Drought score[a] | | Recovery score[b] at 10 bars |
|---|---|---|---|
| | 5 bars[c] | 10 bars | |
| IR45 | 1 | 3 | 3 |
| IR3259-P5-160-1 | 1 | 3 | 1 |
| IR5624-110-2-$A_1$ | 3 | 3 | 1 |
| IR5793-55-1-1-1 | 3 | 3 | 3 |
| IR7790-18-1-2 | 3 | 3 | 3 |
| IR8098-194-2 | 2 | 3 | 3 |
| IR8103-120-3-$A_1$ | 3 | 3 | 3 |
| IR8235-194 | 3 | 3 | 3 |
| IR9266-124 | 3 | 3 | 3 |
| IR9669 selection | 3 | 3 | 1 |
| IR9782-111-2-1-2 | 3 | 3 | 3 |
| IR9852-19-2 | 2 | 3 | 3 |
| IR9852-22-3 | 2 | 3 | 3 |
| IR9852-53-2 | 2 | 3 | 3 |
| IR10206-29-2 | 2 | 3 | 3 |
| IR11288-8-8-288-1 | 3 | 3 | 3 |
| IR11297-170-3-2 | 3 | 3 | 3 |
| IR13149-23-2 | 3 | 3 | 3 |
| IRl3149-71-3-2-3 | 3 | 3 | 3 |
| IR13576-18-2-3-1 | 3 | 3 | 3 |
| IR15718-28-2-2 | 2 | 3 | 3 |
| IR15821-73-2 | 2 | 3 | 1 |
| IRl5849-132-3-3 | 2 | 3 | 1 |
| IRl7076-61-1 | 3 | 3 | 3 |
| RD19 (BKN6986-147-2) | 2 | 3 | 3 |
| BL169 | 1 | 3 | 5 |
| LAC 23 | 2 | 3 | 5 |
| Mal Siraz | 2 | 2 | 3 |
| IR442-2-58 (tolerant check) | 4 | 6 | 3 |
| Salumpikit (tolerant check) | 4 | 5 | 4 |
| IR20 (susceptible check) | 6 | 8 | 5 |
| IRAT 9 (susceptible check) | 7 | 8 | 8 |

[a] Standard Evaluation System for Rice (SES) 1-9 scale: 1 = no to slight effects of soil moisture stress, 9 = all plants apparently dead.
[b] SES 1-9 scale: 1 = 90% plants fully recovered, 9 = no plants fully recovered.
[c] Soil moisture tension (SMT) at drought scoring time.

the 1980 dry season screening test (Table 3) had from 70 to 100% fully recovered plants 10 days after irrigation (recovery scores of 1-3). In that test, the susceptible check IRAT 9 had a score of 8. In the 1980 test, rices showing both excellent drought tolerance and recovery ability were IR3259-P5-160-1, IR5624-110-2-A1, IR9669 selection, IR15821-73-2, and IR15849-132-3-3 (Table 3).

## Reproducibility of field screening results

Relatively uniform drought reactions (scores of 1-3) were observed among the drought tolerant varieties and lines up to 5 bars SMT. There were some variations (mostly differences of 2 units) in reactions at 10 bars SMT. On the whole, the 3-year test showed reproducible reactions to moisture stress of the tolerant to moderately tolerant and susceptible to moderately susceptible rices (Table 2).

## MULTILOCATION TESTING FOR DROUGHT RESPONSE

The IRRI-coordinated IRTP organizes exchange and multilocation testing of breeding lines and varieties in an effort to speed up identification of superior germplasm for diverse rice cultures and stresses. Among the IRTP nurseries are a group for rainfed conditions, including separate observational sets for dryland (IURON), wetland (IRLRON), and deepwater (IRDWON) conditions. For these three categories of rainfed rice, drought tolerance has varying importance and nurseries are screened, among other things, for tolerance to drought.

The dryland observational screening nursery (IURON), in progress since 1975, has been screened more intensively for drought stress. The current results are primarily confined to IURON. Test material for IURON included semidwarfs, intermediates, and talls with a wide range in maturity. Several entries were included on the basis of preliminary information from screening tests at IRRI and from reports from national programs. The countries that participated in the nursery are from Asia, Africa, and Latin America. The test sites represent a wide range in physical and chemical properties of soils and rainfall distribution. The sites experienced varied spells of rainless days in relation to different growth stages.

The IURON entries with the best overall ratings for drought tolerance during

**Table 4. Entries in the International Upland Rice Observational Nursery (1975-79) with best overall ratings for drought tolerance.**

| Year | Test entries (no.) | Entries rated good for drought tolerance |
|---|---|---|
| 1975 | 146 | Aus 8, Aus 61, Azucena, BKN651-23-3-2, Dinalaga, IRl746-226-1-1-2, IR2035-120-3, IR442-2-58<br>(based on 10 tests) |
| 1976 | 185 | Binaritos, ARC7001, ARC7046*, ARC7060*, ARC7102*, ARC10372*, Dular*, Surjamukhi, E425, IRATIO, Aus 61*. DV110*, DZ41, M1-48<br>(based on 14 tests) |
| 1977 | 153 | Sein Ta Lay, Aus 61*, DM59*, DJ29*, DV110* ASD7, DZ41, ARC10372*, Dular*, FH109, IR2035-349-2*, Salumpikit*, Surjamukhi, IRAT13*, IR442-2-58, IR45, BR51-46-5<br>(based on 12 tests) |
| 1978 | 190 | C166-135, DV110, M148, IR7777-7-1-1, IR5, Surjamukhi, IRATl04*, IRAT108*, IRAT109* IRAT110*, CTG1516<br>(based on 10 tests) |
| 1979 | 141 | IR5260-1, RP1158-111-1, BG35-2*, IR3880-29, ARC1175*, IR5931-81-1-1, IR8103-34-1*, KMP12, BPI &6 (NS)*, B995-BCI-1B-113, IAC25*, Salumpikit*<br>(based on 12 tests) |

* Also rated good for recovery.

1975-79 are summarized in Table 4. Promising entries include semidwarfs (IR2035-349-2), intermediates (C166-135), and talls (Salumpikit). They vary in maturity from early (Dular), medium (IR45), and late (IR5). Some entries most frequently rated good for drought tolerance include Aus 61, DV110, Salumpikit, Surjamukhi, ARC10372, M1-48, and IR442-2-58. The entries consistently rated good for both tolerance to and recovery from drought were Aus 61, DV110, ARC10372, and Salumpikit.

These entries were identified on the basis of average scores over different locations in different years, where the conditions of drought in respect to duration and occurrence in relation to crop growth stage are not the same from trial to trial. They reflect potential for generalized performance. To assess varietal performance in relation to specific situations, selected case studies are summarized in Table 5.

The screening results suggest these points:

1. Traits tolerance to and recovery from drought do not appear to be associated with plant height or growth duration. However, good performance of some early-maturing varieties might result from an escape mechanism, either singly or in combination with a certain degree of tolerance. It should be noted that root-shoot ratio rather than plant height contributes to the ability of a plant to withstand drought. Early seedling vigor is another important criterion for which varietal differences are discernible.
2. Lack of consistent performance in some entries may be due to a) specificity of tolerance in relation to growth stage or duration of stress, or both, and b) confounding effects of associated soil problems for which varietal differences exist. A variety may be tolerant of drought but may not be able to express this trait under natural field conditions. It may be affected by some location-specific problems, either independent of or resulting indirectly from low levels of moisture. This would explain, at least in some instances, why a certain entry rated good for drought tolerance at one location did not rate as high at another location that had comparable moisture stress in terms of duration and growth stage period.
3. Despite the climatic, physiographic, and edaphic variations among the test sites, entries such as Salumpikit have shown a greater degree of consistent performance (Table 5).
4. The multilocation screening results confirm the drought tolerance in some of the varieties or breeding lines identified earlier at IRRI (Salumpikit, IR5, Dular, M1-48, IR442-2-58, ARC10372, CTG1516, BPI 76 (NS), IR3880-29).
5. The Assam Rice Collection from Northeast India proved to be a good source of donor material for various biological stresses. Several also are identified as tolerant of drought. Among those, ARC10372 appears outstanding.
6. BKN6986-108-2 and IR442-2-58 are bred for medium deepwater rice culture, which often experiences drought in the early growth stage. The tolerance for drought in these two cultivars at seedling and tillering stages, as evidenced by the IURON tests, is significant.
7. The entries rated good for drought tolerance included both panicle number types (IR442-2-58) and panicle weight types (IRAT 10). Some tolerant

**Table 5. Performance of entries in International Upland Rice Observational Nursery under selected situations representing range in drought pattern and soil characteristics, 1976-79.**

| Year | Location or country | Soil | | Rainfall | | Drought occurrence | Entries (no.) | Entries rated good on phenotypic judgment |
|---|---|---|---|---|---|---|---|---|
| | | Texture | pH | Amount (mm) | Days | | | |
| 1976 | Khonkaen, Thailand | Sandy loam | 5.0 | 608 | 77 | Several shorter spells during seedling and tillering stages, long spell during reproductive stage | 185 | IR1746-226-1-1-4, IR1754-F5B-16, Azucena, IR9575, Sel., Dinalaga, Kinandang Patong, M148, E425, IRAT13, C22. |
| 1976 | Coimbatore, India | Loamy (red) | 7.1 | 334 | 24 | Two long spells, one at vegetative and one at reproductive stage | 185 | IR1754-F5B-22, IR3880-13, Binaritos, C22, M148, Salumpikit, BPI76(NS), G1 1b-Si-141-2. ARC10372, Dular, Surjamukhi, Aus 61, CTG1516, IET1444, SE322B-19, ACC3. |
| 1977 | Nakornrajasima, Thailand | Clay loam | 5.5 | 547 | 46 | At booting and flowering stages | 153 | Aus 8, Aus 61, Salumpikit, DJ29, SE322B-19, Surjamukhi. |
| 1977 | Goiania, Brazil | Sandy loam | 5.2 | 1122 | 86 | Severe drought at tillering and moderate at reproductive stage | 153 | ASD7, N22, LAC 23, Pinulot 330, BG96-3, BG375-1, IR442-2-58. |
| 1977 | Chetumal, Mexico | Clay | 7.2 | 453 | 31 | At reproductive stage | 153 | Aus, DV110, ARC10372, Dular, N22, B981d-Si-28-2, IR2035-349-2, IRAT3, M1-48, Salumpikit, CIG-1516, IR9575 Sel. IR1746-F5B-24, Pah Yan, IR2035-117-3. |
| 1978 | Bhubaneswar, India | Sandy loam | 6.5 | 793 | 85 | Two spells, one at vegetative and one at panicle initiation stage | 190 | B44b-50-2-25, IR5, IR3259-P5-160-1, IR442-2-58, B9c-Md-3-3, Gama 318, BG35-2, IR4528-2-1-2, IR9669 Sel., IRAT111. |
| 1978 | Mtwango, Zanzibar | Clay loam | 6.5 | 986 | 51 | At vegetative stage | 190 | Dular, Pinulot 330, Salumpikit, IR3880-17, RAT107, IRAT110, IRAT111. |
| 1979 | Mahasarakham, Thailand | Sandy loam | – | 593 | 33 | Severe drought at panicle initiation and flowering stages | 141 | Salumpikit, IAC 25, OS6, TOX504-14-11-1, TOX503-7-16-1. |

varieties are bred under irrigated wetland conditions (IR5). This implies that screening for drought tolerance should not be limited to any particular category of rices. Some rice varieties grown under irrigated culture have the potential to adjust under limited moisture supply.

## YIELD AND GENERAL PERFORMANCE UNDER NONASSURED MOISTURE CONDITIONS

Yield performance under nonassured moisture conditions is a result of interaction of the genetic yield potential with several confounding environmental effects. Moisture stress is more frequently a key component of environmental effects under rainfed conditions. This stress varies in intensity, duration, and time of occurrence in relation to crop growth. Yield performance, in a way, reflects the degree of genotypic resilience to aberrant moisture status. One IRTP nursery has been designed for yield testing under rainfed dryland conditions (IURYN). The IURYN entries that produced the highest overall yields over different locations from 1975 to 1979 are listed in Table 6.

Entries which produced statistically higher yields than local checks at selected locations with varying degrees of moisture stress are listed in Table 7. The promising entries included semidwarfs (IR43) and intermediates (MRC172-9). They are either early (IET1444) or medium-duration (IR9669 sel.). IR36, IR43, IR45, and IET1444, semidwarfs developed for wetland irrigated culture, exhibited a high degree of consistency in yield performance over 1975-1979. In several instances, they yielded well compared to traditional tall dryland check varieties.

The results from these yield trials should be assessed in terms of the range of conditions that exist in dryland or in drought-prone areas. In many areas in South and Southeast Asia, frequency of moderate drought is probably higher than frequency of severe drought. Although severe drought conditions provide excellent opportunities to screen rices for yield ability under that situation, genetic variability for severe drought-prone areas is not high, as was pointed out by Jennings et al (1981).

**Table 6. Overall highest yields in the International Upland Rice Yield Nurseries, 1975-79.**

| Year | Trials (no.) | Highest yielding entries |
|---|---|---|
| 1975 | 24 | IR43, IR9575 sel., IR45, MRC172-9, IR2035-108-2 |
| 1976 | 24 | IET1444, IR36, IR43, IR2061-522-6-9, B541b-Kn-19-3-4 |
| 1977 | 27 | IET1444, IR36, C22, IR43, IR2061-522-6-9, IR3839-1 |
| 1978 | 17 | IR43, IR9669 sel., IET1444, IR36, B541b-Kn-19-3-4, IR45, IR3839-1 |
| 1979 | 16 | UPLRi-5, IR9669 sel., BG35-2, IR2061-522-6-9, IR45 |

**Table 7. Entries statistically superior in yield to local checks at selected locations with varying degrees of moisture stress, 1975–79 IURYN.**

| Location | Country | Year | Soil pH | Soil texture | Rainy days (no.) | Total rainfall (mm) | Local check | Entries superior in yield to local check |
|---|---|---|---|---|---|---|---|---|
| ASIA | | | | | | | | |
| Heho | Burma | 1977 | 5.6 | Clay loam | 52 | 1042 | Khao Pa Pyu | KN361-1-8-6 |
| Ilagan | Philippines | 1978 | – | – | 60 | 1963 | BPI 76 (NS) | IR43, IR36, IR3839-1. IR9669 sel. |
| Batangas | Philippines | 1979 | – | – | 103 | 1946 | BPI 76 (NS) | IR9669 sel., MW10, IR45, IR52, KN96 |
| Ranchi | India | 1976 | – | – | 62 | 1314 | – | IR3880-17, B541b-Kn-19-34, IR45 |
| Mandya | India | 1975 | 6.5 | Sandy loam | 45 | 510 | RP79–14 | IR43, IET1444, IR9575 sel., IR5, MRC172-9 |
| Mugad | India | 1979 | 6.3 | Clay loam | – | – | A67 | Gama 318, IR2061-522-6-9, KN96 |
| Faizabad | India | 1975 | 7.5 | Sandy loam | 53 | 651 | N22 | IET1444, IR43, IR45, IR1154-243 |
| Parwanipur | Nepal | 1978 | 6.0 | Loam | 71 | 1599 | China 45 | IR43, IR9669 sel. |
| AFRICA | | | | | | | | |
| Rokupr | Sierra Leone | 1975 | – | – | – | – | Rok 1 | IR43, IR937-55-3, IR45, IR5, MRC172-9, IR1487-141-6 |
| Santchou | Cameroon | 1979 | 5.0 | Clay loam | – | 973 | IRAT79 | IR2061-522-6-9, IR43, IR45, UPL Ri-5, IR9669 sel., IR52 |
| LATIN AMERICA | | | | | | | | |
| Goiania | Brazil | 1975 | 5.3 | – | – | – | IAC1246 | IET1444 |
| Chetumal | Mexico | 1978 | 7.2 | – | 40 | 860 | Cica 6 | IR43, IR45, MRC172-9, C22 |

In many rainfed areas in South and Southeast Asia and in parts of dryland rice areas in Latin America, rice is grown on flat lands with an average annual rainfall of about 2,000 mm over a period of 6-8 months. In those areas, no severe dry periods occur during the rainy season. Substantial areas in the Philippines planted to dryland rice fall into that category (Garrity et al 1978). Similar situations exist in parts of Central America, Colombia, and elsewhere (Jennings et al 1981). In these moisture regimes, some semidwarf varieties developed for wetland rice culture have performed well under well-drained aerobic soil conditions (Tables 8 and 9).

**Table 8. Grain yield of medium- and late-maturing rices that performed well under dryland rice culture in 2 years of yield trials in 4-5 Philippine locations.**

| Designation | Grain yield (t/ha) | | | | |
|---|---|---|---|---|---|
| | 1977 | 1978 | 1979 | 1980 | Av |
| IR43 | 3.6 | 3.3 | 2.8 | 3.9 | 3.4 |
| IR52 | – | 3.5 | 2.5 | 3.1 | 3.0 |
| IR9560-2-6-3-1 | – | – | 3.2 | 3.6 | 3.4 |
| IR9669 sel. | 3.5 | 3.6 | 3.2 | 3.5 | 3.4 |
| C166-135 | – | – | 2.6 | 3.1 | 2.8 |
| Gama 318 | 3.5 | 3.4 | 2.8 | 3.4 | 3.3 |
| IET1785 | – | 3.2 | 2.6 | 3.3 | 3.0 |
| C22 (local check) | 3.4 | 2.8 | 2.2 | 2.8 | 2.8 |

**Table 9. Grain yield (t/ha) range and means of IR36, IR43, and IR45 in International Upland Rice Yield Nursery (IURYN) under the International Rice Testing Program (IRTP) from 1975 to 1978.**

| Year | Locations (no.) | Countries (no.) | Variety | Grain yield (t/ha) | |
|---|---|---|---|---|---|
| | | | | Range | Mean |
| 1975 | 16 | 5 | IR43 | 1.0-4.7 | 2.9 |
| | | | IR45 | 0.3-4.5 | 2.7 |
| | | | Local check[a] | 0.9-3.1 | 2.0 |
| 1976 | 17 | 4 | IR36 | 1.4-4.8 | 3.1 |
| | | | IR43 | 1.2-5.5 | 3.1 |
| | | | IR45 | 0.3-4.3 | 2.7 |
| | | | Local check[a] | 0.4-4.0 | 2.6 |
| 1977 | 20 | 9 | IR36 | 1.8-4.9 | 3.0 |
| | | | IR43 | 1.0-5.7 | 2.9 |
| | | | IR45 | 0.4-5.5 | 2.7 |
| | | | Local check[a] | 0.9-5.8 | 3.0 |
| 1978 | 13 | 5 | IR36 | 1.8-5.4 | 3.4 |
| | | | IR43 | 1.6-6.4 | 3.5 |
| | | | IR45 | 1.2-6.5 | 3.1 |
| | | | Local check[a] | 0.7-4.0 | 2.6 |
| 1979 | 10 | 3 | IR43 | 1.3-4.8 | 2.5 |
| | | | IR45 | 1.2-4.4 | 2.7 |
| | | | Local check[a] | 1.1-5.0 | 2.7 |

[a] In some instances, especially in later years, modern varieties were used as local checks. Source: Final reports of IRTP nurseries, 1975-1979 (IRRI 1975-1979).

Similarly, IR43 and IR45, two semidwarf modern varieties developed for wetland rice culture, have yielded well in multilocation yield trials (Table 9).

In the West Africa Rice Development Association (WARDA) program, average grain yields of several modern semidwarfs varied from 2 to 3 t/ha (Table 10). Some semidwarfs produced considerably higher than the local check OS6. Yields as high as 7.8 t/ha have been reported for the north coast of Colombia under generally favorable moisture regimes (Table 11). In these areas, semidwarfs recovered well following a brief dry spell when moisture supply was renewed by rain.

On the other hand, if severe moisture stress occurs during the reproductive and ripening stages, as in the case of veranico-affected rice areas in Brazil, most semidwarfs such as IR36, IR43, and IR45, intermediate-statured rice such as KN 361-1-8-6 from Indonesia, or even the local checks produced none to extremely

**Table 10. Grain yield performance of medium-duration rices under dryland culture in West Africa. West Africa Rice Development Association (WARDA) coordinated variety trial, 1973-1979 (adapted from Choudhury and Abifarin 1981).**

| Rice | No. of years tested[a] | Average growth duration (days) | Average grain yield (t/ha) |
|---|---|---|---|
| IR442-2-58 | 6 | 124 | 3.2 |
| IR1529-680-3 | 4 | 128 | 2.7 |
| ROK2 | 4 | 128 | 2.4 |
| IRAT13 | 5 | 117 | 2.4 |
| ROK 1 | 5 | 124 | 2.3 |
| IRAT9 | 4 | 115 | 2.2 |
| LAC23 | 7 | 131 | 2.1 |
| 63 -83 | 4 | 118 | 2.1 |
| Iguape Cateto | 5 | 124 | 2.0 |
| OS6 | 4 | 119 | 2.0 |
| ROK3 | 4 | 135 | 2.0 |
| Moroberekan | 5 | 127 | 1.8 |

[a] Several locations each year.

**Table 11. Yields of 4 promising lines under favored dryland conditions in Colombia. Regional trials 1979 B-1980 A (adapted from Jennings et al 1981).**

| Entry number | Yield (t/ha) | | | |
|---|---|---|---|---|
| | North Coast | | Eastern Plain | |
| | 1979 B[a] | 1980[b] | 1979 B | 1980 A |
| 5685 | 3.2 | 6.0 | 6.0 | 5.2 |
| 5709 | 2.6 | 6.3 | 5.2 | 5.5 |
| 5715 | 2.0 | — | 4.3 | — |
| 5738 | 2.5 | 7.8 | 4.7 | 4.6 |
| CICA8 | 2.7 | 6.7 | 5.2 | 5.2 |
| CICA4 | 2.7 | 4.7 | 2.6 | 4.5 |

[a] Low rainfall.
[b] Good rainfall.

**Table 12. Performance of several lines and varieties under dryland conditions in Brazil. VIRAL-S, 1978 (adapted from Jennings et al 1981).**

| Line, variety | Yield (t/ha) | | | | |
|---|---|---|---|---|---|
| | UEPAE$^a$ Bacabal | CNPAF$^b$ Goiania | IAC$^b$ Campinas | EPAMIG$^b$ Uberaba | UEPAE$^a$ Rio Branco |
| KN361-18-6 | 4.9 | 2.6 | 0.5 | 0.7 | 4.0 |
| IR36 | 5.4 | 2.2 | 0.2 | 0.6 | 3.9 |
| IR43 | 5.6 | 1.7 | 0.2 | 0.1 | 4.3 |
| IR45 | 6.3 | 0.5 | – | 0.2 | 3.8 |
| CICA8 | 6.3 | 0.8 | – | 2.0 | 3.3 |
| CR1113 | 5.3 | 0.1 | – | 3.5 | 3.0 |
| Local check$^c$ | 4.9 | 3.2 | 0.8 | 1.7 | 3.3 |

$^a$Favored upland.
$^b$Unfavored upland.
$^c$Local check = IAC1246, IAC47, IAC25.

**Table 13. Entries with best overall phenotypic ratings, IURON, 1976-79.**

| Year | Trials (no.) | Entries rated good for acceptability |
|---|---|---|
| 1976 | 20 | IR1746-226-1-1-4, IR2061-522-6-9, IR3880-29 IR33W-23, Binaritos, IR9575 sel. BPI 76 (NS), C22, Dinalaga, Kinandang Patong, M1–48, ARC10372, DV110, DJ29, MRC172-9 |
| 1977 | 24 | Aus 61, P901-22-11-2-6, KN96, DJ29, KN361-1-84. IR3880-17. IR9575 sel., IRAT13, C22, IR1746-F5B-24 |
| 1978 | 18 | Azucena, B733c-67-3-2, BPI 76 (NS), IR3273-339-2-5, IR4503-12-1-3-1, KN96, IR3880-13, IRAT13, IR3646-9-3-1, Kinandang Patong, IR9575 sel., IAC1246. IRAT105, IRAT106, KN361-1-8-7 |
| 1979 | 17 | C8W-21, C732-14, C424-2, KN96, MRC172-9, Salumpikit, C22, Gama 318, IR3880-29, IR9575 sel., BPI 76 (NS), BG35-2, IR5929-12-3 |

low yields of 0.2-0.8 t/ha (Table 12).

These results suggest a lack of apparent association between yield and genetic height potential under dryland conditions. This is possibly due to the lack of relationship between semidwarfing genes and water uptake patterns under those conditions.

In the dryland observational nursery, phenotypic judgment scores are substituted for yield measurement. The phenotypic scores reflect general acceptance for a given situation. Drought tolerance plays a key role in the determination of phenotypic acceptability, but several other factors also are involved. The IURON entries that received the best phenotypic ratings at most locations 1976-1979 are listed in Table 13. Several entries with broad phenotypic acceptability are those that also received good ratings for drought tolerance (Table 4).

These results clearly suggest that, as we continue to identify rices for high levels of drought tolerance, we also should identify rice that would yield well under somewhat milder drought situations. These rices must recover quickly upon renewal of moisture supply to express higher yield potential than many traditional rices. Traditional rices more often have extremely low but stable, yields under droughty conditions but do not respond well to favorable moisture regimes when drought stress is relieved.

## REFERENCES CITED

Chang, T. T., G. C. Loresto, and O. Tagumpay. 1974. Screening rice germplasm for drought resistance. SABRAO J. 6:9-16.

Chang, T. T., B. Somrith, and J. C. O'Toole. 1979. Potential for improving drought resistance in rainfed rice. Pages 149-164 *in* International Rice Research Institute. Rainfed lowland rice: selected papers from the 1978 International Rice Research Conference. Los Baños, Philippines.

Choudhury, M. A., and A. O. Abifarin. 1981. Present and future upland rice improvement strategies at West Africa Rice Development Association (WARDA). Paper presented at the Travelling Workshop on Blast and Upland Rice, 8-14 March 1981, Goiania, Brazil, EMBRAPA, CNPAF. (unpubl. mimeo.)

De Datta, S. K., and H. M. Beachell. 1972. Varietal response to some factors affecting production of upland rice. Pages 685-700 *in* International Rice Research Institute. Rice breeding. Los Baños, Philippines.

De Datta, S. K., T. T. Chang, and S. Yoshida. 1975. Drought tolerance in upland rice. Pages 101-116 *in* International Rice Research Institute. Major research in upland rice. Los Baños, Philippines.

De Datta, S. K., and P. G. Vicencio. 1976. Dry season field screening for drought tolerance in rice at various moisture tension. Paper presented at the American Society of Agronomy Meetings, 28 November-3 December 1976, Houston, Texas, USA. (abstr.)

De Datta, S. K., and J. C. O' Toole. 1977. Screening deep-water rices for drought tolerance. Pages 83-91 *in* International Rice Research Institute. Proceedings, 1976 deepwater rice workshop, 8-10 November 1976, Bangkok, Thailand. Los Baños, Philippines.

De Datta, S. K., J. A. Malabuyoc, N. Supapoj, C. Prechachat, and B. R. Jackson. 1979. International cooperation to screen deepwater rice for drought tolerance at the seedling and early vegetative stages. Pages 277-289 *in* International Rice Research Institute. Proceedings of the 1978 international deepwater rice workshop. International Rice Research Institute, Los Baños, Philippines.

Gangadharan, C., and R. N. Misra. 1979. Importance of mass screening of mutagenized populations for drought, disease and pest tolerant genotypes in rice. J. Nuclear Agric. Biol. 8(1):30-32.

Garrity, D. P., H. G. Zandstra, and R. R. Harwood. 1978. A classification of Philippine upland rice-growing environment for use in cropping systems research. Philipp. J. Crop Sci. 3(1):25-37.

IRRI (International Rice Research Institute). 1974. Annual report for 1973. Los Baños, Philippines. 265 p.

IRRI (International Rice Research Institute). 1975a. Standard evaluation system for rice. Los Baños, Philippines. 64 p.

IRRI (International Rice Research Institute). 1975b. Final report of International Upland Rice Yield Nursery, International Rice Testing Program (IRTP). 35 p.

IRRI (International Rice Research Institute). 1976. Final report of International Upland Rice Yield Nursery, International Rice Testing Program (IRTP). 34 p.

IRRI (International Rice Research Institute). 1977. Final report of International Upland Rice Yield Nursery, International Rice Testing Program (IRTP). 38 p.

IRRI (International Rice Research Institute). 1978. Final report of International Upland Rice Yield Nursery, International Rice Testing Program. 34 p.

IRRI (International Rice Research Institute). 1979a. Highlights of 1978 IRTP nurseries. Los Baños, Philippines. 26 p.

IRRI (International Rice Research Institute). 1979b. Final report of International Upland Rice Yield Nursery, International Rice Testing Program (IRTP). 34 p.

Jacquot, M. 1981. IRAT research to improve and develop upland rice cultivation. Paper presented at the Travelling Workshop on Blast and Upland Rice in Goiania, Brazil, EMBRAPA, CNPAF, 8-14 March 1981. (unpubl. mimeo.)

Jana, R. K., and S. K. De Datta. 1971. Effects of solar energy and soil moisture tension on the nitrogen response of upland rice. Proc. Int. Symp. on Soil Fert. Eval., New Delhi, 9-14 February 1971. 1:487-497.

Jennings, P. R., H. Weeraratne, and C. Martinez. 1981. The CIAT strategy for upland improvement. Paper presented at the Travelling Workshop on Blast and Upland Rice 8-14 March 1981, Goiania, Brazil, EMBRAPA, CNPAF. (unpubl. mimeo.)

Malabuyoc, J. A., E. L. Aragon, and S. K. De Datta. 1980. A field screening technique for evaluating rice for drought tolerance. Paper presented at the 11th annual meeting of the Crop Science Society of the Philippines, 27-29 April 1980. Baybay, Leyte.

Reyniers, F. N., and M. Jacquot. 1978. Demarche pour l'obtention de la resistance varietale a la secheresse. L'Agric. Trop. 33(4):313-317.

Sullivan, C. Y. 1971. Techniques for measuring plant drought stress. *In* Drought injury and research in crops. Crop Sci. Soc. Amer. Spec. Publ. 2.

Yoshida, S., M. Shioya, E. de los Reyes, V. Coronel, and F. T. Parao. 1974. Physiological basis and techniques for screening drought resistance. Paper presented at a Saturday seminar, 16 March 1974, International Rice Research Institute, Los Baños, Laguna, Philippines. (unpubl. mimeo.)

# BREEDING RICE VARIETIES FOR DRYLAND AND DROUGHT-PRONE AREAS OF INDIA

D. CHAUDHARY AND M. J. B. K. RAO

Almost 15% of India's rice area is planted to rainfed dryland rice. Its production depends on the distribution and amount of rainfall. Average rice yield in rainfed dryland areas is low because of periodic drought, adverse soils, and lack of improved varieties. Drought resistance appears to be the most important single factor in increasing and stabilizing of rice production in the dryland area.

Cultivated dryland rice varieties comprise both the traditional tall plant types grown on 80% of the cropped area and modem semidwarfs grown on the remaining areas.

Drought resistance is a relatively new breeding objective in rice. Progress has been limited because past efforts have been based on empirical testing and selection methods. Genetic studies show that all adaptive mechanisms to drought in rice are heritable and are controlled by complex quantitative characters. Greater progress can be expected through interdisciplinary research efforts and appropriate breeding methodology.

Dryland rice occupies 15% of India's total rice area, which varies greatly in topography, land, and soil type. Dryland soils are characterized by low nitrogen, phosphorus, and iron and also have poor capacity for retaining moisture and nutrients.

---

Scientist-S1, Division of Genetics and Plant Breeding, CRRI, Cuttack 753006 (presently postdoctoral fellow, IRRI, P.O. Box 933, Manila, Philippines); and head, Division of Genetics and Plant Breeding, Central Rice Research Institute, Cuttack, India.

Dryland rice is distributed in both high and low rainfall zones. The dryland rice areas in Kerala, West Bengal, part of Orissa, and the northeastern states comprise the high rainfall category. The large dryland rice areas with low rainfall (700-1100 mm/year) are in Uttar Pradesh, Madhya Pradesh, Gujarat, Rajasthan, and parts of Bihar, Andhra Pradesh, Maharashtra, and Tamil Nadu. These areas suffer periodic drought because rainfall is uneven (Rao et al 1971).

The average yield of dryland rice is poor partly because of the lack of improved varieties. The dryland rice area is so large that even marginal increases in average yield would substantially improve living conditions in this area and might influence the total rice production of India. Research shows that production and productivity can be improved through varietal improvement and improved agronomic practices.

## PRESENT STATUS OF DRYLAND RICE

Based on rainfall pattern and intensity, the dryland rice tracts can be categorized as: 1) areas with adequate rainfall (1,100–2,000 mm/year) and 2) areas with low to moderate rainfall (700-1,100 mm/year). Soil nutrient problems cause low yields in areas of adequate rainfall (Ponnamperuma 1975). In the low rainfall areas, stress at critical crop growth phases is the major factor limiting yields. An analysis of rainfall patterns over 80 years (Table 1) showed that maximum drought spells lasted only 8–9 days from July to September (George et al 1974). Short-duration varieties with drought resistance are needed to help crops escape drought.

Table 2 shows popular dryland rice varieties under cultivation in India. Some possess drought resistance and wide adaptability, but all yield poorly (0.7-1.5 t/ha). Most have coarse grains with red kernels. The main advantage of these varieties appears to be their inherent earliness, which allows them to mature before the cessation of the monsoon rains.

### Breeding and selection procedure

*Basis of drought tolerance.* Research on standardization of breeding techniques for drought resistance has been minimal—largely because of the complexity of the

**Table 1. Number of breaks in the monsoon rains in 80 years (George et al 1974).**

| Duration breaks (days) | | Breaks (no.) | |
|---|---|---|---|
| | July | August | July-August |
| 3-4 | 28 | 25 | 2 |
| 5-6 | 10 | 12 | – |
| 7-8 | 8 | 9 | 1 |
| 9-10 | 3 | 4 | – |
| 11-12 | 2 | 3 | 1 |
| 13-16 | 1 | 1 | – |
| 17-21 | 1 | 1 | 1 |
| Total | 53 | 55 | 5 |

**Table 2. Popular dryland varieties in different states of India.**

| Variety | State | Total duration (days) | Grain characteristics |
|---|---|---|---|
| MTU 17 | Andhra Pradesh | 90 | Coarse, red kernel |
| Mettasannavari | Andhra Pradesh | 100 | Medium, white kernel |
| Black Gora | Bihar | 100 | Coarse, red kernel |
| Brown Gora | Bihar | 100 | Coarse, red kernel |
| CH45 | Bihar | 105 | Medium, white kernel |
| Sathi 34-36 | Gujarat | 95 | Coarse, white kernel |
| PTB28 | Kerala | 100 | Coarse, red kernel |
| PTB29 | Kerala | 95 | Coarse, red kernel |
| PTB30 | Kerala | 90 | Coarse, red kernel |
| Teenpakhia | Maharashtra | 70 | Medium, white kernel |
| 876 | Orissa | 100 | Medium, red kernel |
| Kalakari | Orissa | 700 | Coarse, red kernel |
| Lalnakanda 41 | Punjab | 95 | Coarse, white kernel |
| TKM1 | Tamil Nadu | 100 | Coarse, red kernel |
| N22 | Uttar Pradesh | 90 | Medium, white kernel |
| Sudha | Uttar Pradesh | 85 | Coarse, red kernel |
| Dular | West Bengal | 95 | Medium, white kernel |

problem rather than a lack of recognition of its importance. But research efforts on drought resistance have been intensified at the Central Rice Research Institute (CRRI), the All-India Coordinated Rice Improvement Project (AICRIP), and IRRI.

At CRRI, considerable work has been done to evaluate existing early varieties for adaptability in dryland areas of sufficient and deficit moisture regimes (Murty et a1 1967, Bhattacharjee et a1 1971). Even conventional dryland varieties and land races vary widely in drought resistance and in adaptability to withstand drought at different growth stages. Varieties such as Lalnakanda 41 and CH 45 showed better drought tolerance at the seedling and tillering stages, while MTU 17 could stand moderate drought even at the flowering stage. Donors for drought resistance at different growth stages are available.

Techniques for assessing the relative drought resistance of varieties under known stress conditions are important prerequisites for breeding. The survival rate of seedlings under prolonged soil desiccation gave reliable information on relative drought tolerance. This was confirmed with controlled pot culture and field trials (Murty et a1 1967).

*Early attempts.* Dryland rice improvement programs in their earlier phases primarily involved the isolation of pure lines of land or popular local varieties by single plant selection. For example, N 22 was selected from Rajbhog in U.P. and PTB 10 from Thaval Kannan in Kerala. Richharia and Govindaswami (1966) listed more than 150 improved tall varieties with varying maturity durations (80-110 days) for dryland or autumn cropping developed in different states during the first half of the 19th century.

Attempts to develop varieties by hybridization to withstand drought began in Tamil Nadu and Kerala in 1955. Thedrought-resistant variety CO 31 was released from Coimbatore, Tamil Nadu (Rajagopalan 1966), while a few promising cultivars such as Culture 356 were isolated from the cross Krasnodar/Kattamodan at Pattambi, Kerala. CO 31 has long growth duration and is sensitive to photoperiod. Culture 356 is selected under and is suitable for dryland, high-rainfall areas.

*Work in progress.* Currently, the objective for the development of varieties for rainfed dryland areas has been shifted to the isolation of varieties maturing in 90-110 days to fit in the southwest monsoon season that also have resistance to moisture stress when exposed to drought spells.

CRRI has made numerous crosses with selected dryland varieties such as MTU 17, Lalnakanda, and Taichung Native 1 (TN1). The segregating populations of the crosses were direct-seeded and raised in rainfed dryland condition during the wet season. The generations also were advanced during the dry season under field drought conditions induced by withholding irrigation during the vegetative stage. The selection for drought resistance was made on the basis of uniformity in flowering and of normal expression of productive tillers with high panicle fertility. In kharif, the populations were grown under normal rainfall, which was fairly high, and selections were made for seedling vigor, tillering ability, and yield.

Only one variety, CR42-38 (Bala) from the cross N22/TN1 was isolated as a promising variety for direct-seeded dryland conditions (Rao and Chaudhary 1969). The successful adoption of this early-maturing, drought-resistant, semidwarf variety by farmers in the drought-prone states of Madhya Pradesh, Uttar Pradesh, and Bihar attests that there is scope for varietal improvement for dryland droughty conditions.

Rao et al (1971) reviewed the philosophy developed and applied in the evolution of Bala. The general strategy was to identify drought-resistant traditional varieties that were well-adapted to local conditions, cross them with modern varieties with more desirable agronomic traits, and select progeny in situ at drought-prone sites.

Breeding programs for developing dryland strains with 100-day maturity continue to intensify at CRRI, AICRIP, and in certain state programs. In the early phases, well-known traditional dryland varieties were crossed with exotic semidwarf strains (Mohanty 1978). As a result, many varieties with early duration were evolved. Table 3 shows promising semidwarf strains released by the Central Variety Release Committee and by various states by 1978.

CRRI is using induced mutation as a varietal improvement tool. A promising mutant, CRM13-3241, has been isolated that matures in 70 days and can be grown in drylands even with low, erratic rainfall.

Some researchers express doubt about breeding varieties for nonspecific stresses such as drought and advocate the use of early, high-yielding varieties developed under normal irrigated conditions even for stress situations (Krishnamurty et al 1971, Kawano et al 1972). But the constellation of physiological traits and factors that govern productivity in dryland, drought-prone rice differ considerably from those of wetland rice.

The adaptive mechanisms of the component traits for field resistance have been classified as escape, avoidance, tolerance, and recovery. These mechanisms are observed to be heritable (O'Toole and Chang 1978). Hung and Chang (1976) reported the occurrence of aberrant segregation in crosses involving traditional

**Table 3. Dryland rice varieties released by Central Variety Release Committee and by state departments and agricultural universities in India.**

| Variety | Parentage | Flowering duration (days) | Origin[a] |
|---|---|---|---|
| Akashi | IR8/N22 | 80 | AICRIP |
| Annapurna | PTB10/TN1 | 70 | Kerala |
| Anupma | IR6/SLO 16 | 85 | Madhya Pradesh |
| Bala | N22/TN1 | 80 | CRRI |
| Cauvery | TN1/TKM6 | 87 | Tamil Nadu |
| Gaur 3 | N19/IR9-60 | 70 | Gujarat |
| Kanchan | IR8/N22 | 70 | Bihar |
| Karuna | IR8/ADT 27 | 80 | Tamil Nadu |
| Kiran | N22/TN1/T90/IR8 | 70 | Bihar |
| Parijat | TN1/TKM6 | 78 | Orissa |
| Pennai | TN1/ASD1 | 80 | Tamil Nadu |
| Pusa 2-21 | IR8/TKM6 | 80 | IARI |
| Rajendra | IJ52/TN1 | 77 | Andhra Pradesh |
| Rasi | TN1/CO 29 | 85 | AICRIP |
| Rohini | PTB10/IR8 | 78 | Kerala |
| Saket 4 | TKM6/IR8 | 85 | Utter Pradesh |
| Sarjoo 49 | TG5/TN1 | 85 | Utter Pradesh |
| Sarjoo 50 | TN1/T21 | 80 | Utter Pradesh |

[a] AICRIP = All India Coordinated Rice Improvement Project, CRRI = Central Rice Research Institute, IARI = Indian Agricultural Research Institute.

dryland varieties with semidwarf wetland varieties, indicating restrictions in genetic recombination.

Thus the proper choice of parents for a specific character is crucial (Chang et al 1975). Furthermore, three-way and double-crosses appeared to be more effective than single crosses for combining traits from diverse parents. Basic segregating populations can be developed by crossing large numbers of diverse donor parents and advancing the pedigree populations to the $F_4$ or $F_5$ without selection. By selection among such large segregating populations under appropriate environments, a full spectrum of genetic materials adapted to various edaphic conditions can be fixed (Chang et al 1975, IRRI 1978).

Since 1975, efforts to identify and study the most drought-resistant varieties and breeding lines have been made by AICRIP and cooperating plant physiologists at several stations. Studies revealed a high interrelationship of yield and yield components with climatic factors, soil moisture, and plant moisture status. Striking differences among varieties have been identified (AICRIP 1978, 1979).

AICRIP studied moisture stress at the most problematic drought-prone locations of India, including Hathwara, West Bengal; Ranchi, Bihar; Faizabad, Uttar Pradesh; Derol, Gujarat; and Hyderabad, Andhra Pradesh. Although yields varied greatly, several entries proved to be consistently high yielders across years and sites (Table 4).

Currently, agricultural universities with responsibility for drought-prone areas, such as Faizabad, U.P.; Ranchi, Bihar; Bhubaneshwar, Orissa; and Madurai,

**Table 4. Pedigrees of selected top-yielding entries, 1978, 1979, and 1980 AICRIP Studies on Moisture Stress Trials (AICRIP 1978, 1979, and 1980).**

| Entry | Crosses |
|---|---|
| CR141-192 | N22/TN1 //T90/IR8 |
| CR143-2-2 | N22/TN1 //Lal Nakanda |
| IET1444 (Rasi) | TN1 /Co 29 |
| IET2914 | IR8/N22 |
| IET4106 | Cauvery//Baok/N22//Red |
| IET5849 | RPA5824//IR8/N22 |
| IET5850 | RPA5824//IR8/N22 |
| IET5858 | RPA5824//IR8/N22 |
| IET5860 | RPA 5824//IR8/N22 |
| IET5878 | Bala Mutant |
| IET6148 | N22/TN1 //Co 13 |
| IET6155 | IR20/IR24 |
| IET6223 | MRU 15/Waikoku |

Tamil Nadu, have launched specific breeding projects for developing drought-resistant varieties.

Through the India-IRRI Collaborative Program, eight experiment stations in drought-prone areas have undertaken specific research. Segregating materials are generated at IRRI from crosses suggested by the breeding group and the progeny are raised at the participating stations for selection under stress situations.

The national programs are reassessing the problems of rainfed rice. Strategies for breeding drought-resistant rice varieties were discussed in depth at a 1978 symposium and a 1980 group meeting held at CRRI on research priorities in rice improvement for drought-prone areas. A new central dryland rice research station has been established at Hazaribagh, Bihar — an ideal spot for dryland and drought-resistance studies.

## Plant types for dryland and drought conditions

Based on research experience in India and the problems associated with drylands that are often subjected to moisture stress, the following is suggested for an ideal plant type:

- Roots — Well-developed, deep root system with thick, long roots.
- Leaf character — Seedling vigor with rapid buildup of leaf area index at early stages; thick, medium-long leaves that are erect or moderately droopy; good cell elongation; slow leaf senescence; maintenance of high water potential in leaf by stomatal and cuticular resistance.
- Plant characters — Intermediate height (90-100 cm under drought conditions); high root-shoot ratio; ability to survive internal water stress and recover and grow rapidly on hydration; panicle weight type; resistance to major insects and diseases.
- Flowering — Stability and synchrony in flowering with full panicle expression and low sterility.
- Duration — Short growth duration (85-100 days), depending on the location-specific rainfall pattern.

## Breeding methods

Dryland conditions vary from place-to-place, depending on factors such as the soil type, and amount and intensity of rainfall. Therefore, varietal reaction to drought is diverse, even within a group of dryland rice varieties. The search for new donors should be continued. So far, breeding programs have screened a limited number of varieties for dryland adaptability because varietal requirements are poorly understood.

Hybridization programs involving multiple crosses of several genotypes with drought resistance coupled with resistance to adverse soils, diseases, and insects must be designed. Large segregating populations with wider recombinations must be generated and selected under stress at several centers. Immediate attention must be given to the standardization of selection procedures.

It is currently difficult to create known moisture stress or known drought conditions in the field. Hence, there is also a need to devise laboratory techniques based on sound physiological principles for preliminary screening of varieties or segregating material.

## REFERENCES CITED

AICRIP (All-India Coordinated Rice Improvement Project). 1978. Studies on moisture stress. Annual report, kharif, 1978. p. 6.1-6.2.

AICRIP (All-India Coordinated Rice Improvement Project). 1979. Studies on moisture stress. Annual report, kharif, 1979. p. 6.1-6.28.

AICRIP (All-India Coordinated Rice Improvement Project). 1980. Studies on moisture stress. Annual report, kharif, 1980. p. 6.1-6.3.

Bhattacharjee, D. P., G. Ramakrishnayya, and S. C. Paul. 1971. Physiological basis of drought resistance in rice and varietal reaction under drought conditions. Oryza 8(2):75-84.

Chang, T. T., S. K. De Datta, and W. R. Coffman. 1975. Breeding methods for upland rice. Pages 143-157 *in* International Rice Research Institute. Major research in upland rice. Los Baños, Philippines.

George, C. T., P. E. Moray, and V. P. Athyankar. 1974. Rainfall pattern of rice growing areas prone to drought in India. Meteorol. Monogr. Agrimeteorol. 6. Indian Meteorological Department, Poona.

Hung, H. H., and T. T. Chang. 1976. Aberrant segregation of three marker-genes in crosses between upland and semidwarf-lowland varieties of rice. SABRAO J. 8:127-184.

IRRI (International Rice Research Institute). 1978. Annual report for 1977. Los Baños, Philippines. 548 p.

Kawano, K., P. A. Sanchez, M. A. Nuvena, and J. R. Velez. 1972. Upland rice in the Peruvian jungle. Pages 637-643 *in* International Rice Research Institute. Rice breeding. Los Baños, Philippines.

Krishnamurthy, Ch., S. V. S. Shastry, and W. H. Freeman. 1971. Breeding rice for tolerance to drought and salinity. Oryza 8(2):47-54.

Mohanty, H. K. 1978. Breeding rice varieties for upland. Pages 157-178 *in* Indian Council of Agricultural Research. National symposium on increasing rice yield in kharif (February 8-11, 1978). Central Rice Research Institute, Cuttack, India,

Murty, K. S., D. P. Bhattacharjee, S. C. Paul, and A. P. Singh. 1967. Rice varieties for drought stress. *In* National Institute of Sciences Symposium. Science and India's Food Problem, New Delhi, October, 1967.

O'Toole, J. C., and T. T. Chang. 1978. Drought and rice improvement in perspective. IRRI Res. Paper Ser. 14. 27 p.

Ponnamperuma, F. N. 1975. Varietal resistance to adverse chemical environments of upland rice soils. Pages 136-142 *in* International Rice Research Institute. Major research in upland rice. Los Baños, Philippines.

Rajagopalan, K. 1966. Drought resistance paddy strain CO 31. Madras Agric. J. 58:840-841.

Rao, M. J. B. K., and D. Chaudhary. 1969. CR42-38, a new promising upland rice culture. *In* Symposium on planning for drought areas. Abstract of papers, National Institute of Science, India.

Rao, M. J. B. K., K. S. Murty, K. Srinivasulu, and C. Gangadharan. 1971. Breeding for drought and upland conditions in rice. Oryza 8(2):75-84.

Richharia, R. H., and S. Govindaswami. 1966. Rices of India. Sci. Book Co., Patna, India.

# BREEDING FOR DROUGHT RESISTANCE IN DRYLAND RICE

F. N. REYNIERS, TRUONG-BINH, L. JACQUINOT, AND R. NICOU

The aspects of breeding for drought resistance in dryland rice presented here are drought tolerance and agronomic resistance to drought.

Roots were studied under three conditions: 1) in an aeroponic system without constraints, 2) in more or less compacted soils, and 3) in the field using radioactive $^{32}P$ placement. An important varietal difference found was that $^{32}P$ absorption seemed to be related to root weight. The most discriminant root characteristics related to drought resistance are presented.

Resistance to transpiration presented important differences independent of genetic group.

Apparent translocation represents a genetic variability. The effect of drought on this character and on $^{14}C$ migration from stem to grains were compared.

The effects of drought at different growth stages on grain yield showed that susceptibility is highest within ± 20 days to heading. Varieties differ in this susceptibility.

We propose two complementary approaches for breeding. The first is more prospective and tends to assemble resistance factors in the same genotype. The second, already available to breeders, selects lines or varieties showing agronomic resistance to drought at different developmental stages and assembles them in one variety.

---

Institut de Recherches Agronomiques Tropicales et des Cultures Vivrieres, 110 Rue de Universite, 75340 Paris Cedex 07, France.

The results of breeding for drought resistance in dryland rice at the Institut des Savanes, Ivory Coast, and at the Research Institute for Tropical Agronomy and Food Crops (IRAT), Montpellier, are presented. Water conditions in dryland rice in the Ivory Coast were described by Kalms and Forest (1981).

This paper deals with three aspects of varietal selection:

- drought resistance factors: root systems, resistance to transpiration, and use of stem reserves;
- yield differences caused by drought;
- approaches to breeding for drought resistance.

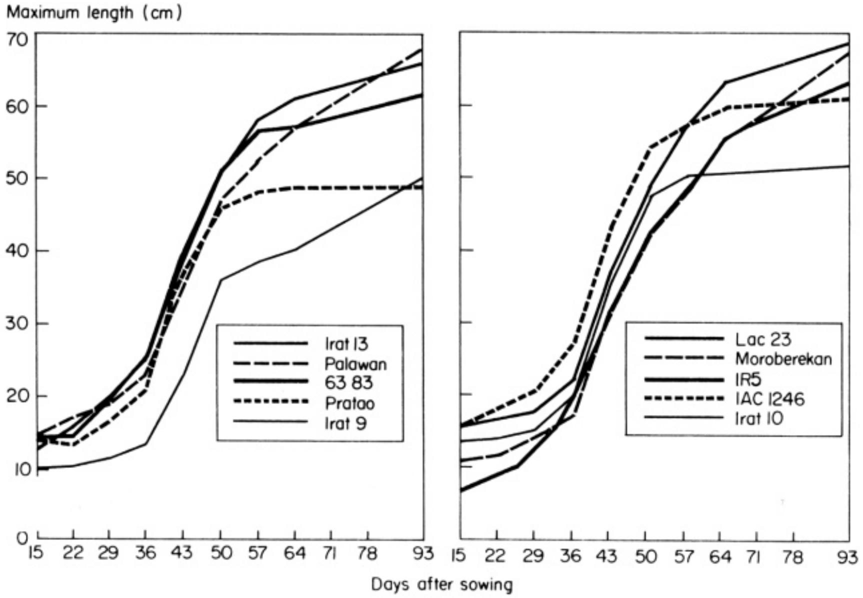
## DROUGHT RESISTANCE FACTORS

### Rooting

Drought resistance in dryland rice is determined partly by rooting characteristics. Our research focused on testing methods to compare varieties for specific characters and limitations.

*Aeroponic system.* Culture on a nutrient mist makes it possible to observe roots continuously during the growth cycle but does not take into account environmental constraints. This system permits the measurement of varietal differences in rooting characteristics.

The method was first tested on 10 rice varieties to estimate the genetic variability of roots (Truong Binh and Beunard 1978). The 10 varieties were chosen for differences in growth cycle, stem height, and tillering — traits that *a priori* can have an effect on rooting. The varieties were IRAT9, IRAT10, IRAT13, IR5, 63-83, Moroberekan, Pratao, LAC23, IAC1246, and Palawan.



**1.** Varietal difference in root growth in aeroponic culture.

The method consists of intermittently spraying a complete nutrient solution as an aerosol in a closed space. A rectangular polyvinyl chloride (PVC) box 150 cm high, 105 cm long, and 65 cm wide was used. The cover was made of 10 PVC jointed sheets 20 mm thick with a series of holes in which seedlings were placed. Seeds were germinated in sand and transplanted to the box after 8 days.

Figure 1 shows the change in length of the longest root during the vegetative period. Growth was slow until 30 days after sowing (DS), probably because of difficulties in adaptation. Then it became rapid (about 2 cm/day) until 60 DS, when a relatively stable level was reached. Growth curves for the 10 varieties were similar, but appeared to differ more distinctly in the last phase.

Important varietal differences in the characteristics measured were found at 90 DS (Table 1). For some varieties, intravariety fluctuations did not permit identification of significant differences. Variety ranking for root length and number was almost inverse. Maximum root length and ratio of root weight to aerial part weight, probably the two most interesting root characteristics for drought resist-

**Table 1. Root characteristics in aeroponic solution 90 days after sowing.**[a]

| Variety | Primary roots (no.) | Primary root length (m) | Max length (m) | Dry matter (mg) | Dry root wt: dry shoot wt | Dry root wt > 30 cm: dry shoot wt |
|---|---|---|---|---|---|---|
| IR5 | 52 b | 15.14 ab | 63 abc | 386 a | 0.132 c | 0.027 ab |
| IRAT9 | 93 a | 20.78 a | 50 cd | 261 a | 0.142 bc | 0.015 ab |
| IRAT10 | 70 a | 17.01 ab | 51 bcd | 547 a | 0.157 bc | 0.024 ab |
| IRAT13 | 48 b | 14.31 ab | 65 ab | 430 a | 0.141 bc | 0.025 ab |
| 63-83 | 56 ab | 15.72 ab | 61 abc | 710 a | 0.169 b | 0.032 a |
| Moroberekan | 42 b | 14.03 ab | 67 ab | 500 a | 0.237 a | 0.063 a |
| Pratao | 64 ab | 13.42 ab | 48 d | 525 a | 0.156 bc | 0.009 b |
| LAC23 | 49 b | 16.14 ab | 68 a | 642 a | 0.232 a | 0.053 a |
| IAC1246 | 47 b | 11.87 b | 60 ab | 440 a | 0.171 b | 0.032 a |
| Palawan | 50 b | 15.51 ab | 67 ab | 416 a | 0.206 a | 0.043 a |
| Mean | 57 | 15.39 | 59 | 485 | 0.174 | 0.032 |
| C.V. % | 28 | 39 | 16 | 51 | 19 | 48 |

[a] Data followed by the same letter are not different from each other by Duncan's multiple range test.

**Table 2. Classification of varieties by 2 root characteristics in aeroponic conditions 90 days after sowing. The characteristics were linked with drought tolerance.**

| Maximum root length (cm) | Varieties with dry root wt-dry shoot wt ratio of | | |
|---|---|---|---|
| | 0.25-0.20 mg | 0.20-0.15 mg | 0.15-0.10 mg |
| 70-61 | Lac 23<br>Moroberekan<br>Palawan | 63-83 | IRAT13<br>IR5 |
| 60-51 | | IRAT10<br>IAC1246 | |
| 50-41 | | PRATAO | IRAT9 |

ance, were among the most discriminant factors. The three traditional varieties ranked first in these while the semidwarf variety IRAT9 ranked last (Table 2). Other varieties were intermediate.

## Root sensitivity to soil compaction

Studies on the effect of plowing often show that soil compaction affects root growth. The aim of this study was to determine whether rice varieties differ in the ability of roots to enter compacted soils and whether the compaction method can be used for varietal screening (Bayogo 1980).

The method consists of compacting 700 g soil at 11% water content with a proctor to obtain 2 densities: $D_1 = 1.8$ and $D_2 = 1.6$. In this trial, a sandy soil (9% clay) from the Montpellier area was used. The core sample was put in a PVC tube. The trial consisted of 10 replications, a total of 70 randomized plants.

Eight seeds were sown on each core sample and covered with 1 cm of noncompacted soil. Seedlings were subjected to an artificial light of 12,000 lx during alternate 12-hour periods. An amount of water equal to that lost by evaporation was supplied daily to each pot.

After 15 days, the core samples were cut into 3 horizons: $H_0$ = 1 cm (noncompacted), $H_1$ = 3 cm, and $H_2$ = 5 cm. Roots were separated by wet sieving, dried at 60° C, and weighed.

Table 3 shows the weight of roots in the three horizons and at the two compaction levels. Results in horizons $H_0$ and $H_2$ were too heterogeneous for statistical classification. On the whole, varieties 63-83, KU86, and Zakpale ranked first in root production in all treatments.

In view of the experiment objective, to study how roots react to soil compaction and how deeply they are able to penetrate the soil, the

$$( 1 - \frac{D1}{D2} ) \times 100$$

**Table 3. Effect of soil compaction[a] on dry weight of root per plant**

| Variety | Root dry wt (0.1 mg/plant) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | $H_0$ | | $H_1$ | | $H_2$ | | Total | |
| | $D_1$ | $D_2$ | $D_1$ | $D_2$ | $D_1$ | $D_2$ | $D_1$ | $D_2$ |
| Zakpalé | 5 | 4 | 41 | 27 c | 22 | 44 | 67 | 75 b |
| Lung Sheng 1 | 5 | 5 | 23 | 18 d | 5 | 12 | 33 | 35 e |
| Moroberekan | 8 | 6 | 29 | 23 c | 5 | 22 | 41 | 51 d |
| 63-83 | 19 | 12 | 57 | 39 a | 14 | 39 | 90 | 91 a |
| IRAT13 | 14 | 10 | 36 | 22 c | 8 | 27 | 59 | 59 c |
| IR5 | 9 | 6 | 21 | 18 d | 7 | 20 | 38 | 44 de |
| KU86 | 15 | 10 | 47 | 35 b | 12 | 35 | 75 | 80 b |
| Mean | 9.1 | | 31.2 | | 19.5 | | 59.9 | |
| C.V. % | 28.4 | | 23.9 | | 34.9 | | 19.1 | |

[a] Density: $D_1$ = 1.8, $D_2$ = 1.6. Horizon: $H_0$ = 1 cm, $H_1$ = 3 cm, $H_2$ = 5 cm. Classification of varieties $\frac{D_1 + D_2}{2}$ : data followed by the same letter are not significantly different by Duncan's multiple range test.

ratio in horizon $H_2$ best expresses production losses in root depth caused by increased compaction. The lower the ratio, the better the adaptation of one variety (Table 4). For this criterion, the varieties that adapted best to constraints were Zakpalé (*O. glaberrima*) and Lung Sheng 1 (*O. sativa, juponica*). Both varieties showed the highest resistance to compaction. Moroberekan showed the lowest.

Both the quantity of roots produced and root sensitivity to soil compaction must be taken into account in characterizing root penetration capacity. Varietal differences in these characters were noted at the seedling stage. Under test conditions, the most favorable combination was found in Zakpalé. Further observations of root quantity and compaction sensitivity on more advanced plants are needed before they can be used as selection criteria.

## Characterization of in situ rooting using $^{32}P$ placement

Rooting must be studied in field conditions to integrate all the factors of root growth in the crop environment. It is too difficult to use digging and washing roots as a screening method. Using a radioactive tracer might be a relatively simple solution.

The principle is to place $^{32}P$ solution in the soil at different depths and distances from the plant and to test and measure the radioactivity absorbed by the aerial parts of the plant (Reyniers et al 1978, Truong Binh 1977).

The method was used on 50 varieties to see whether they have roots at 1-m depth (Reyniers and Truong Binh 1977). The qualitative response was not very discriminating.

A quantitative value of $^{32}P$ absorption was needed. It was advisable, on the one hand, to verify whether this value was related to other root parameters and, on the other hand, to determine the best depth for placement.

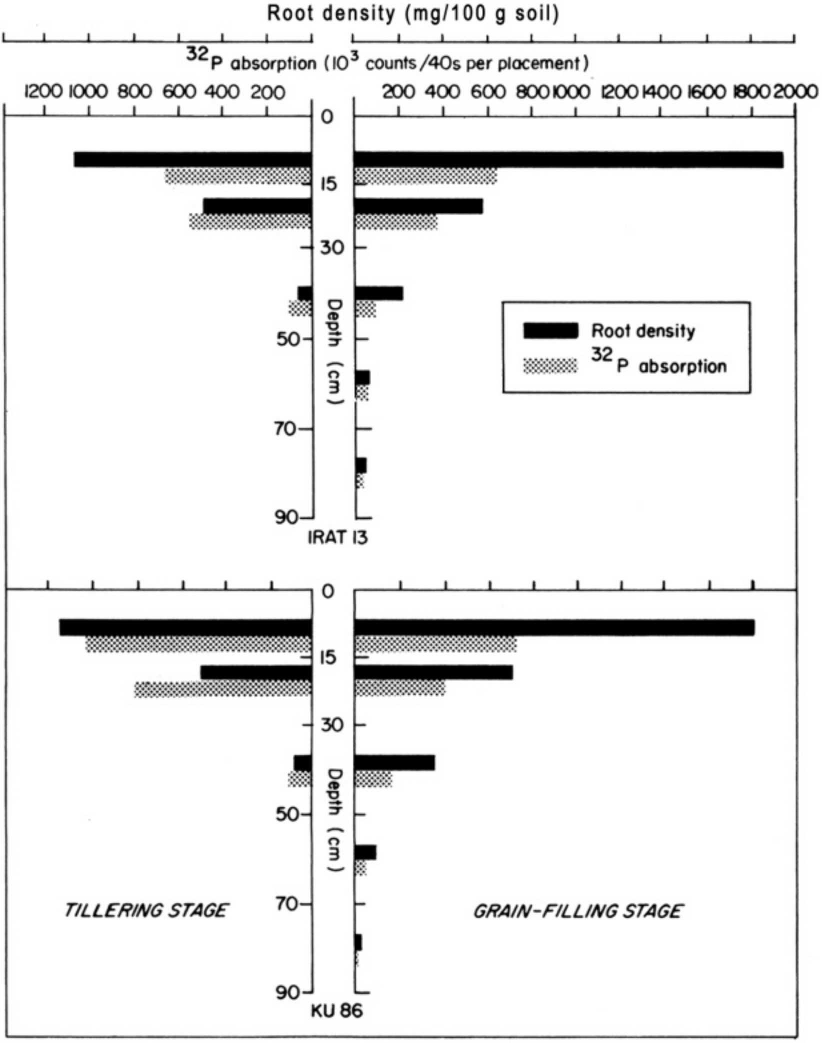
A trial was conducted with 2 varieties — IRAT13 and KU86 — at 2 development stages, 5 depths and 3 lateral distances: at tillering at depths of 10, 20, and 40 cm; at heading at depths of 10, 20, 40, 60, and 80 cm; both at distances of 0, 15, and 30 cm.

$^{32}P$ placements were made on 6 plants/elementary plot and in 6 plots (36 replications). Parallel core samples of roots were taken vertically at the same depths under the $^{32}P$-labeled plants. Roots were separated by wet sieving, dried, and weighed. Figure 2 shows the comparison of the two parameter profiles at

**Table 4. Sensitivity to soil compaction.**

| Variety | Root loss[a] (%) |
|---|---|
| Zakpalé | 51 |
| Lung Sheng 1 | 56 |
| IR35 | 62 |
| 63-83 | 64 |
| KU86 | 66 |
| IRAT13 | 69 |
| Moroberekan | 78 |

[a] Root loss = $(1-\frac{D_1}{D_2})$ 100.

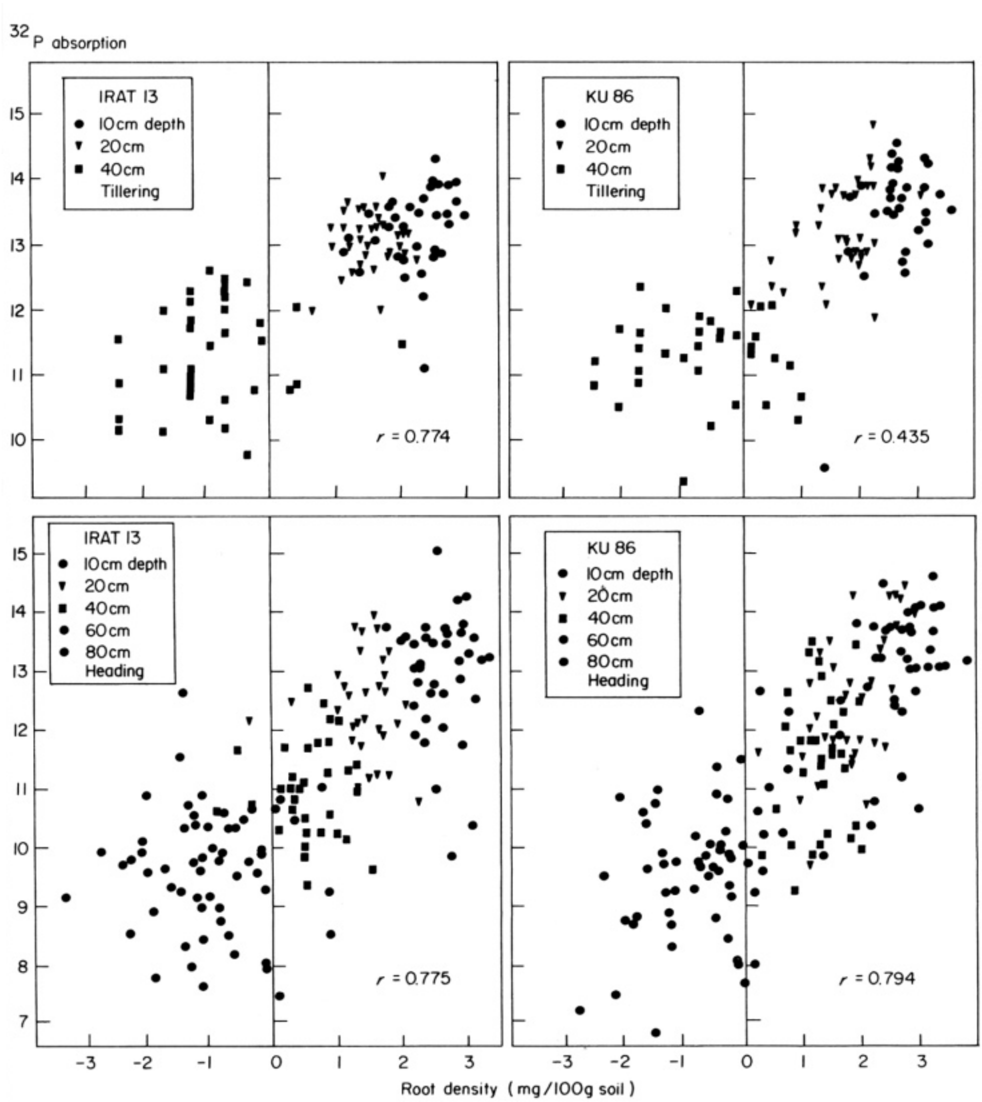


**2.** $^{32}$P absorption profile and root density in situ.

different stages. Figure 3 shows their relationship.

At tillering, $^{32}$P absorption gives relatively more abundant roots at 20 and 40 cm than at the surface horizon. At heading, the two profiles are homogeneous. The same regularity is found in the coefficients of correlation that, on the average, are higher at heading (0.775 and 0.794) than at tillering (0.774 and 0.435). $^{32}$P absorption can be considered representative of root quantities and a good means for comparing *in situ* rooting.

*Variety screening.* About 100 varieties classified as of early, medium-, or late-maturing were cultivated in a field in central Ivory Coast under natural rainfall



**3.** Relationship between $^{32}$P absorption and root density in 2 varieties.

that resulted in an important water deficit during 15 out of 24 weeks. Sowing was adjusted so that all varieties would reach the reproductive stage at the same time to be screened under the same conditions (heading stage).

Root activity at 60-cm depth was evaluated. Radioactive $^{32}$P solution was placed around 3 plants/plot. The treatment was repeated 4 times (12 replications). Table 5 shows that varietal differences exist, irrespective of growth duration.

**Table 5. Varietal differences in $^{32}$P absorbed by roots at 60 cm depth.**

| Varieties | $^{32}$P absorbed at 60-cm depth (counts/per labeled place) |
|---|---|
| *Short-duration varieties* | |
| NO IKU MOCHI | 1757 |
| R 23 K | 1688 |
| SE 349 D | 1453 |
| R 75 | 1189 |
| NO IKU 1517 | 1189 |
| RE 107 | 1142 |
| KU 78 | 1142 |
| KHAO HAY (SDB 18) | 1076 |
| E 425 | 847 |
| LAURENT | 821 |
| TAINAN IKU 512 | 797 |
| IRAT 13/IRAT10 126/3 | 774 |
| KU 113-2 | 766 |
| KU 117 | 766 |
| SECUEMANI L | 714 |
| R 60 | 693 |
| CHUN 139-12 | 666 |
| IRAT 13/DOURADO PRECOCE 598/5 | 642 |
| IRAT I3/IRAT10 287/10 | 621 |
| KU 87-1 | 609 |
| KHAO CHAO (SBB 31) | 602 |
| TAVA LAKKANNAN PTB9 | 567 |
| HOHONO | 539 |
| IRAT13/IRAT10 129/8 | 539 |
| KU86 | 524 |
| IRAT13/IRAT10 163/7 | 479 |
| IRAT110 | 474 |
| RE 19 M | 442 |
| IRAT107 | 429 |
| IRAT108 | 416 |
| KU 56-2 | 408 |
| IRAT10 TEMOIN | 384 |
| IRAT111 | 355 |
| R 54 | 334 |
| IRAT13/IRAT10 244/1 | 302 |
| HAO KHAO (VTB 10) | 282 |
| KU 115 | 276 |
| MACK 0 | 193 |
| CHAO HAY (a) (LBB 40) | 178 |
| PRATAO PRECOCE | 158 |
| *Medium-duration varieties* | |
| IRAT/MOROBEREKAN2603/10 | 3276 |
| IRAT116 | 3169 |
| IRAT13/MOROBEREKAN2303/4/9 | 3137 |
| IRAT13/MOROBEREKAN2303/7/8 | 2647 |
| IRAT13/MOROBEREKAN2532/10 | 2167 |
| IRAM31/8/6 | 1213 |
| IRAT114 | 1201 |
| TAINAN 5 | 1065 |
| TP Sel/ (B 52-4820) 182 | 936 |
| IRAM115/A/2 | 908 |

CONTINUED ON OPPOSITE PAGE

**Table 5. Continued.**

| Varieties | $^{32}P$ absorbed at 60-cm depth (counts/per labeled place) |
|---|---|
| MACK FAY DENG | 846 |
| M 949 m/9/1 | 766 |
| RE 352 V | 736 |
| IRAT106 | 707 |
| IRAT115 | 686 |
| IRAM1632 | 673 |
| IRAM115/B/15/8 | 673 |
| KHAO MONE TIA | 659 |
| IRAT78 | 633 |
| IAC3100 | 602 |
| IRAT138 | 567 |
| IRAM31/6/12 | 562 |
| RT 1077-III A | 524 |
| HT 74-7 | 524 |
| IRAT132 | 519 |
| IRAM31/8/12 | 488 |
| 63-83 | 479 |
| IRAM115/A/2/13 | 446 |
| 63-41 | 442 |
| REUNION HN | 437 |
| KHAO LAY | 408 |
| IGUAPE CATETO | 396 |
| RE 352 GS 24 | 365 |
| IRAT140 | 358 |
| KH-CHE BROCK ATB 7 | 341 |
| I TAME | 334 |
| MAKOUTA | 321 |
| KHAO MONE SOUNG | 318 |
| IRAT13 TEMOIN | 315 |
| IRAM44-9-2 | 311 |
| YRIKPO KOLOTCHIE | 299 |
| IRAT117 | 299 |
| IRAM31-1-4 | 285 |
| RE 352 GS10 | 276 |
| IRAT139 | 265 |
| IRAT104 | 258 |
| IRAT136 | 245 |
| IRAT105 | 245 |
| CS 10 G2 | 219 |
| HYB1229/5/9 | 213 |
| RE 19 A | 189 |
| CI 345 | 163 |
| IRAT103 | 149 |
| *Long-duration varieties* | |
| IRAT13/MOROBEREKAN 2532/8 | 1705 |
| LAC 23 | 983 |
| GBANTE | 872 |
| KH CHERO (ATB 13) | 813 |
| 434 | 693 |
| P 44 | 686 |
| IRAM5/9/12/S | 529 |
| IRAM118/13 | 484 |
| IRAT13/MOROBEREKAN 245318 | 469 |
| IRAT13/MOROBEREKAN 253517 | 420 |

CONTINUED ON NEXT PAGE

**Table 5.** Continued.

| Varieties | $^{32}$P absorbed at 60-cm depth (counts/per labeled place) |
|---|---|
| MACALINO | 420 |
| IRAT137 | 404 |
| K2 C54 | 396 |
| H 5 | 392 |
| MURUNGAKAYAN | 377 |
| IRAM31/5/9 | 351 |
| IRAT113 | 324 |
| K2 B32 | 268 |
| LAC 48 | 250 |
| PATEYON A | 235 |
| HT 74/75 | 226 |
| LAC 73 B | 173 |
| MOROBEREKAN | 136 |
| LINE/MOROBEREKAN 1827/3 | 130 |

Among early-maturing varieties, three (No Iku Mochi, R 23 K, and SE 349 D) were statistically different from the control IRAT10 but not different from many other varieties. Screening medium-duration varieties makes it possible to show the importance of the IRAT13/Moroberekan cross, with four lines (2603/10, 2303/4/9, 2303/7/8, and 2532/10) having markedly higher activity than most other varieties. Two mutants of Moroberekan, IRAT116 and IRAT114, also were promising. In the late varieties, some IRAT13/Moroberekan progeny were notable.

This screening method can be recommended.

## Dryland rice resistance to transpiration

Losses to any other element of water usage must be reduced. For this reason, we studied transpiration regulation. The resistance to transpiration of a cultivated plant is considered one of the major parameters affecting drought resistance (Stigter 1972). Our aim is to define a breeding criterion that is easy to measure and inheritable. Jacquinot et al (1981) defined a method measurement and compared some varieties.

Resistance to transpiration was chosen for physiological and feasibility reasons. From a physiological point of view, high resistance enables the plant to remain somewhat turgescent, not calling on the properties of drying resistance that are generally detrimental to useful yield (Turner 1979).

When several hundred lines must be screened, measurements must be easily reproducible, rapid, and simple. Several available methods meet these criteria.

Methods and materials. Our method was drawn from one used by Henzell et al (1975), who cultivated two sorghum varieties—one control and one test variety—in the same pot. After a time, the roots of the two varieties are closely imbricated. They are continually subjected to the same soil water potential $y_s$. $R_a$ is the leaf resistance to transpiration measured on a given leafofthe control and $R_b$ measured on the test variety.

Both measures ($R_a$, $R_b$) are obtained by subjecting plants $a$ and $b$ in the same pot to the same environmental conditions at the same time. They find the same water potential $\psi_{os}$ in the soil and the same relative humidity, temperature, and radiative energy in the air.

Because this study was aimed at evaluating the response of various genetic materials to drought and, if possible, at rating them as more or less resistant to transpiration, the graphic method was used principally as an illustration, not quantitatively.

Porometer measures made it possible to calculate the R resistance to transpiration from the function $R = \alpha\Delta_t + \beta$, where $\alpha$ and $\beta$ are experimental coefficients depending upon temperature and captor type.

For simplicity in comparing varieties, we adopted the mean value:

$$\bar{Y} = \frac{\sum_1^n (\Delta t_b - \Delta t_a)}{n}$$

where $t_a$ and $t_b$ are porometer readings for the varieties $a$ and $b$ and $n$ is the number of measurement couples ($\Delta t_b$, $\Delta t_a$) made during drought evolution. As

$$R_b = \alpha\Delta t_b + \beta$$

$$R_a = \alpha\Delta t_a + \beta$$

we have

$$\bar{Y} = \frac{1}{9} \frac{\sum_1^n (R_b - R_a)}{n}$$

$Y$ is the mean of the differences obtained during $n$ days of drought with one measurement per day, per plant.

Measurements were made on the lower surface in the middle of the second youngest leaf at a temperature of 29°C.

Plants were cultivated in pots containing 12 liters of clay - calcareous medium to give an adequate moisture-retention capacity to avoid too rapid drying. Pots were watered with a complete nutrient solution (Jacquinot 1969) for a normal water supply.

Drought was obtained by stopping watering until wilting. Light from metal halide lamps was about 850 micro E $m^2$/s. Photoperiod was 10.5-hours light and a 13.5-hours dark.

Control varieties were IRAT13 and the doubled haploids IRAT149, IRAT156, and IRAT157 (Asselin de Beauville 1980). Test varieties were *Oryza glaberrima:* 96, Sangaré; *Oryza brevigulata:* CAS V5; *Oryza sativa, japonica:* Chinei, Lung Sheng 1, Chianan 8; *Oryza sativa,* dryland rice: Pat6 blanc LA, Moroberekan, Pateyon A, Gouantzeti, E 425, Iguape Cateto, 63-83, IRAT10, IRAT106, IRAT110, IRAT112, IRAT133, IRAT140, IRAT146; and *Oryza sativa, indica:* H105, Teksichut, Carreon, IM16, IR8.

*Variety screening.* When compared with itself, differences in control variety

**Table 6. Varietal differences in resistance to transpiration.**

IRAT13 as control

| More resistant | | Equivalent | | Less resistant | |
|---|---|---|---|---|---|
| | $\bar{Y}$ | | $\bar{Y}$ | | $\bar{Y}$ |
| IRAT110 | 9.2 | CAS V5 | 1.3 | H105 | –2.8 |
| 96 | 7.3 | IRAT133 | 0.1 | Carreon | –3.4 |
| IR8 | 6.6 | IRAT73 | 0 | Iguape Cateto | –4.0 |
| Tainan 1 | 5.1 | IRAT140 | –0.3 | Chinei | –4.1 |
| Lung Sheng 1 | 4.5 | IRATI 06 | –0.9 | IRAT146 | –4.3 |
| Gouantzeti J | 2.5 | IRATI 0 | –0.9 | | |
| | | 63-83 | –1.0 | | |
| | | Pate Blanc LA | –1.5 | | |
| | | IM16 | –1.7 | | |
| | | IRAT112 | –1.7 | | |

Double haploids as control

| IRATI 56 | | | IRAT149 | | | IRAT157 | | |
|---|---|---|---|---|---|---|---|---|
| | $\bar{Y} + 0.4^a$ | | | $\bar{Y} - 0.9^a$ | | | $\bar{Y} + 0.1^a$ | |
| Lung Sheng 1 | 1.5 | 1.9 | 96 | 2.5 | 1.6 | 96 | 2.1 | 2.2 |
| 96 | 0.7 | 1.1 | Lung Sheng 1 | 1.7 | 0.8 | Lung Sheng 1 | 1.5 | 1.6 |
| IRATI 10 | 0.5 | 0.99 | IR8 | 1.6 | 0.7 | IRAT110 | 0.9 | 1.0 |
| Iguape Cateto | 0.3 | 0.7 | Moroberekan | 1.3 | 0.4 | IR8 | 0.3 | 0.4 |
| IRAT13 | –0.4 | 0 | IRAT13 | 0.9 | 0 | IRAT13 | –0.1 | 0 |
| IR8 | –0.8 | –0.4 | IRATI 10 | –0 | –0.9 | Iguape Cateto | –0.8 | –0.9 |
| Moroberekan | –0.9 | –0.5 | Iguape Cateto | –0.1 | –1.0 | Moroberekan | –1.6 | –1.7 |

[a] $\bar{Y}$ corrected of the averaged value of IRAT13.

IRAT13 were insignificant, leading to its use as a basis for comparison. Table 6 shows the mean algebraic values of $\bar{Y}$ obtained with different varieties used as control.

Four varieties had a persistently higher resistance to transpiration than IRAT13. They were 96, IRAT110, IR8, and Lung Sheng 1. Differences between the four varieties were not sufficient for ranking. However, other experiments confirmed the good performance of IR8 and the poor performance of Iguape Cateto for resistance to transpiration.

Results were confirmed using other, more stable controls. In the first variety comparisons, when ranking was far from strictly reproducible, it was nevertheless constant when groups corresponding to mean deviations $\bar{Y}$ + 2.5 were considered.

These genetically different varieties had quite similar behavior: 96 ( *O. glaberrima* ), IRAT110 ( *O. sativa,* dryland ), IR8 ( *O. sativa, indica ),* and Lung Sheng 1 ( *O. sativa, japonica* ) were all highly resistant to transpiration. A genetic relationship between IRAT110 and Lung Sheng 1 was noted. Interestingly, two varieties as different as IRAT110 and IR8 showed resistance to transpiration. This character is associated with drought resistance in the dryland rice variety IRAT110 but also exists in other genomes that do not necessarily control drought resistance.

This test seems suitable as a first phase to characterize the types of plants most resistant to transpiration.

## Use of stem reserves to fill grain

If moisture is adequate during the vegetative stage, rices should be able to store assimilates for subsequent use if moisture stress occurs during spikelet filling. Such translocations have been studied in some cereals, but few results have been obtained on varietal differences and drought effect in dryland rice.

Two methods were compared to study varietal differences: apparent translocation and trace $^{14}C$.

Apparent translocation (ATR) was estimated by using the ratio:

$$ATR = \frac{WSF - WSM}{WPM - WPF}$$

where

*WSF* = dry weight of stems at flowering time,
*WSM* = dry weight of stems at maturity time,
*WPM* = dry weight of panicles at maturity time, and
*WPF* = dry weight of panicles at flowering time.

The translocation of photosynthates from the vegetative parts toward grain also was evaluated by using a $^{14}C$ tracer. The vegetative parts are labeled by $^{14}CO_2$ absorption at different developmental stages of the stems from panicle initiation to heading. The ratio of the quantity of tracer in grains at harvest to the initial quantity absorbed by the plant expresses the proportion of photosynthates assimilated before flowering time and used to fill grains. Grain filling during a drought period is compared with a control variety.

*Results.* Apparent translocation was increased by water stress during the grain filling stage, from an average of 23% to 57 per cent (Table 7).

Assimilates labeled by $^{14}C$ before flowering were translocated to grain, from 15% to 45% when labeling proceeded from panicle initiation to heading. But water stress did not increase the phenomenon. It seems it is more adequate to use $^{14}C$

**Table 7. Effect of postflowering drought on apparent translocation and $^{14}C$ translocation assimilated before flowering.**

| Assimilation of $^{14}CO_2$ (DS[a]) | $^{14}C$ in panicle in % of total assimilate | | Apparent translocation | |
|---|---|---|---|---|
| | Control | Water deficit | Control | Water deficit |
| 74 | 14.4 | 10.3 | 41 | 82 |
| 81 | 25.4 | 28.7 | 28 | 63 |
| 93 | 45.3 | 41 | 8 | 27 |
| 101 | 43.3 | 39.05 | 16 | 56 |

[a] Days after sowing.

than apparent translocation to evaluate translocation in rice between vegetative and reproductive organs.

Yet there is large variability in apparent translocation among varieties, even if the exact significance of this character is not clear.

Variety comparison. Fourteen dryland rice varieties were cultivated in the field with natural water supply or with supplementary irrigation during the vegetative phase. Apparent translocation was measured on samples of eight plants each from five replications.

Apparent translocation can be negative when stems continue to grow after flowering (Table 8). Some varieties, such as Moroberekan, showed this characteristic in both treatments. Others, such as Khao Hay, show it when they have not been subjected to water deficit. In both treatments, IRAT104 showed one of the highest apparent translocations and gave the best yields.

Important differences among the varieties make apparent translocation or the direct measurement using $^{14}CO_2$ labeling of photosynthate movement from the vegetative parts toward the grain a character to be taken into account in improving the resistance of dryland rice to drought.

## EFFECT OF DROUGHT AT DIFFERENT STAGES ON GRAIN PRODUCTION

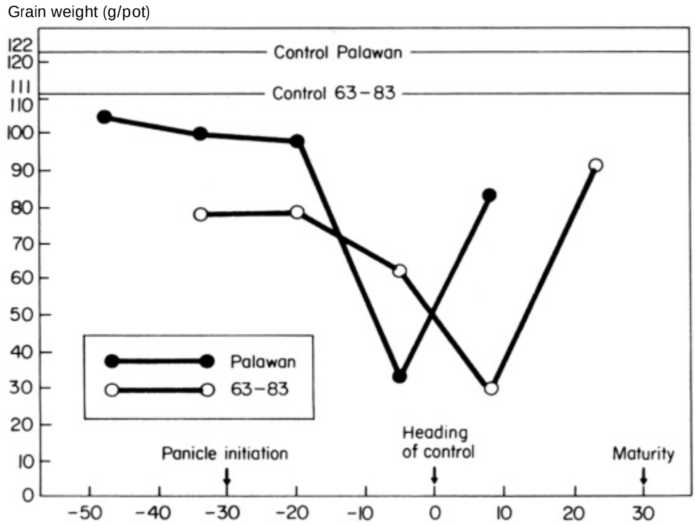
### Pot trial

Grain production as a function of drought at different developmental stages was measured on plants cultivated in pots (Reyniers 1976). For 2 weeks, the water supplied was only 50% of plant requirements. Varieties 63-83 and Palawan were compared.

Susceptibility was highest in the interval ± 20 days toward heading (Fig. 4), with a decrease in production of 30-70%, depending on variety and growth stage.

**Table 8. Varietal differences in apparent translocation with and without drought stress at the vegetative stage.**

| Variety | Apparent translocation | |
|---|---|---|
| | Control | Water deficit at vegetative stage |
| IRAT137 | 0.079 | –0.600 |
| Moroberekan | –0.150 | –0.270 |
| Makouta | –0.027 | –0.120 |
| RE 19 A | 0.340 | –0.230 |
| I Tame | 0.432 | 0.045 |
| M 949 m/0/1 | 0.491 | 0.034 |
| IRAT104 | 0.170 | 0.380 |
| IRAT13 | –0.040 | –0.002 |
| No Iku Mochi | –0.133 | –0.162 |
| Khao Hay | –0.425 | 0.064 |
| KU86 | –0.080 | –0.034 |
| KU115 | –0.102 | 0.340 |
| IRAT133 | –0.735 | 0.023 |
| IRAT10 | –1.491 | –0.470 |



4. Grain production as function of the stage with drought. Drought characteristics:

$$2 \text{ weeks with } \frac{\text{ETR}}{\text{ETM}} = 0.5$$

Production at other growth stages tested was not affected very much. Variety 63-83 was less affected by drought just before heading, but Palawan was less affected by drought just after heading. Spikelet sterility was higher with a post-heading drought period in 63-83 and with a pre-heading drought period in Palawan.

## Field trials

Varietal differences in yield were observed in field trials with imposed drought periods or under natural rainfall. In all cases rainfall distribution was compared with maximum evapotranspiration (ETM) to determine the development periods at which a plant is affected by drought. Varieties were compared only if they had been subjected to water stress of the same intensity at the same growth stages.

### Effect of drought during reproductive period

Reyniers and Kalms (1975) described the design. A 3-week period without irrigation started at the start of the dry season in late November. Sowing dates were chosen so that all varieties would reach testing stages at a particular time. The stages ranged from before panicle initiation to grain filling.

The mean water deficit for the 21 drought days was about 50 mm, half the ETM calculated from climatic data (Kalms 1980). Except during the dry period, irrigation rates equaled ETM, with a few exceptions.

About 60 varieties representing a wide range of genetic variability were tested. Varieties susceptible to blast disease under rainfed conditions at Bouaké were discarded.

**Table 9. Varieties with best yields at given periods of the reproductive stage.**

| Latent stage | | Heading | | Filling stage | |
|---|---|---|---|---|---|
| Variety | Yield[a] | Variety | Yield[a] | Variety | Yield[a] |
| Palawan | 175 | IRAT104 | 129 | IRAT113 | 103 |
| Moroberekan[b] | 100 | IRAT109 | 129 | IRAT13[b] | 100 |
| | | IRAT13[b] | 100 | IRAT104 | 91 |
| | | 63-83 | 78 | Moroberekan | 85 |
| | | IR480 | 69 | IRAT140 | 70 |
| | | Moroberekan | 50 | | |
| | | Palawan | 41 | | |

[a] Yield is % of control. [b] Control.

**Table 10. Yield without (control) or with water deficit at different stages of the reproductive period.**

| Variety | Yield ($g/m^2$) | |
|---|---|---|
| | Control | With drought |
| | *Booting stage* | |
| Moroberekan | 347 | 133 |
| Palawan | 397 | 113 |
| Fossa | 348 | 110 |
| IR5 | 200 | 146 |
| 63-83 | 493 | 232 |
| IRAT13 | 485 | 296 |
| IRAT9 | 414 | 173 |
| | *Panicle initiation and postflowering* | |
| Moroberekan | 317 | 198 |
| Palawan | 321 | 304 |
| Fossa | 380 | 311 |
| | *Heading and flowering* | |
| 63-83 | 483 | 188 |
| IRAT13 | 568 | 272 |
| IRAT9 | 415 | 165 |

Varieties with the best yields at each stage of the reproductive period are listed in Table 9. Ranking was the same from year to year. The most tolerant varieties were IRAT104 and IRAT109 for a drought period at the booting stage and IRAT13 for a drought period at the grain-filling stage.

Table 10 shows the results of a trial with an irrigated control during the drought period. Palawan and Moroberekan were subjected to stress at the panicle initiation stage. An unplanned stress at flowering time caused by a very high evaporation demand due to a dry hot wind and inadequate irrigation made it impossible to determine precisely at what stage Palawan was more tolerant than Moroberekan. Yet from earlier results, Palawan would seem to be more tolerant at the flowering stage. Other authors also found that Palawan showed a particular tolerance at that stage (IRRI 1979).

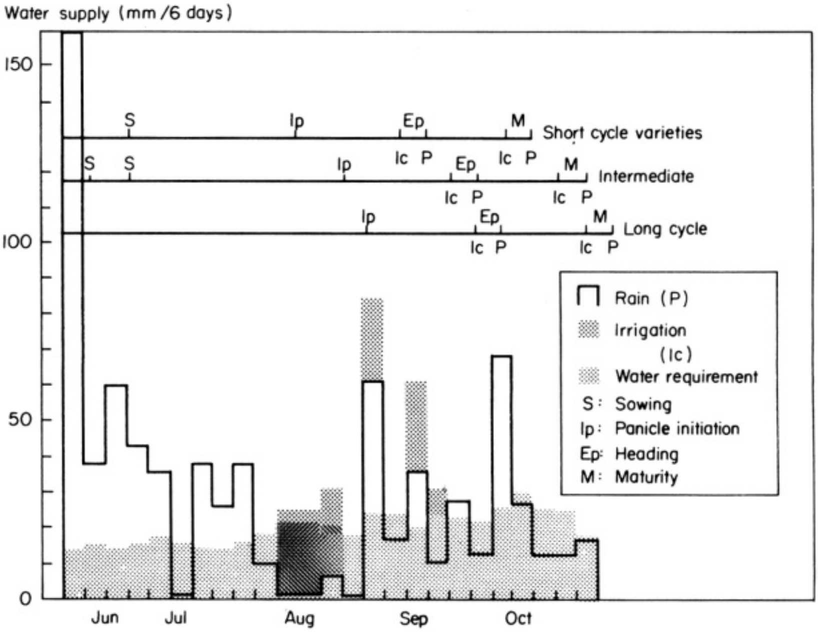
## Tolerance for drought during vegetative period

Sixteen varieties were chosen according to yield stability over several years (Arraudeau 1980). Yields of varieties grown under strict dryland conditions or with supplementary irrigation during the vegetative phase were compared. The

**Table 11. Yield with rainfed conditions and with complementary irrigation at the vegetative stage.**[a]

| Variety | Yield (t/ha) | | Susceptibility coefficient |
|---|---|---|---|
| | Rainfed and complementary irrigation | Rainfed | |
| IRAT104 | 3.38 a | 2.43 a | 0.28* |
| KU86 | 3.30 a | 1.80 | 0.45** |
| KU115 | 3.24 ab | 1.97 cd | 0.39** |
| $K_2C_{54}$ | 3.19 ab | 2.17 abcd | 0.32** |
| 949m/9/1 | 3.11 ab | 2.14 abc | 0.31* |
| IRAT13 | 2.93 abc | 2.23 a | 0.24* |
| Khao Hay | 2.10 abc | 2.10 abc | 0.25 |
| RE19 A | 2.79 abc | 2.21 ab | 0.27* |
| Makouta | 2.58 abcd | 1.75 cde | 0.32* |
| No Iku Mochi | 2.57 abcd | 1.54 de | 0.37 |
| I Tame | 2.49 bcd | 1.90 bcd | 0.23 |
| IRAT 137 | 2.14 cd | 1.42 de | 0.33 |
| KH Chero (ATB13) | 1.76 de | 1.97 abc | –0.12 |
| Moroberekan | 1.32 e | 1.21 e | 0.08 |
| Mean | 2.89 | 1.92 | |

[a] *Significant at 5% level. **Significant at 1% level. In a column, means followed by a common letter are not significantly different.



**5.** Rain, irrigation, and development stages.

coefficient of drought susceptibility was determined as:

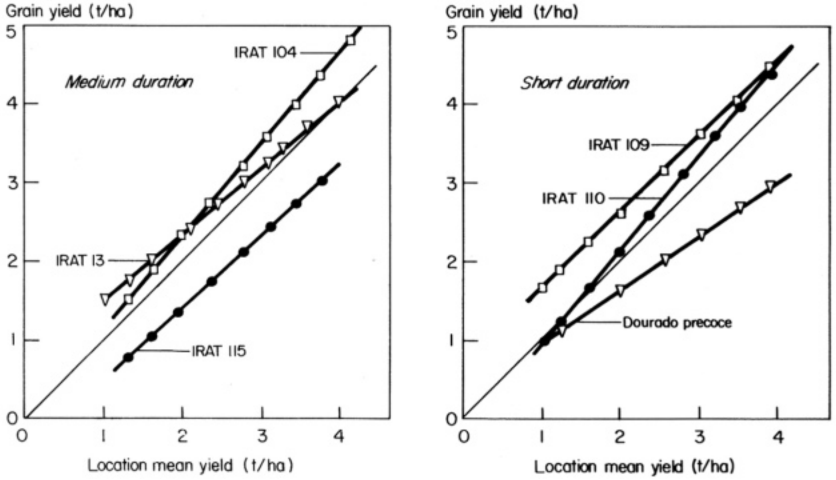
$$S = \frac{Y_i - Y_d}{Y_i}$$

where $Y_i$ = yield with irrigation and
$Y_d$ = yield with a drought period.

*Variety screening.* Variety ranking (Table 11) was not quite the same as ranking by water treatment (Fig. 5). IRAT104 proved best under both conditions. Varieties having lower yields than IRAT104 with supplementary irrigation were I Tame, IRATl37, KH Chero (ATB13), Moroberekan, and, under strictly rainfed conditions, Makouta, No Iku Mochi, IRAT137, and Moroberekan.

Yield rankings according to drought conditions and the coefficient of susceptibility partly correlated with yields under irrigated conditions ($r$ = 0.67). Fischer and Wood (1979) found the same phenomenon with wheat. More stable varieties frequently have lower yields under good conditions.

Effects on yield of drought during the vegetative period was significant on IRAT104, IRAT13, RE19 A, K2 C54, KU115, KU86, and Makouta. Varieties



6. Adaptability analysis of varieties with medium and short duration.

**Table 12. Yields in different regions of the Ivory Coast.**

| Variety | Yield (t/ha) | | |
|---|---|---|---|
| | Bouaké | Odienne | Man |
| IRAT170<br>(from IRAT13/Palawan) | 3.76 | 4.39 | 3.19 |
| IRAT13 | 2.90 | 4.42 | 3.04 |
| RAT104 | 3.36 | 3.90 | 4.03 |

with significant responses to stress were the most productive under both conditions, except for KH Chero, which ranked well only under stress conditions.

## BREEDING FOR DROUGHT RESISTANCE

Two approaches can be envisaged to improve drought resistance, each with two steps.

- First approach
  Step 1. Breed varieties for each factor of drought resistance, in particular deep rooting, high transpiration resistance, and good translocation from the stems toward the grain.
  Step 2. Cross the varieties showing such good characters to accumulate them in the same cultivar.
- Second approach
  Step 1. Select the most tolerant varieties of each stage in a series of field tests, each with drought stress at a different developmental stage.
  Step 2. Cross varieties producing the best yields for each test and screen the lines accumulating tolerance at different stages.

The first approach is prospective. It tries to gather resistance factors not necessarily assembled through natural or artificial breeding in the same genotype.

The second approach has already produced some results. IRAT13, IRAT104, and IRAT109 have been selected in step 1. These varieties showed a wide range of adaptability in West African Rice Development Association multilocational trials of 10 biotypes in West Africa (Fig. 6a,b).

In step 2, it is too early to know if progeny of a cross between IRAT13 and Palawan have combined tolerances at different stages but one, IRAT170, appears interesting (Table 12).

In any case, the approaches appear complementary.

## REFERENCES CITED

Arraudeau, M. 1980. Results of a multidisciplinary trial. DCV/IDESSA, Bouaké, Côte d'Ivoire. 23 p.

Asselin de Beauville, M. 1980. Haplomethod on rice at IRAT. In Celebrating the 20th anniversary of IRRI Spec. Plan. Conf. on Rice Tissue Culture. 28–30 Apr 1980. Los Baños, Philippines.

Bayogo, A. J. 1980. A research for a breeding test for drought resistant varieties of upland rice. Study of root response to soil compactness. Memoire DEA. ENSA, Montpellier. 78 p.

Fischer, R. A., and J. T. Wood. 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. Aust. J. Agro. Res. 80:1001-1020.

Henzell, R. G., K. J. McCree, C. H. M. Van Bavel, K. F. Shertz. 1975. Method for screening sorghum genotypes for stomatal sensitivity to water deficits. Crop Sci. 16:516–518.

IRRI (International Rice Research Institute). 1979. Annual report for 1978. Los Baños, Philippines.

Jacquinot, L. 1969. Millet mineral nutrition. I. Effect of the nature of nitrogenous feeding on nitrogen absorption and growth. L'Agr. Trop. 24(12): 1129-1138.

Jacquinot, L., M. Forget, and K. A. Edah. 1981. Transpiration resistance of upland rice (*Oryza sativa* ). Study of a variety screening test. Institut de Recherches Agronomiques Tropicales et des Cultures Vivrières. (in press)

Jacquot, M., and M. Arnaud. 1979. Numerical classification of rice varieties. L'Agr. Trop. 33(4):307-313.

Kalms, J. M. 1980. Evapotranspiration maxima of upland rice in the center of Ivory Coast. DCV/ IDESSA, Bouake, Côte d' Ivoire. 10 p.

Kalms, J. M., and F. Forest. 1981. Influence of pedoclimatic conditions on upland rice yield in the center of Ivory Coast. Institut de Recherches Agronomiques Tropicales et des Cultures Vivrieres. (in press)

Reyniers, F. N., and J. M. Kalms. 1975. Study of varietal drought resistance in rice for its improvement. *In* Proceedings of physiology program workshop. International Institute of Tropical Agriculture, Ibadan, Nigeria.

Reyniers, F. N. 1976. Annual reports for 1974 and 1975. Physiology department. DCV/IDESSA, Bouake, Côte d'Ivoire.

Reyniers, F. N., Truong Binh, J. F. Bois, E. Bonnin, and G. Thomin. 1979. Characteristics of in situ upland rice rooting with $^{32}P$. *In* Proceedings of isotopes and radiation in research on soil-plant relationships. IAEA. Vienna, Austria.

Reyniers, F. N., and Truong Binh. 1977. Screening with $^{32}P$ for rooting depth among varieties of rainfed rice. *In* Rice in Africa. International Institute of Tropical Agriculture, Ibadan. Nigeria.

Stigter, C. J. 1972. Leaf diffusion resistance to water vapor and its direct measurement. Meded. Land Bouwhogeschool Wageningen, 72-3.47 p.

Truong Binh. 1977. Use of radioactive tracers to study upland rice rooting in Ivory Coast. Rapport AIEA n° 1205.24 p.

Truong Binh and P. Beunard. 1978. Study of the root growth of six upland rice varieties under aeroponic system culture. L'Agr. Trop. 33(3):231-236.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. Pages 343-372 *in* H. Mussel and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

# BREEDING AND SELECTION FOR PLANT TYPE IN DRYLAND RICE

K. ALLURI, J. YAMAGUCHI, J. C. ADJA, AND KAUNG ZAN

High yield potential semidwarf cultivars developed for irrigated wetland conditions do not seem to express their high yield potential in dryland conditions.

IITA research to identify an ideotype for drylands indicated that semidwarf performance in dryland is a variety-specific, not a general plant type characteristic. Dryland semidwarfs should differ from irrigated paddy semidwarfs by having moderate numbers (150-200/$m^2$) of panicles, thicker roots, droopy lower leaves, erect upper leaves, and, even under drought, well-exserted panicles with good grain filling.

An approach to selection for short stature and thick roots indicated that seedling stage selection should be possible. To obtain superior semidwarf cultivars adapted for dryland, it is suggested that a large proportion of semidwarfs with thick roots be selected at the seedling stage in $F_2$ and evaluated under dryland conditions at $F_3$.

Most of the dryland soils where rice is traditionally grown in Africa have low water-holding capacities. When coupled with the relatively shallow rooting habits of improved wetland semidwarfs, this limits the soil volume which plants can exploit for moisture and nutrients. Semidwarfs developed for wetland paddy culture are unsuitable for drylands, where they do not have the capacity to express high yield potentials. Semidwarfs with extensive root development might be

---

The International Institute of Tropical Agriculture, Ibadan, Nigeria.

suitable, but the appropriate plant characteristics for drylands have not been well defined.

Research efforts at the International Institute of Tropical Agriculture (IITA) have focused on identifying ideotype for dryland rice culture. The approach was based on agronomic evaluation and growth analysis of rice varieties under three moisture regimes — free draining dryland, valley bottom near saturated hydromorphic, and well-managed irrigated paddy.

In the initial experiment (Alluri et al 1979), high yield potential, wetland semidwarf cultivar BG90-2; local dryland tall cultivar OS6; and intermediate-statured cultivar TOs 2583 were evaluated under three moisture regimes.

Growth and yield comparisons under three spacings and three water regimes (Table 1) showed the superiority of high yield potential semidwarf BGW-2 in the absence of moisture stress, both under paddy and hydromorphic conditions. In dryland, BG90-2 failed to yield while TOs 2583 and OS6 yielded moderately. Blast disease reduced grain yields of BG90-2 in the hydromorphic location. A combination of severe drought and blast stress ruined productivity in dryland.

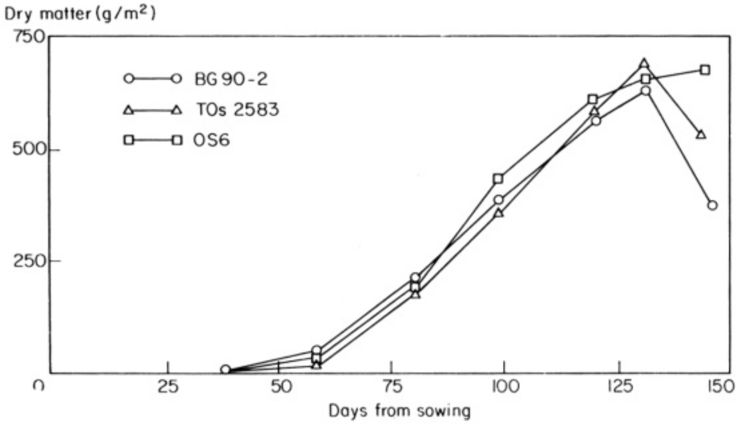
In dryland, there was little difference among cultivars in dry matter production at 60 × 60 cm up to flowering stage (Fig. 1), indicating that growth *per se* was not limiting for BG90-2. High susceptibility to drought and neck blast caused the collapse of BG90-2 after flowering (Fig. 2).

To identify superior cultivars that can resist drought and blast for high yields under dryland conditions, 68 cultivars, including 10 upland talk and 58 semidwarfs, were evaluated in dryland (Ibadan, Ikenne, Onne) and paddy (Ibadan) in Nigeria. Severe moisture and blast stress occurred 90 days after sowing at Ibadan. At Ikenne, moderate moisture stress, brown spot, and neck blast occurred 100

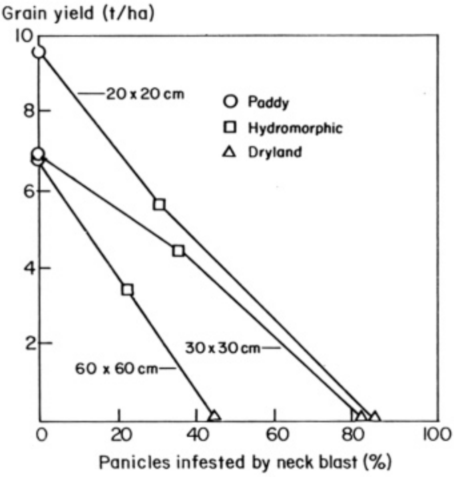
**Table 1. Growth and yield performance of semidwarf, intermediate, and tall ricevarieties under different water regimes. [a]**

| | Grain yield (t/ha) | | | Plant height (cm) | | | Tillers (no./m$^2$) | | | Harvest index (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P | H | D | P | H | D | P | H | D | P | H | D |
| 20 × 20 cm | | | | | | | | | | | | |
| BG90-2 | 9.7 | 5.6 | 0.0 | 115 | 104 | 77 | 265 | 218 | 333 | 54 | 48 | 19 |
| TOs 2583 | 5.4 | 4.3 | 1.9 | 150 | 144 | 124 | 243 | 168 | 332 | 47 | 46 | 27 |
| OS6 | 6.6 | 3.5 | 2.2 | 178 | 182 | 130 | 151 | 156 | 228 | 47 | 40 | 35 |
| 30 × 30 cm | | | | | | | | | | | | |
| BG90-2 | 6.8 | 7.1 | 0.0 | 111 | 108 | 73 | 182 | 170 | 321 | 56 | 51 | 22 |
| TOs 2583 | 4.3 | 4.1 | 2.1 | 148 | 141 | 130 | 158 | 125 | 223 | 50 | 47 | 32 |
| OS6 | 4.2 | 4.4 | 2.1 | 172 | 184 | 142 | 112 | 110 | 166 | 46 | 44 | 34 |
| 60 × 60 cm | | | | | | | | | | | | |
| BG90-2 | 6.7 | 4.3 | 0.1 | 115 | 104 | 78 | 126 | 119 | 165 | 56 | 42 | 33 |
| TOs 2583 | 2.1 | 2.9 | 1.6 | 128 | 147 | 127 | 76 | 83 | 105 | 46 | 50 | 40 |
| OS6 | 2.3 | 2.8 | 1.8 | 164 | 170 | 148 | 49 | 55 | 100 | 49 | 49 | 40 |
| s.e. + | 0.64 | 0.45 | 0.29 | | | | | | | 1.4 | 1.2 | 2.4 |
| C.V. % | 36.0 | 31.0 | 42.6 | | | | | | | 8.3 | 8.1 | 23.7 |

[a] P = paddy field, H = hydromorphic field, D = dryland field.



**1.** Dry matter production per day in BG90-2, TOs 2583, and OS6 at 60 × 60 cm spacing in dryland.



**2.** Effects of drought: blast stress on grain yield of BG90-2.

days after sowing. At Onne, no blast was prevalent. Drought occurred 95 to 100 days after sowing. Soils at Onne are highly leached Ultisols with low organic matter, low CEC, and low pH.

At IITA, most semidwarf yields were extremely low. Some produced no grain because of their susceptibility to the drought and blast complex (Alluri et al 1979). However, their grain yields in paddy were high. The top 15 gave yields ranging from 5.8 to 8.2 t/ha (Table 2). At Ikenne, most yielded reasonably well in the

**Table 2. Performance of rice cultivars with high yield potential at different locations in Nigeria, 1978.**

| Cultivar | Grain yield[a] (t/ha) | | | | Growth duration (days) | Plant height (cm) | Panicles (no./$m^2$) |
|---|---|---|---|---|---|---|---|
| | Paddy Ibadan | Dryland | | | | | |
| | | Onne | Ikenne | Ibadan | | | |
| BG66-1 | 6.7 | 0.8 | 3.1 | 0.0 | 135 | 110 | 248 |
| C4-63 | 7.2 | NT | 0.8 | 0.3 | 157 | 127 | 306 |
| IET 1996 | 6.88 | 0.69 | 2.61 | 0.20 | 147 | 92 | 376 |
| IR8 | 6.7 | 1.0 | 3.6 | 0.0 | 130 | 91 | 207 |
| IR1416-131-5 | 6.6 | 0.6 | NT | 1.2 | 140 | 98 | 331 |
| IR43 | 6.9 | 1.2 | 3.2 | 0.0 | 124 | 85 | 237 |
| IR2035-120-3 | 8.2 | 1.7 | 4.4 | 0.4 | 138 | 107 | 305 |
| IR2035-244-3-2-2 | 7.2 | 0.7 | 3.3 | 0.3 | 153 | 95 | 374 |
| IR2061-228-3-9 | 6.9 | 0.9 | 1.7 | 0.3 | 125 | 131 | 288 |
| IR2071-586-5-6-3 | 5.8 | NT | 2.4 | 0.8 | 132 | 108 | 330 |
| IR2071-588-3 | 6.0 | 0.8 | 2.3 | 1.4 | 154 | 108 | 418 |
| PMI 6624-257-1 | 7.0 | 1.5 | 2.5 | 0.0 | 138 | 118 | 199 |
| RP4-14 | 7.2 | 1.2 | 2.4 | 0.0 | 146 | 110 | 254 |
| RPW6-17 | 6.9 | NT | 3.2 | 0.0 | 139 | 104 | 285 |
| TOX514-16-101-1-1 | 7.7 | NT | 4.6 | 1.2 | 114 | 113 | 350 |
| BG90-2 (check) | 7.9 | 1.2 | 2.4 | 0.0 | 129 | 106 | 258 |
| OS6 (check) | NT | 1.9 | 2.4 | 0.9 | 120 | 180 | – |

[a] NT = not tested.

absence of severe dryland stresses.

The data suggest that most semidwarfs selected for paddy do not have resistance to dryland stresses. However, grain yields of IR1416-131-5, IR2035-120-3, IR2071-588-3, and TOX514-16-101-1-1 in some dryland locations were better than the yield of the local dryland variety OS6. This indicates that performance in dryland is variety-specific, not a general plant type characteristic. As such, the semidwarf plant type *per se* should not be a limitation for dryland cultivation.

To identify the grain yield components and plant characters important for

**Table 3. Correlation matrix between selected plant parameters for 36 varieties under 4 drought treatments.**

| Plant parameter | Mean value | Plant height (cm) | Panicle exsertion (cm) | Panicle number (per hill) | Grain weight (g/hill) | 1,000 grain weight (g) | Weight per panicle (g) |
|---|---|---|---|---|---|---|---|
| Plant height (cm) | 107 | 1.0 | | | | | |
| Panicle exsertion (cm) | 3.9 | .45* | 1.0 | | | | |
| Panicle number (per hill) | 9.2 | .01 | –.06 | 1.0 | | | |
| Grain weight (g/hill) | 14.5 | .46* | .28* | .30* | 1.0 | | |
| 1,000 grain weight (g) | 13.8 | .46* | 27* | .28* | .98* | 1.0 | |
| Weight per panicle (g) | 2.0 | .45* | .29* | –.11 | .86* | .87* | 1.0 |
| Harvest index (%) | 30.5 | .26 | .10 | .07 | .49* | .48* | .44* |

*Significant at 1 % level.

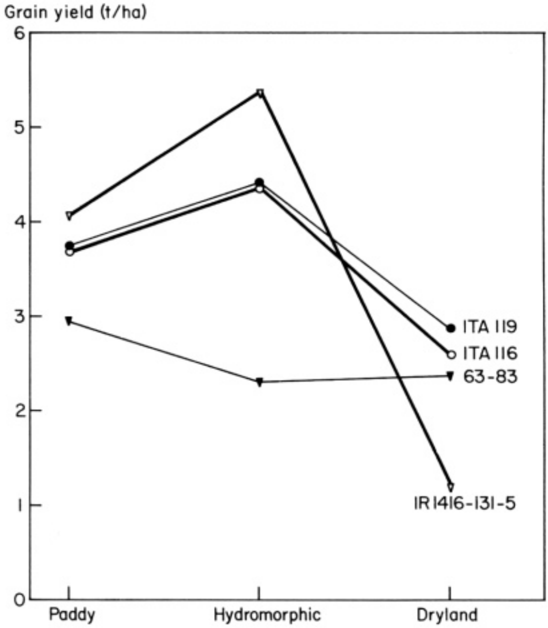
dryland, 36 cultivars, including advanced dryland selections from IITA; IRAT13, an improved dryland variety; and OS6 were evaluated under 4 moisture regimes (IITA 1981). Grain yield correlations with 1,000 grain weight and unit panicle weight show the importance of good grain filling under drought stress (Table 3).

Morphological expressions of cell elongation, plant height, and panicle exsertion are correlated with grain yield. Hsiao et al (1970) and Boyer (1973) reported that cell elongation, an essential component of growth, is retarded by only slight stress levels. Poor panicle exsertion directly affects grain filling and grain yield by causing sterility of the lower spikelets, which remain enclosed in the leaf sheath. However, field observations suggest it is possible to select for good exsertion among semidwarf plants.

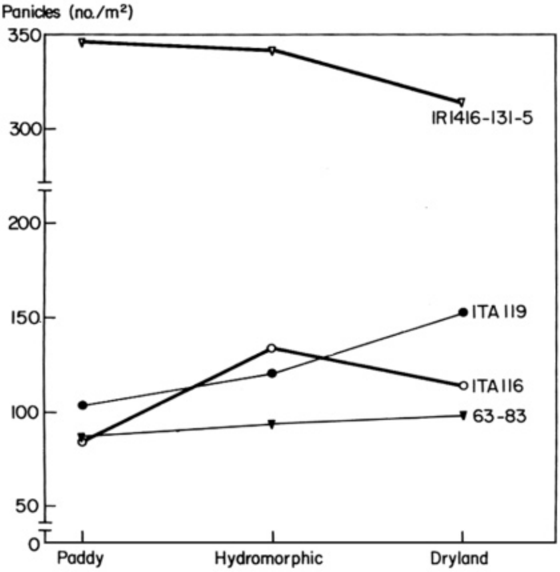
In another study, 16 cultivars of wide genetic background were evaluated under three ecologies (Yamaguchi, unpubl.). The performance of 4 cultivars — 63-83, ITA116, ITA119, and IR1416-131-5 — representing dryland tall (130-160 cm), dryland intermediate (110-130 cm), dryland semidwarf (80-100cm), and wetland semidwarf (80-100 cm) groups is presented in Figures 3 and 4 and Table 4.

The grain yield of IR1416-131-5 was superior to that of the three other cultivars in both paddy and hydromorphic ecologies but was inferior in dryland. The traditional tall, low tillering dryland cultivar 63-83 had relatively low but stable yields across three environments. ITA116 and ITA119, which were developed from crosses involving a traditional, tall, dryland and an improved semidwarf, wetland varieties, had higher yields than 63-83 in all three ecologies.

ITA119, apart from being a semidwarf, differs from IR1416-131-5 by having lower tillering ability, higher 1,000-grain weight, lower root volume, and thicker roots. ITA119 also has droopy lower leaves, which enable it to compete with



**3.** Grain yield of rice varieties in 3 ecologies.



4. Panicles of 4 varieties in 3 ecologies.

**Table 4. One thousand-grain weight, root dry weight, and root thickness of 4 varieties with different plant types in 3 ecologies.**[a]

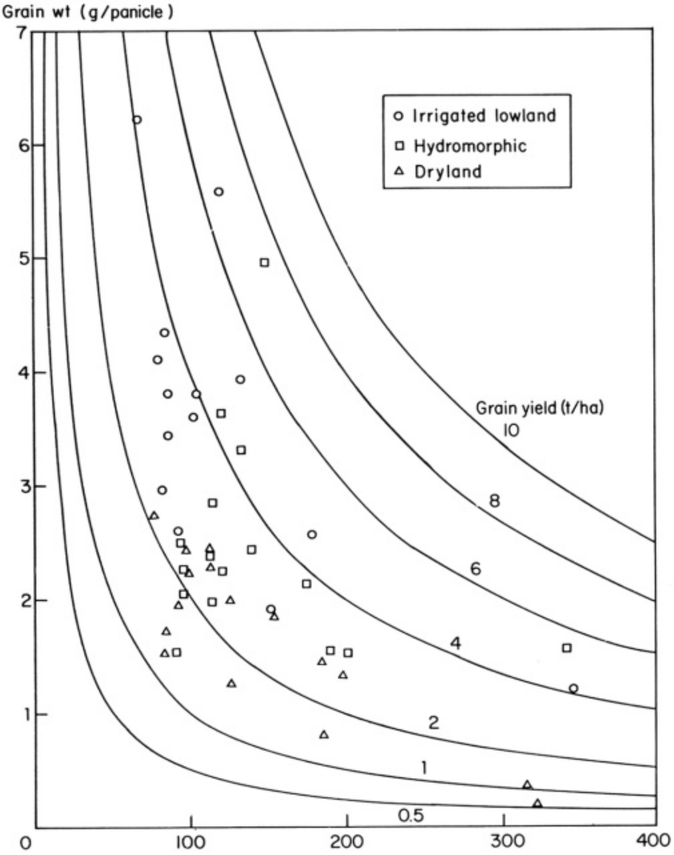
| Variety | 1,000-grain weight (g) | | | Root dry weight (g) | | | Root thickness score[b] | | |
|---|---|---|---|---|---|---|---|---|---|
| | P | H | D | P | H | D | P | H | D |
| 63-83 | 37.3 | 38.8 | 39.1 | 48 | 80 | 65 | 6 | 9 | 6 |
| ITA116 | 32.6 | 35.1 | 33.8 | 61 | 72 | 76 | 7 | 8 | 6 |
| ITA119 | 31.5 | 32.9 | 29.8 | 48 | 68 | 91 | 7 | 8 | 7 |
| IR1416-131-5 | 27.1 | 26.9 | 17.7 | 107 | 134 | 172 | 5 | 5 | 3 |

[a] P = paddy, H = hydromorphic, D = dryland.
[b] 1-9 scale; 1 : all roots thinner than 1 mm, 9: all roots thicker than 2 mm.

weeds, and erect upper leaves, for efficient utilization of solar radiation. Multilocational tests in Nigeria indicated the superiority of ITA119 under dryland conditions. ITA119 also maintained high leafwater potential under drought conditions (IITA 1981). These data demonstrate that this semidwarf plant type is realistic for dryland cultivation.

Increasing panicle number could raise the grain yield potential of this plant type. This trait is closely associated with high yields in wetlands. However, it appears that high tillering (300 or more panicles/m$^2$) , such as in wetland semidwarf IR1416-131-5, could be detrimental under dryland conditions. Similar observations were made for another semidwarf cultivar under drought conditions (Alluri 1979, IITA 1980).

The data on panicle number and grain weight per panicle and the corresponding



**5.** Relationship between panicle number and grain weight per panicle.

grain yields of all 16 cultivars studied under 3 moisture regimes are presented in Figure 5. In dryland, no cultivar produced up to 4.0 t/ha. To obtain 4.0-6.0 t grain/ha, a cultivar should have grain weight of 2.5-3.0 g/panicle and 150-200 panicles/m$^2$. A possible approach is to select for higher tillering while retaining grain weight per panicle at around 3.0 g.

Traditional dryland African cultivars have deeper and thicker roots than wetland paddy cultivars. Deep-rooted cultivars generally have a larger proportion of thicker roots than shallow-rooted cultivars. When compared with data for root dry weight and root thickness in dryland rice (Table 4), the grain yield data (Fig. 3) suggest no relationship with root dry weight but indicate thicker roots have an advantage. Although IR1416-131-5 had nearly twice the root weight of other cultivars, most of its roots were thin. Its grain yield in dryland was the lowest. The mean diameter of roots among 35 rice cultivars correlated with the field drought score (Chang et al, unpubl.).

Visual scoring for thick roots is relatively simple. However, the combination of short height and thick roots is less common, probably because breeding for short height has been directed toward developing paddy varieties.

An approach to recombining short stature with a thick root system is through the evaluation and selection of a large $F_2$ population from a cross of appropriate parents. No convenient methods are available to evaluate for root characteristics for breeding purposes, where the size of the $F_2$ population needs to be large. We explore the possibility of evaluating for root and height characteristics at the seedling stage, when the probability of obtaining the desirable plant type would be increased.

Preliminary studies on the $F_2$ population of TOX936 (IR43/Iguape Cateto), a semidwarf-dryland tall cross, indicated that seedling stage selection should be possible. The fitness of seedling stage selection and adult plant performance of root thickness in short-statured plants was as high as 95%. Plant height and root thickness behaved as independent characters. These two desirable traits could be recognized at the seedling stage.

For efficient seedling stage selection, care should be taken to enable a good, early expression of these characteristics. Selected seedlings may be transplanted in paddy. Root thickness can be verified at maturity, since the expression of this character under dryland and paddy does not seem to change much (Yamaguchi, unpubl.). The selected seedlings of the $F_2$ population are transplanted in wetlands. However, because of the absence of dryland stresses in paddy, it is recommended that only a limited negative selection be done at maturity. The critical selection is initiated from the $F_3$ stage under dryland conditions.

## REFERENCES CITED

Alluri, K. 1979. Method of planting for the evaluation of upland rice cultivars ofdifferent plant types. WARDA Tech. Newsl. l(1).

Alluri, K., I. C. Mahapatra, and T. L. Lawson. 1979. Production constraints for upland rice in West Africa. *In* First Annual Research Conference, The International Institute of Tropical Agriculture, Ibadan, October 15-19, 1979.

Boyer, J. S. 1973. Response of metabolism to low water potentials in plants. Phytopathology 63:466-472.

Hsiao, T. C., E. Acebedo, and D. W. Henderson. 1970. Maize leafelongation: Continuous measurements and close dependance on plant water status. Science 168:590-591.

IITA (International Institute of Tropical Agriculture). 1980. Annual report for 1979. Ibadan, Nigeria.

IITA (International Institute of Tropical Agriculture). 1981, Annual report for 1980. Ibadan, Nigeria.

# BREEDING AND SELECTION APPROACHES FOR DROUGHT-PRONE AREAS — OTHER CROPS

# BREEDING AND SELECTING FOR DROUGHT RESISTANCE IN WHEAT

R. A. RICHARDS

Breeding and selecting for better wheat yields in water-limited environments have been accomplished more successfully using traditional breeding methods in environments where water was not limited. This has been due mainly to the contribution of dwarfing genes that are yield positive in dry environments as well as in the irrigated environments for which they were originally developed. To identify ways to further improve yields in dry environments, two breeding approaches are discussed: first, the traditional or empirical approach where selection is for yield, and second, an analytical approach where selection is for a character other than yield that may be advantageous under drought. Emphasis in the traditional approach is on the best environment in which to select and in the analytical approach on characters that are yield positive in dry environments but unlikely to be yield negative in wetter environments.

Wheat, in terms of area sown and production, is the major cereal of the semiarid regions of the world. In nonirrigated areas, it is the most important crop economically (Arnon 1972b). The two major wheat types, hexaploid bread wheat (*Triticum aestivum,* 2n= 42) and tetraploid durum wheat (*T. turgidum* L. var. group durum,

---

Division of plant Industry, Commonwealth Scientific and Industrial Research Organization, P.O. Box 1600, Canberra City, 2601, Australia.

2n = 28), evolved in the semiarid Middle East from wild diploid and tetraploid progenitors. Both species show remarkable adaptation to a wide range of conditions. They are grown in both semiarid and humid climates. They are sown and harvested where temperatures are increasing or decreasing. Typically, however, wheat is sown so that its early growth and development occur during the coolest months and grain ripening occurs during the warmest months. The amount of rain required to produce an economic yield varies with rainfall distribution, but is about 300 mm in areas with winter rain. However, actual crop water requirements can be much less. In a recent study, a crop achieved a yield of 3 t/ha with only 200 mm of predominantly stored soil moisture (Angus et al 1980).

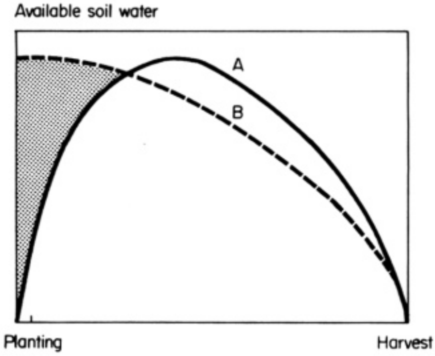
The most significant yield increases in wheat have not come from breeding for yield *per se* but from decreasing height and manipulating phenology to suit a particular climate or ecological zone. In breeding for drought resistance, considerations of climate and ecological zone are equally important.

## CLIMATIC CONSIDERATIONS

The availability of soil water to most wheat crops between sowing and maturity is shown schematically in Figure 1. One extreme (A) is typical of a winter rainfall pattern in a mediterranean climate. The other extreme (B) is typical of a summer rainfall pattern in a climate where the crop relies primarily on soil water accumulated before sowing. The shaded area indicates the period when the amount of soil water is likely to be most variable, depending upon the region and the season.

It can be seen that wheat is generally sown when soil moisture reserves are adequate because of previous rainfall or a fallow period or are expected to increase because of the high probability of rainfall exceeding evapotranspiration. Crop development continues as evapotranspiration increases and by crop maturity, all of the available soil water is generally used. Although drought in a wheat crop can occur at any time, its probability is highest late rather than early in the growing season, regardless of whether the rainfall pattern is predominantly during the summer or the winter or whether rainfall is distributed equally throughout the year.

Despite the similarity in crop time of the likely occurrence of drought stress



**1.** Schematic representation of available soil water between sowing and maturity of a wheat crop. A represents a winter rainfall pattern, where the crop is grown on current rainfall, and B represents a summer rainfall pattern, where the crop relies largely on soil water accumulated before sowing. The shaded area represents the period when the amount of soil water is likely to be most variable.

with different rainfall patterns, it does not follow that selection procedures for yield improvement in these different droughts are the same. For example, a crop growing in a region with a summer rainfall (B in Fig. 1) would be favored by a water conservation pattern such as a reduced early leaf area to save water for grain filling, whereas a crop growing in a mediterranean climate where the soil surface is often wet (A in Fig. 1) may be favored by rapid development of early leaf area to increase the proportion of transpiration over soil evaporation.

Despite the predictability of seasonal rainfall patterns, year-to-year fluctuations in the amount, frequency, and duration of rain in most dryland wheat regions are great. The result is years in which there is total crop failure and years in which water is nonlimiting. Superimposed on these considerations of water supply and variability in a particular climatic region are other factors which also influence crop growth and yield, such as high temperatures that may terminate grain filling, the risk of frost, and photoperiod.

Breeding and selection for drought resistance in wheat should be viewed within this general framework.

## BREEDING OBJECTIVES

Breeding for drought resistance can have opposing objectives. For the subsistence farmer, breeding for plant survival in the worst years may be the major objective to ensure some grain production (Jennings 1976). For other dryland farmers the major objective may be high yields in the best years, since they contribute the most to long-term yields. It is unlikely that factors that contribute to plant survival in the most extreme dry environments also contribute to high yield in wetter environments. This is borne out in yield trials showing that cultivar yields in the driest and wettest environments are not closely related (Arnon 1972, Laing and Fischer 1977, Fischer and Maurer 1978).

Attention here will focus on maximizing long-term yields in dryland environments by developing drought-resistant cultivars able to yield more grain under drought ($Y_D$) without sacrificing yield potential ($Y_p$) in wetter years. Emphasis will be on developing cultivars with the highest absolute yields ($Y_D$) rather than the highest relative yields ($Y_D/Y_p$). Because long-term yields are influenced more by the wetter years, breeding emphasis will be on drought intensities where $Y_D/Y_p$ exceeds 0.2.

## BREEDING APPROACHES

Two very different approaches have been used in breeding for high average yield in water-limited environments. The first approach, which has been referred to as the traditional or empirical approach, relies on grain yield as the selection criterion, since this integrates all the components that determine yield in a water-limited environment and is, after all, the economic product. The second, called here the analytical approach, relies on the different physiological mechanisms of adaptation in a drought environment, with the possibility that breeding and selection for these adaptations will contribute to growth and yield under drought. Few plant breeders have been prepared to undertake selection programs based on physiological criteria. This is either because the value of the specific adaptations in crops has not been demonstrated or because rapid selection methods are not available to detect worthwhile genetic variability in a character. But both breeding approaches are likely to contribute significantly to yield improvements under drought in the future. They should be seen as complementary rather than opposing. The real question is not which approach is best but, for the traditional approach, what is the most efficient way to select directly for yield and, for the analytical approach, which criteria are likely to be most influential in improving yields that also satisfy breeders' needs for characters that can be rapidly screened and that have high heritabilities.

## Empirical

Normally several different facets of an empirical breeding program can be identified. One involves maintaining yield by breeding for resistance to pests and diseases and at the same time maintaining adequate quality. Another involves breeding for yield potential. Breeding for yield potential will be discussed here, although it should be remembered that breeding for disease resistance indirectly affects yield through maintaining an efficient photosynthetic area for efficient crop water use.

The most important question in a traditional breeding program for dry environments is what is the most efficient environment in which to select. Hurd (1976) recommends the use of dry environments, where he has been successful in selecting for yield. However, he attributes part of this success to emphasis on phenotype of the original parents (Hurd 1974). Richards (1978) found a drought environment ($Y_D/Y_P$ of 0.35 and 0.75) more efficient than a wetter environment within which to select for yield for dry conditions in two species of rapeseed. However, others have found the wetter environments more efficient (Johnson and Frey 1967, Roy and Murty 1976). These apparently contrasting findings are not necessarily opposed. In the example given by Hurd, yield in the dry environment depended more on the crop's ability to extract water at depth so that plants with deeper roots were at a selective advantage over plants with shallower roots. When deeper roots do not have a selective advantage, selection in a more optimal environment may be more efficient. Richards (1978) found that selection for yield in a wet environment also would result in yield improvements in a dry environment.

Since the breeder cannot specify the drought intensity within which to select, an approximate target yield level ($Y_D/Y_P$) which is characteristic of the drought intensity in the area he is breeding for should be the aim. However, the most efficient environment within which to select may be some other environment. It will depend on the heritability ($h^2$) and the phenotypic variation ($O_p{}^2$) in yield and also on the genetic correlation ($r_A$) between yields in the different environments. The response to selection in environment $Y$ ($R_y$) is given by:

$$R_y = i\ h_y^2 O_{py} \qquad (1)$$

where $i$ is the selection intensity, $hy^2$ the heritability, $O_{py}$ the standard deviation of yield in environment *Y*. If the target environment is *X* and selection is made in *Y*, the correlated response of yield in the target environment ( $CR_x$ ) is given by:

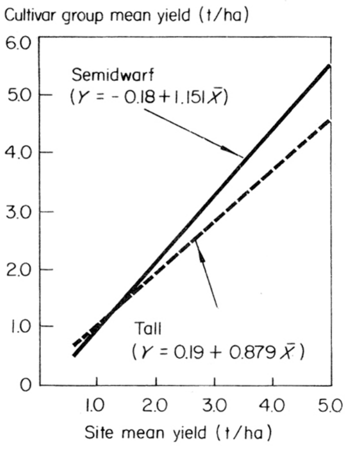
$$CR_x = \frac{r_A h_y}{h_x} \cdot R_y \tag{2}$$

If $r_A h_y$, is greater than $h_x$, selection for yield in the target environment will be less efficient than if selection were made in environment *Y*. On the other hand, if $r_A h_y$ is less than $h_x$, the target environment would be the most efficient within which to select.

In wheat, as in other crops, the expression of genetic variability is greater in good environments than in poor ones. The association between yields in these environments must also be high. Cultivars with high yield potentials and cultivars bred in good environments also have yielded the most in suboptimal environments in Canada (Harrington 1935, Walton 1968) and performed better than cultivars developed in dryland environments in Australia (Syme 1970) and on farmers' fields in Tunisia (Purvis 1973). Laing and Fischer (1977) compared yields over a large number of rainfed sites of semidwarf wheats developed for irrigated high fertility conditions with taller varieties developed for dryland lower fertility conditions. They used results from 44 rainfed environments of the 6th and 7th International Spring Wheat Yield Nurseries to determine the relationship between cultivar yield and site mean yield for 33 common wheat cultivars.

Figure 2 contrasts the mean yield of semidwarf cultivars developed in good conditions with the mean yield of tall cultivars developed in dryland conditions over a range of water-limited environments. Flowering times of the two groups of cultivars were similar. The yield superiority of semidwarf cultivars developed in irrigated high fertility conditions was evident. Although the highest yielding cultivars suffered the greatest absolute yield loss with decreasing water supply, their high yield potential was enough to offset this loss in all except the most extreme environments. Thus, the higher yield potential of the shorter wheats in

**2.** Mean grain yield of 18 semidwarf cultivars and 10 tall cultivars with similar flowering times, as a function of mean yield at 44 rainfed sites of the 6th and 7th international Spring Wheat Yield Nurseries (Fischer 1981).



optimal environments was also expressed in a wide range of dry environments, leading to their remarkably wide adaptation. This also was evident in other studies with shorter wheats (Arnon 1972a, Walton 1968). Fischer and Maurer (1978) compared common wheats of different height classes bred under good conditions, taller wheats bred under dryland conditions, and a number of durum wheats, barleys, and triticales. Cultivars were grown under good conditions and in a series of terminal droughts of different intensities. The yields of shorter wheats bred in good conditions were again superior to wheats bred in dryland areas.

Thus, the general observation in wheat is that selection for yield under optimal conditions also results in marked improvements under less optimal conditions. However, this may not always be the case. These comparisons are dominated by the yield superiority of cultivars containing the Norin 10 dwarfing genes. Maybe the traditional taller dryland cultivars possess specific drought resistance attributes that shorter wheats do not have so that for further progress in breeding for yield in dryland environments it may be possible to combine the yield potential of shorter cultivars with the possible drought resistance of taller wheats. In other words, maybe there are yield positive traits in dry conditions that are neutral or even negative in their effect under optimal conditions and which may be lost in breeding programs carried out in good conditions. One such phenotype that could be lost in good environments would be deep roots. Fischer and Wood (1979) were able to examine this in part by looking at the associations between yield under drought ($Y_D$), yield under irrigation (wet) ($Y_p$), a drought susceptibility index proportional to ($1-Y_D/Y_p$), and various morphophysiological traits of a genetically diverse array of cultivars. They concluded that combining yield potential with drought resistance may be difficult physiologically because of the trade-off between yield potential and yield resistance to stress.

Another aspect of drought resistance that has been considered in traditional breeding programs is the modification of drought response by selecting for early maturity or drought escape (Reitz 1974). However, further improvements in adaptation by selecting for time of flowering are unlikely in currently grown cultivars because flowering time has a higher heritability than yield itself. Selection for yield over the years in dryland environments has probably optimized flowering times to maximize yield and adaptation. This is not to say that modification of flowering date would not be worthwhile, but it may depend on other environmental constraints such as frost. With more frost-resistant cultivars, an earlier flowering date may be useful (Nix 1976, Fischer 1979). More subtle changes, such as the proportion of time a crop spends in each phenological period rather than the actual time of anthesis, may also provide opportunities to improve yields in dry environments. These changes would be independent of the stabilizing selection pressures imposed by the environment on a critical event such as flowering time.

A major criticism of the empirical approach is that a radically improved assortment of characters may be missed in early generations because of their poor performance as isolated plants in a competitive situation (Donald 1968, 1981). Characters that confer a competitive disadvantage to a plant in a genetically heterogeneous population may confer a yield advantage in a homogeneous crop population. This can be a strong argument for using such breeding techniques as single seed descent rather than the more traditional bulk breeding or pedigree methods, since in single seed descent, no selection pressure (artificial or natural) is imposed on the population as is done in pedigree and bulk breeding methods. Tincurrin, a recently released wheat in Western Australia, was developed by single seed descent (Reeves et al 1978). As a club wheat, it is a radical departure morphologically from comparable cultivars and, whether by coincidence or not, it was the outstanding wheat throughout Australia in the exceptionally dry year of 1977.

## Analytical

The analytical approach to breeding for drought resistance stems from two basic philosophies. First, plants that are competitively inferior in isolation or in a genetically mixed population may be superior in a genetically pure stand (Donald 1968). Second, yield is the ultimate expression of a number of individual processes that have interacted with and been modulated by the prevailing climate and crop environment so that selection for these traits or processes may be more efficient than selection for yield itself.

Both physiologists and breeders have attempted to identify indirect selection criteria for improved yield or drought resistance (Hurd 1976, Turner and Kramer 1980). Traits examined have been metabolic—proline (Singh et al 1973), abscisic acid (Quarrie 1980); physiological—stomatal regulation (Jones 1979), osmotic regulation (Turner and Jones, 1980); morphological—awns (Evans et al 1972); developmental—tillers (Islam and Sedgely 1981), and whole plant characteristics —germination, growth, and survival (Blum et al 1980).

Use of these criteria in breeding programs has been almost nonexistent for several reasons. First, breeders have not been convinced that using these criteria will improve the efficiency of their breeding programs. Second, no clear association has been shown between these characters and yield. One reason may be that too much attention has focused on the components of drought resistance, such as escape, avoidance, and tolerance (Levitt 1972), which are more applicable to the ecological situation than to the agricultural situation, where productivity is the major consideration. Passioura (1976) has argued that too much emphasis may have been placed on processes important over a short-time scale rather than on slower and more influential processes that operate over a longer time scale.

Fischer (1981) has distinguished between two analytical approaches—a deductive black box approach in which underlying causes of yield differences are sought and an ideotype approach in which predictions are made of possible causes of yield differences. An example of the first approach, which also indicates the inherent difficulties associated with finding causes of differences in yield under drought, is given by Fischer and Wood (1979), who did an extensive study on bread and durum wheats, barley, and triticale grown in a set of unrelieved droughts of different intensities as well as in an environment with ample water. They measured the components of yield, aspects of crop development, growth, morphological characters, and plant water relations in wet and dry environments, then examined the associations of these characters with yield under drought (dry yield) and a drought susceptibility index calculated from drought intensity, yield potential (wet yield), and dry yield. Due consideration also was given to the influence of anthesis date on dry yield. From the associations between the traits and dry yield and drought susceptibility, it was hoped that specific indicators could be found that were yield positive under drought and that also contributed to drought resistance. Neither yield under drought nor the drought susceptibility index was closely associated with plant water relations traits — a conclusion also reached in other studies (Jones 1977, Kaul and Crowle 1974). Furthermore, no single wet or dry trait could be considered a reasonable alternative to selection for yield under drought.

The ideotype approach will be discussed around a general framework prepared by Passioura (1977) for yield of wheat grown with a limited water supply. He proposed that yield should be viewed as the product of the amount of usable water, the water use efficiency (ratio of dry matter to water used), and the harvest index (ratio of grain yield to aboveground biological yield). He argues that, since each of these traits is likely to be independent of one another, improving any one of them should result in yield improvement in a water limited environment. This overcomes some of the problems associated with analytical breeding approaches, such as the indiscriminate recommendation of selection criteria, since it enables specific criteria to be seen in relation to the major determinants of yield under drought.

By considering each of these components primarily from a breeder's point of view, criteria for fruitful selection in wheat can be suggested. These criteria should be considered in relation to the genetic architecture of a typical wheat crop (a genetically homogenous population of plants) and the nature of the water-limited environment in which it is to be grown (Fig. 1).

*Amount of water.* Deep rooting increases the availability of water to the plant, provided water is available at depth (Hurd 1974). The extra water would enable greater yields, since it would be used efficiently. However, deep-rooted plants would not be of benefit in all situations, since there is often no water at depth or, if there is, the recharge rate may be extremely slow (Passioura 1977). On the other hand, it has been suggested that the investment of photosynthate in the roots of modern-day cultivars may be excessive and, although deep rooting may have had adaptive value in a heterogeneous population competing for water, it may be of little value in a genetically homogeneous population (Passioura 1981). Indeed in rapeseed, a large root weight was negatively associated with yield in dry environments (Richards and Thurling 1978). Unfortunately, little information is available on useful genetic variation in the morphology of root systems and, until better techniques for the study of roots in soil rather than in nutrient solution are developed, further progress seems unlikely. The most useful ways to study root systems may be to use the shoots as indicators of what is happening below the ground.

A considerable quantity of water that would otherwise be used by the plant is lost by soil evaporation. This is greatest in areas with a rainfall pattern such as B in Figure 1, where the crop relies on current rainfall. Fischer (1980) suggests that selection for early ground cover should be effective in redirecting some of this water through the plant, thereby increasing transpiration at the expense of soil evaporation. Although this may reduce the amount of soil water available for grain filling, areas that have a high probability of rain around anthesis should benefit. Two characteristics of wheat that can easily be selected to achieve this are the early accumulation of dry matter and early leaf cover of interrow leaf display.

*Water use efficiency.* Water use efficiency (WUE) is used here in the broad sense as dry matter per unit of water used and in the narrow sense as the assimilation ratio (photosynthesis divided by transpiration). Evidence for significant variation among cultivars in WUE has been reported (Passioura 1977) however, roots were not included in total dry matter and it is possible that the differences may have been due to variation in root/shoot ratios. This variation is nonetheless of considerable value, because of the lesser investment of photosynthate in roots.

For breeding purposes, it may be more instructive to examine characters that may alter the assimilation ratio, such as characters that differentially affect photosynthesis and transpiration. These characters are likely to be under more simple genetic control and therefore be more amenable to breeding and selection. Fortunately, relative differences in WUE at the leaf level are likely to remain unchanged in a canopy (Fischer and Turner 1978), so that the effects of selection practiced on isolated leaves or plants should translate to a crop canopy. A vast array of characters could conceivably influence the assimilation ratio, for example, any character or trait that influences the resistance to diffusion of carbon dioxide and water vapor, respiration rates, or energy loads on the leaf. When these characters are considered in relation to the normal growth climate, the possible interactions with other factors (pleiotropic effects), and the available genetic variation and ease of manipulation, several can be identified as possibly useful in a breeding program to increase water use efficiency in wheat.

In *Triticum,* it was found that species with a high specific leafweight (weight per unit area) also had a thicker leaf and a higher photosynthetic rate per unit area (Khan and Tsunoda 1970). Thus, if transpiration is dependent on area, specific leaf weight could be associated with improved WUE. I have attempted to screen segregating populations of wheat for leaf thickness to increase specific leaf weight indirectly. However, even though considerable attention was paid to possible confounding due to pubescence and cuticle thickness, the selected lines became dominated by types with protruding veins. It seems that both leaf area and weight must be considered together when selecting for specific leaf weight.

Leaf surface morphology, such as pubescence and waxiness, also may alter the assimilation ratio. The specific effect of these characters is speculative, but it is conceivable that they may influence leaf or spike temperature which in turn may influence the degree of senescence and spike tipping (premature senescence of the upper half of the spike, a common feature reducing grain number in droughts), respiration rate, cuticular and boundary layer resistance, and duration of the grain-filling period. Pubescence and waxiness are controlled by separate single genes whose contrasting expressions are easily identified. Separate genes also control leaf and stem and glume pubescence and wax, so that it is easy to differentially alter different plant parts. Even though the characters are under the control of separate single genes, their expression can be further enhanced or reduced by selection within the background genotype.

Other adaptations where significant genetic variation exists that could alter WUE are characters such as leaf rolling, leaf size, erectness, and stomatal sensitivity. However, with the exception of erectness, because these characters are more susceptible to environmental fluctuations and are more complex genetically, they have less intrinsic value in a breeding program. Awns also may alter WUE in wheat, as they do in barley (Johnson et al 1975). Their influence and value will be discussed later.

*Harvest index.* Harvest index, the partitioning component of the equation, is perhaps the most important. If advances are made in increasing dry matter by increasing either the amount of water used or WUE, part of this dry matter must then be converted into grain. Increased harvest index has been identified as the major factor responsible for the yield increases attributed to the semidwarf wheats in dry and wet environments and it seems that genotype has a greater direct influence on assimilate allocation than it has on either WUE or the amount of water used. Improving the harvest index per se must result in yield improvements in all drought affected environments, provided total dry matter does not decrease. In this discussion, attention is focused on ways that are likely to result in a high grain-to-straw ratio.

Passioura (1977) has shown the dependence of harvest index (and grain yield) of wheat on the proportion of water used after anthesis. He suggests that, for cereals relying largely on stored soil water (B in Fig.1), restricting water use before anthesis would result in a greater availability of water after anthesis and a higher grain yield. He also has suggested that the pattern of water use can be changed by altering hydraulic resistance in the seminal root system (Passioura 1972).

We have embarked on a breeding program in wheat aimed specifically at increasing hydraulic resistance in the seminal root system. Theoretical and practical breeding considerations indicate that selecting for smaller diameter xylem vessels in the seminal roots would be the most effective method of increasing hydraulic resistance (Richards and Passioura 1981a, b). Fortunately, selection for xylem vessel diameter does not seem to be complicated by large genotype-by-environment interactions or a low heritability. Despite some environmental and seed factors that do alter expression of the character, selection can be done in the greenhouse, where several generations each year can be grown.

There are two major drawbacks to the breeding program. First, the character is polygenically controlled, so the backcross breeding program which we are attempting becomes more difficult. Second, for the new phenotype to be effective in a population of plants, all plants must possess the narrow xylem vessels. If variation is present in the crop population, plants possessing narrow vessels are likely to be at a competitive disadvantage relative to plants with wider vessels.

So far, we have successfully manipulated and maintained the character through several backcross and filial generations to introduce the genes into two high yielding cultivars that also have good quality characteristics and disease resistance. These lines will be field tested after eliminating unwanted variation in vessel diameter.

There are several other ways to possibly increase the proportion of grain to total dry weight in semiarid environments, apart from direct selection for harvest index.

One is to increase the proportion of fertile tillers, since tillers that produce no grain represent wasted photosynthate leaf area and thus water. For example, uniculm barleys and plants surgically restricted to two fertile tillers, when grown under crop conditions, have shown promise in dry regions (Donald 1981, Islam and Sedgely 1981). A second way may be to select for increased sink size or grain number per unit area, since there is evidence that sink size has an influence on the rate of photosynthesis (Evans and Wardlaw 1976). Increasing the size of the sink may enable greater responsiveness to better conditions without affecting yields in the worst years. Grain number has been selected for effectively in wheat (McNeal et al 1978) and ample genetic variation seems to exist.

The investment of photosynthate in awns is one characteristic that is clearly advantageous in conditions where there is a terminal drought, and yet not disadvantageous when water is not limiting. Awns not only contribute significantly to yield in dry years (Patterson and Ohm 1975, Evans et al 1972), but also may improve WUE, as evidence in barley indicates (Johnson et al 1975). Awns, whose presence or absence in wheat is controlled by a single gene, represent an ideal selection criterion for drought resistance. That is, they are yield positive under drought without a negative influence in wet conditions and the character is easily observed in segregating populations.

## FUTURE STRATEGIES AND CONCLUSIONS

Yield increases in wheat as a result of breeding have been achieved in most dryland environments. It is paradoxical that the greatest yield advances in recent years have occurred mainly as a result of breeding under optimal conditions and are attributable to the specific influence of the Norin 10 dwarfing genes. A major factor hindering further yield increases in traditional programs is the inability to identify high yielding types in early generations. This is because, first, selection for yield in early generations is generally ineffective, since yield in segregating populations or yield of single plants is unrelated to yield in pure stands (Donald and Hamblin 1976, Fischer 1981). Second, as a result, when genotypes are rapidly advanced to homozygosis for evaluation in large plots, much of the genetic variation contained within a cross is lost because of limited capacity to test large numbers of pure lines. Hence, any selection technique effective in early generations would result in a significant increase in breeding efficiency. But, unless techniques can be developed, breeders must still rely on evaluating their genotypes in large plots.

Yield increases in wheat made by selecting for specific attributes under drought are to my knowledge nonexistent. The deep-rooting wheats described by Hurd (1974) were selected for their yield rather than their root system (it was the parents that were selected for their deep roots). Awns and even more so the dwarfing genes are the only proven yield positive characters in dry conditions that are either neutral or yield positive in wet conditions for which breeders can select. However, it is likely that most dryland wheats probably already possess both these attributes. Thus, breeders must rely on an empirical approach as the only dependable route to improved drought resistance (i.e. yield under drought) until specific attributes can be shown to be yield positive in drought conditions. It is encouraging from a breeding viewpoint that the two yield positive attributes that have been identified are simply inherited, yet have such a positive influence on yield under drought.

I have tried to identify yield positive attributes under drought based primarily on their possible influence on yield, genetic control, and ease of genetic manipulation in wheat. Only when contrasting phenotypes of each character in a similar genetic background are compared will it be possible to test their specific influence. If a character confers a significant advantage in a dry environment, it can be incorporated into existing cultivars by backcross breeding methods. Alternately, if a character is simply inherited and observed, it can be incorporated into a traditional breeding program where a pedigree method is used.

Success is dependent on the availability of sufficient genetic variability in the character concerned. It is fortunate that in wheat there is access to a huge store of genetic variation, not only from existing cultivars developed in the diverse climates where wheat is grown but also from land races collected from the centers of origin of the species, from closely related wild species, and from even more distantly related genera such as barley, rye, and *Agropyron.* Gene transfer from related species and genera is now possible, largely through the use of the *Ph* locus that suppresses pairing between homeologues, the use of embryo culture, the production of alien addition lines, and translocation induction. The ease of manipulation of the wheat genome and access to alien germplasm is probably not equaled in any other crop species.

The likelihood of developing more drought-resistant wheats looks very promising from the viewpoint of the extent of genetic variation and the range of possible characters that could influence yield under drought. It depends on innovative research efforts to identify appropriate characters and germplasm that would be yield positive in the variable dryland environments and to incorporate them into the appropriate germplasm.

## REFERENCES CITED

Angus, J. F., H. A. Nix, J. S. Russell, and J. E. Kruizinga. 1980. Water use, growth and yield of wheat in a sub-tropical environment. Aust. J. Agric. Res. 31:873-886.

Amon, I. 1972a. Crop production in dry regions. Vol. 1. Background and principles. Leonard Hill, London. 650 p.

Amon, I. 1972b. Crop production in dry regions. Vol. II. Systematic treatment of the principal crop. Leonard Hill, London. 683 p.

Atkins, I. M., and M. J. Norris. 1955. The influence of awns on yield and certain morphological characters of wheat. Agron. J. 47:218-220.

Blum, A., B. Sinmena, and O. Ziu. 1980. An evaluation of seed and seedling drought tolerance screening tests in wheat. Euphytica 29:727-736.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Donald, C. M. 1981. Competitive plants, communal plants, and yield in wheat crops. Pages 223-247 *in* L. T. Evans and W. J. Peacock, eds. Wheat science — today and tomorrow. Cambridge University Press.

Donald, C. M., and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agron. 28:361-405.

Evans, L. T., J. Bingham, P. Jackson, and J. Sutherland. 1972. Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. Ann. Appl. Biol. 70:67-76.

Fischer, R. A. 1980. Influence of water stress on crop yield in semi-arid regions. Pages 323-329 *in*

N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Fischer, R. A. 1981. Optimizing the use of water and nitrogen through breeding of crops. Plant and Soil 58:249-278.

Fischer, R. A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:897-912.

Fischer, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semi-arid zones. Annu. Rev. Plant Physiol. 29:277-317.

Fischer, R. A., and J. T. Wood. 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. Aust. J. Agric. Res. 30:1001-1020.

Harrington, J. B. 1935. Cereal crop improvement for dry farming conditions. Sci. Agric. 16:113-120.

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. Agric. Meteorol. 14:39-55.

Hurd, E. A. 1976. Can we breed for drought resistance? Pages 317-353 *in* T. T. Kozlowski, ed. Water deficits and plant growth. Vol. IV. Academic Press, New York.

Islam, T. M. T., and R. H. Sedgely. 1981. Evidence for a 'uniculm effect' in spring wheat (*Triticum aestivum* L.) in a mediterranean environment. Euphytica 30:277-282.

Jennings, P. R. 1976. The amplification of agricultural production. Sci. An. 235:189-194.

Johnson, G. R., and K. J. Frey. 1967. Heritabilities of quantitative attributes of oats (*Avena* sp.) at varying levels of environmental stress. Crop Sci. 7:4346.

Johnson, R. R., C. M. Wilmer, and D. N. Moss. 1975. Roleofawns in photosynthesis, respiration, and transpiration of barley spikes. Crop. Sci. 15:217-221.

Jones, H. G. 1977. Aspects of the water relations of spring wheat (*Triticum aestivum* L.) in response to induced drought. J. Agric. Sci. 88:267-282.

Jones, H. G. 1979. Stomatal behavior and breeding for drought resistance. Pages 407-428 *in* H. Mussell and R. S. Staples, eds. Stress physiology in crop plants. John Wiley and Sons, New York.

Jones, H. G., and E. J. M. Kirby. 1977. Effect of manipulation of number of tillers and water supply on grain yield in barley. J. Agric. Sci. Camb. 88:391-393.

Kaul, R., and W. L. Crowle. 1974. An index derived from photosynthetic parameters for predicting grain yields of drought-stressed cultivars. Z. Pflanzenzuecht 65:233-243.

Khan, M. A., and S. Tsunoda. 1971. Comparative leaf anatomy ofcultivated wheats and wild relatives with reference to their photosynthetic rates. Jpn. J. Breed. 21:143-150.

Laing, D. R., and R. A. Fischer. 1977. Adaptationofsemi-dwarfwheat cultivars to rainfed conditions. Euphytica 26: 129-139.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York.

McNeal, F. H., C. O. Qualset, D. E. Baldridge, and V. R. Stewart. 1978. Selection for yield and yield components in wheat. Crop Sci. 18:795-799.

Nix, H. A. 1976. Climateandcrop productivity in Australia. *In* International Rice Research Institute. Proceedings of the Symposium on climate and rice. Los Baños, Philippines.

Passioura, J. B. 1972. The effect of wheat geometry on the yield of wheat growing on stored water. Aust. J. Agric. Res. 23:745-752.

Passioura, J. B. 1976. The control of water movement through plants. Pages 373-380 *in* I. F. Wardlaw and J. B. Passioura, eds. Transport and transfer processes in plants. Academic Press, New York.

Passioura, J. B. 198l. The collection of water by roots. Pages 39-53 *in* L. G. Paleg and D. Aspinall, eds. The physiology and biochemistry of drought resistance. Academic Press, New York. (in press)

Patterson, F. C., and H. W. Ohm. 1975. Compensating ability of awns in soft red winter wheat. Crop Sci. 15:403-407.

Purvis, J. M. 1973. The new varieties under dryland conditions: Mexican wheats in Tunisia. Am. J. Agric. Econ. 55:54-57.

Quarrie, S. A. 1980. Genotypic differences in leafwater potential abscisic acid and proline concentration in spring wheat during drought stress. Ann. Bot. 46:383-394.

Reeves, J. T., H. M. Fischer, and G. B. Crosbie. 1978. Tincurrin, a new biscuit wheat. J. Agric. -West Aust. 19:16-18.

Reitz, L. P. 1974. Breeding for more efficient water use — is it real or a mirage? Agric. Meteorol. 14:3-11.

Richards, R. A. 1978. Genetic analysis of drought stress response in rapeseed (*Brassica campestris* and *B. napus*). I. Assessment of environments for maximum selection response in grain yield. Euphytica 27:609-615.

Richards, R. A., and J. B. Passioura. 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. Crop Sci. 21:249-252.

Richards, R. A., and J. B. Passioura. 1981b. Seminal root morphology and water use of wheat. II.

Genetic variation. Crop Sci. 21:253-255.

Richards, R. A., and N. Thurling. 1978. Variation between and within species of rapeseed (*Brassica cumpestris* and *B. napus*) in response to drought stress. I. Sensitivity at different stages of development. Aust. J. Agric. Res. 28:469-477.

Roy, N. N., and B. R. Murty. 1976. A selection procedure in wheat for stress environment. Euphytica 19:509-521.

Singh, T. N., L. G. Paleg, and D. Aspinall. 1973. Stress metabolism. III. Variations in response to water deficit in the barley plant. Aust. J. Biol. Sci. 26:65-76.

Syme, J. R. 1970. A high-yielding Mexican semi-dwarf wheat and the relationship of yield to harvest index and other varietal characteristics. Aust. J. Exp. Agric. Anim. Husb. 10:350-353.

Turner, N. C., and M. M. Jones. 1980. Turgor maintenance by osmotic adjustment. A review and evaluation. Pages 87-103 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Turner, N. C., and P. J. Kramer. 1980. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York. 482 p.

Walton, P. D. 1968. Spring wheat variety trials in the Prairie Provinces. Can. J. Plant Sci. 48:601-609.

# SORGHUM IMPROVEMENT FOR DROUGHT RESISTANCE

N. SEETHARAMA, B. V. SUBBA KEDDY, J. AM. PEACOCK,
AND F. R. BIDINGER

Drought is the major limiting factor in most of the sorghum-growing areas of the world, especially in the semiarid tropics. At the International Crops Research Institute for the Semi-Arid Tropics, sorghum improvement for drought resistance involves using a range of techniques for screening germplasm and elite breeding material. Selections are advanced to multilocation trials in drought-prone areas. The need to incorporate drought-resistance mechanisms in addition to escape and to tailor the plant to suit the target environment is emphasized. Field and laboratory techniques are used to study specific adaptations such as leaf-area adjustment (drought avoidance) and heat and desiccation tolerance and adjustment in osmotic potential (drought tolerance). Future problems and prospects in crop improvement for drought resistance are considered. The requirements for tackling the locational and temporal specificity of drought by problem-oriented training, by better cataloguing of environments coupled with requisite adaptations, and by modeling are noted.

Sorghum, grown on 51 million ha in both tropical and temperate zones, is one of the 5 most important cereals in the world (Doggett 1970). The major ecological zone for sorghum lies between the humid forests near the equator and the deserts

---

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru P.O., Andhra Pradesh 502 324, India.

of the arid and semiarid tropics (SAT). Recently FAO carried out a more complete agroecological description of the sorghum-growing areas of Africa, Southwest and Southeast Asia, and Central and South America (Higgins 1978). The rainfall probability and moisture availability indices for many SAT regions have been compiled and published by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (Virmani et al 1980a,b). But much more has to be done to delineate agroecological zones of the SAT regions of the world.

In Africa, sorghum is grown on 14 million ha in the group of drought-prone countries that extend across the continent between latitudes 10° and 20° N (Motha and Sakamoto 1979), bordered on the north by the Sahara Desert in the Sahelian-Sudanian zones, down through East Africa, and into Central and Southern Africa. It is the major source of food calories in many countries, but yields average only 690 kg/ha (FAO 1979).

In Asia, sorghum grown on 26 million ha yields an average of less than 880 kg/ha. In India, where it is the third major cereal, it is grown on 16 million ha, of which 50% is cultivated on stored moisture during the postrainy season. Regions growing sorghum during the rainy season fall between the wheat- and pearl millet-growing environments in the north and the rice- and finger millet-growing regions in the south (S. J. Reddy, ICRISAT, pers. comm.). They are classified as agricultural subdivisions II and III (Murthy and Pandey 1978). Sorghum usually is intercropped with pigeon pea during the rainy season in India.

In Latin America, especially in Mexico and Argentina, the rate of increase in area sown and yield has been impressive (3.5 t/ha in Mexico and 2.9 t/ha in Argentina in 1979). In Latin America, as in Africa, sorghum is intercropped with other cereals such as pearl millet or maize (depending upon the rainfall) and with a variety of legumes. A ratoon crop also is grown in many countries.

Most countries of the semiarid tropical belt of Africa, Asia, and Latin America have exhibited a dramatic downward trend in levels of food self-sufficiency over the last 15 years. This decline has been reflected by both a general decline in total annual rainfall (Motha and Sakamoto 1979) and large year-to-year fluctuations in the amount of rainfall. These two conditions together have brought drought. The impact has been compounded by population increases.

Drought limits the yield of sorghum, reputedly one of the most drought-resistant crops. Surveys conducted by ICRISAT and the Semi-Arid Food Grain Research and Development (SAFGRAD) show that drought is the major problem limiting sorghum production in SAT (House 1980). Even in high-rainfall (>80 cm) areas, short periods of drought can decrease yield considerably.

The objectives of this paper are:

1. to examine approaches to screening for drought resistance in sorghum, with particular reference to the complexity of the SAT environment and the vast range of germplasm available;
2. to examine the usefulness of different techniques of selection for drought resistance; and
3. to speculate on future problems and prospects of success.

Other authors (Garrity et al, this volume) also deal with sorghum. This paper will be confined to sorghum in the SAT and work at ICRISAT.

## SCREENING AND BREEDING FOR DROUGHT RESISTANCE

### Approaches to screening

The various approaches to screening for drought resistance may be grouped as direct (agronomic or empirical) or indirect (physiological or analytical). Direct selection for resistance implies either selection for absolute performance (growth rate or yield) under actual moisture stress or selection for only a small reduction in performance under stress. Indirect selection implies screening for morphological or physiological characteristics that may be correlated with or that contribute to drought resistance.

An important aspect of the sorghum improvement program at ICRISAT is the availability of more than 18,000 accessions of sorghum germplasm. The diversity of sorghum-growing environments and the resulting plant adaptations suggest that there is scope for using the germplasm to improve drought resistance. To identify the various traits that individually and in combination contribute to drought resistance, accessions have to be grown in the field. Such direct field screening probably can be done only where and when there is little or no rainfall or where moisture supply to the crop can be controlled through use of irrigation and rain-out shelters. Fortunately, this is possible at many sites in the SAT during the dry season, provided irrigation facilities are available.

The complexity of drought has led to the comment that empirical selection may remain the most effective procedure for some time (Evans 1980). Indirect selection and short-term measurements in the field or under controlled environments also are useful.

Selection for tolerance for desiccation and heat (Sullivan and Ross 1979) and selection for stomatal sensitivity to stress (Henzell et al 1975) are examples of indirect selection in sorghum. It is probably unrealistic to expect a correlation between individual physiological responses and final yield or yield maintenance under moisture stress. However, such responses should consistently confer at least some advantages during stress.

To establish the usefulness of such adaptations in reducing moisture stress, direct field screening and yield estimates are essential. For evaluation of a large number of germplasm and breeders' lines, field screening should have priority. The selected lines can be subjected to individual tests so that the diverse components and underlying mechanisms contributing to stress resistance can be identified and better understood. In the long run, the two approaches are complementary, not mutually exclusive.

### Strategies for breeding

Strategies for breeding for drought resistance have been widely discussed (Blum 1979a, Hurd 1976, Sharma and Saxena 1979, Townley-Smith and Hurd 1979, Reddy et al 1980, Fischer 1981). At ICRISAT, it has been postulated that the genes for yield, adaptability, and resistance to stress are separate, at least at some of the loci, and that stress resistance can be further improved without sacrificing yield or adaptability. Segregating materials grown under stress environments can be selected for drought resistance. Selections should be tested repeatedly under environments where the seasonal and interacting patterns of temperature and water stress are similar to those in the target regions.

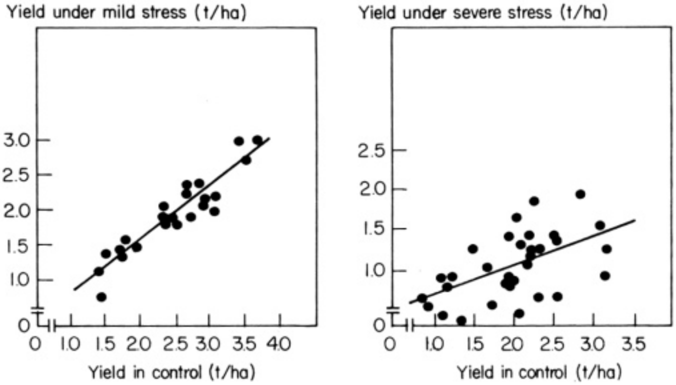
## RESEARCH AT ICRISAT

### Field screening methods

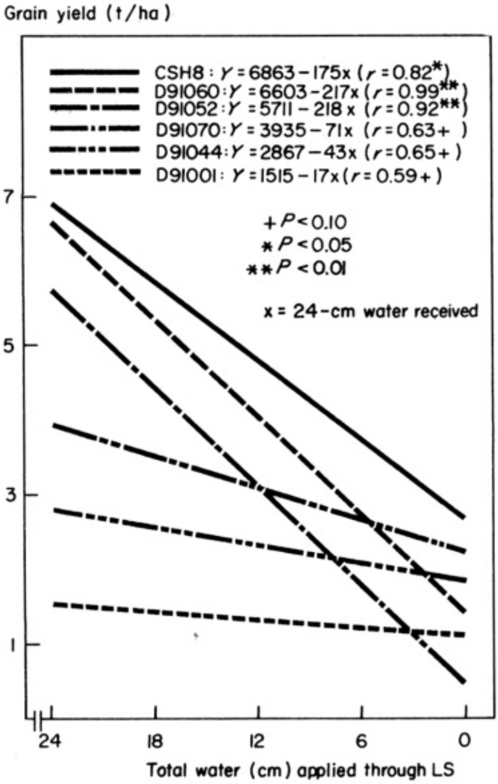
Since 1975, attempts have been made at ICRISAT to evolve simple and direct empirical drought screening methods to evaluate large germplasm accessions and breeder's lines. The experiments were conducted under soil moisture stress in the postrainy (rabi: October-February) and summer (March-June) seasons. Initially, two conditions were imposed: drought during the panicle development stage and receding soil moisture conditions in Vertisols. The first condition represents the midseason drought pattern of the rainy season in many parts of SAT, the second the pattern in rabi crops in India similar to that in crops grown under receding soil moisture conditions in the Mediterranean region (Israel and Yemen) as well as parts of West Africa (Lake Chad area in Nigeria and in Mali).

*Screening for midseason stress.* Comparison of results of early experiments (Seetharama and Bidinger 1979) in postrainy and summer seasons revealed an important aspect of the screening technique (Fig. 1). Yields under moderate stress were closely related to yields without stress. The mean absolute deviation of the measured yield under stress was only 9% of the predicted yield (obtained by regressing stress yield on control yield). This suggests that mild moisture stress is not sufficient for the expression of genotype differences in response to stress. However, severe stress during the summer caused larger deviations from the predicted yield. The mean absolute deviation equaled 26% of the predicted yield and the range of deviation was from –59 to +63%. This provided an opportunity to tentatively identify a number of genotypes which might have different responses to stress.

The stress treatment used did not produce an abnormal crop (despite lower yields). Correlations of yield and other variables (such as yield components, dry weight, and harvest index) were similar in stress and no-stress treatments. How-



1. Relationship between sorghum yields and stress and no stress.



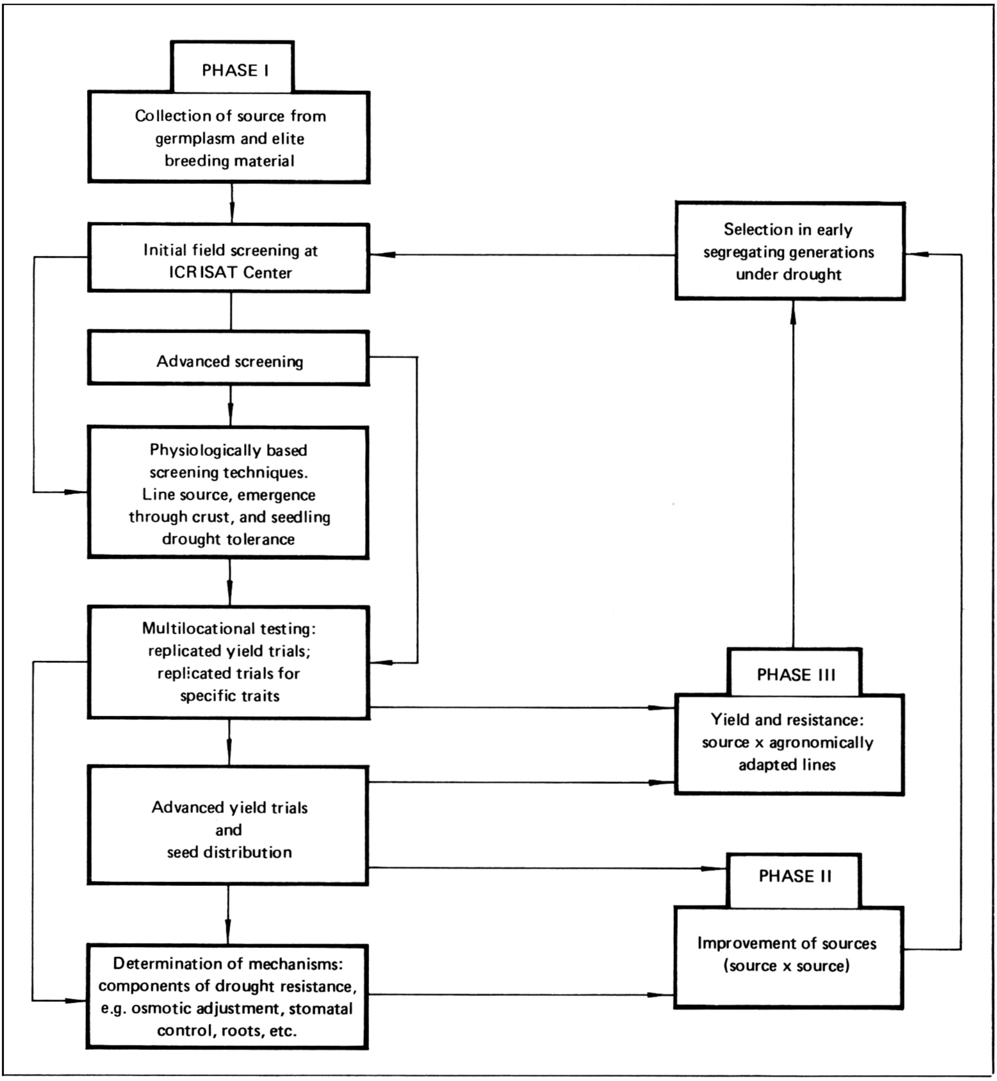
**2.** Relation between grain yield and irrigation water applied through line source (LS) sprinkler irrigation system (after 3 uniform furrow irrigations to recharge the profile during crop establishment phase). Field RA9C; 9.4 cm water available up to 130-cm depth.

ever, phenology differences are important in this type of approach and estimates of cultivar performance under stress may need to be adjusted for them. Simple indices have been proposed for assessing drought resistance in the field which are independent of cultivar yield potential and correlated to yield under stress. The procedure is similar to that described for pearl millet (Bidinger et al, this vol.).

*Screening for rabi pattern of stress.* Comparison of yields on shallow Vertisols or on partially saturated deep Vertisols with yields for an irrigated control can be used to screen genotypes for drought resistance in receding-soil-moisture environments.

*Line source sprinkler irrigation system.* Line source (LS) sprinkler irrigation (Hanks et al 1976) is useful in maintaining a stress gradient at minimum land requirement and cost. A series of test rows of different genotypes planted at right angles to the LS is exposed individually to a uniform gradient of water — from zero to any desired maximum (or adequate to satisfy plant requirements) — from a single row ofoverhead sprinklers. This technique was used in 1980-81 to screen 64 advanced $F_6$ progenies (using 8 checks) from the drought-resistance breeding project.

Genotypic differences in response to the water gradient by LS (after the initial three uniformly applied irrigations needed for crop establishment) can be seen when the yield is plotted against the water applied through LS (Fig. 2). The



**3.** Flow chart of steps in sorghum improvement for drought resistance at ICRISAT (from Reddy et al 1980).

intercepts indicate the yield potential and the slopes indicate susceptibility to decline in water supply. Genotypes with higher intercept and lower degree of slope are selected. When comparing entries such as D91052 and D91070, the areas under regression lines (or overall mean yield across all levels of water supply) are used. Note that, because of its very high yield potential (intercept), the hybrid check CSH8 yielded more than all other entries at all levels of water supply, although it has a steeper slope than D91070, D91044, and D91001. This technique is used at ICRISAT to select for more resistant genotypes (less slope) with high yield potential (intercept) in each maturity group.

### Identification of resistance sources and breeding

The crop improvement strategy at ICRISAT consists of essentially three phases (Fig. 3):

Phase I: identification and characterization of sources of drought resistance.
Phase II: improvement of the sources, for example by bringing together the various genes distributed in germplasm into a smaller number of lines.
Phase III: production of agronomically acceptable types by combining yield and adaptability with drought resistance.

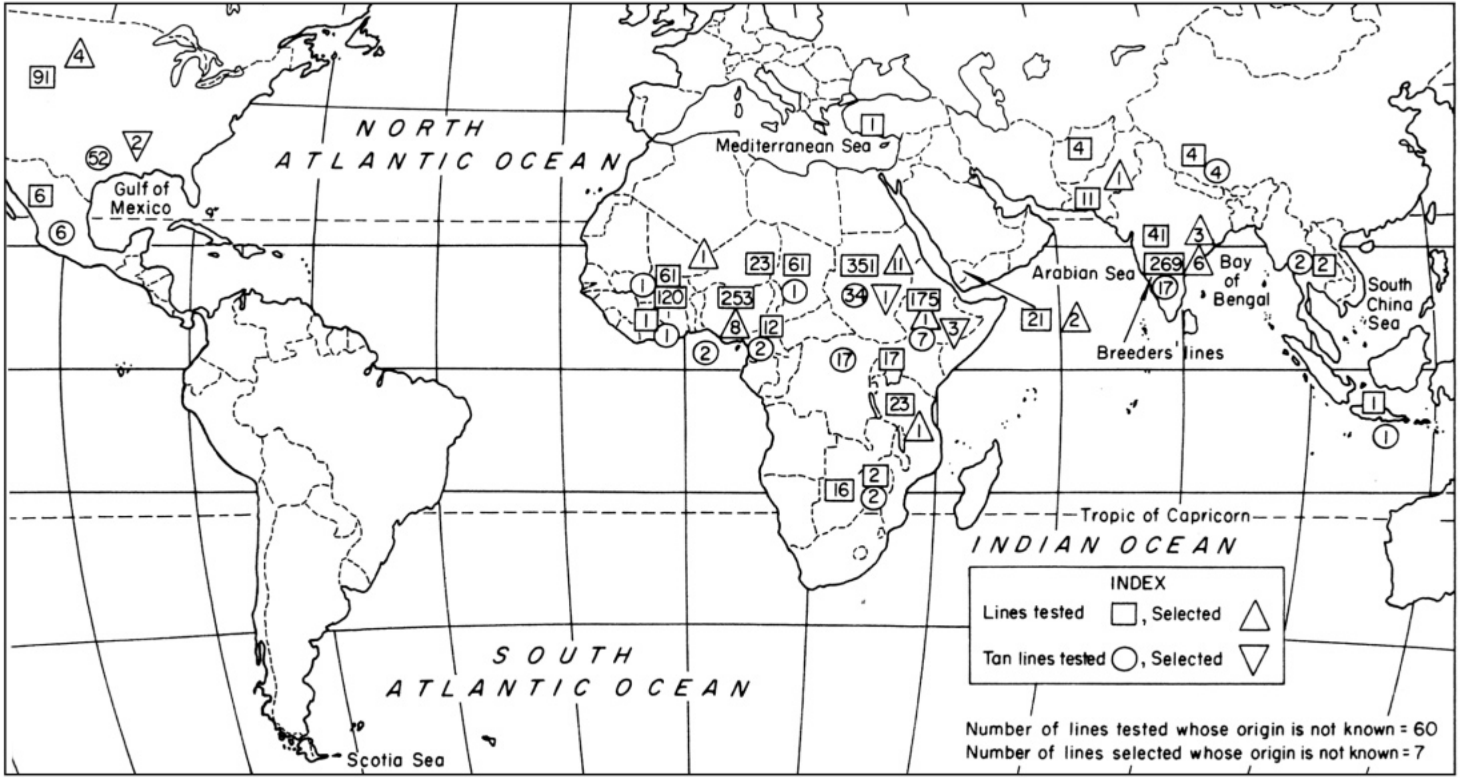
The success of the scheme depends upon the selection of suitable test sites for screening. Both the wet and postrainy dry seasons with controlled irrigation at the ICRISAT center and other sites in India and Africa are used. These sites or environments represent the major patterns of stress being dealt with: 1) intermittent rainy-season drought with emphasis on crop establishment during the first growth stage, and 2) leaf and reproductive growth during the second and third growth stages.

*Germplasm screening.* During 1978 and 1979, 1,255 germplasm accessions from the drier regions (Fig. 4) of SAT and about 600 advanced breeding stocks were subjected to empirical field screening. Based on field performance during drought, 150 promising lines with suitable checks were organized into 3 separate trials and tested at 8 sites. Some promising selections are listed in Table 1.

*Crossing, selection, and testing.* Promising lines were identified and crosses were made with agronomically desirable high-yielding lines. Large populations of early generations were grown at the ICRISAT center during the rainy season. Selections were based on agronomic eliteness and resistance traits such as glossy leaves, mold-free grains, and freedom from pests and diseases. Advanced generations were placed in different trials during all seasons and across many sites wherever water deficits were expected to occur during crop growth. The most promising selections were used in crossing for improving various resistance traits and adaptation (Phase III). They were also crossed among themselves and with new sources to improve the level of resistance to drought (Phase II). Final selections were subjected to special screening under the line source sprinkler irrigation system and were tested for seedling drought resistance.

## MECHANISMS OF DROUGHT RESISTANCE

Crop plants, unlike most of the xerophytes, use more than one mechanism to resist moisture stress (O'Toole and Chang 1978, Gaff 1980). The complete exploitation of genetic diversity requires evaluating mechanisms that ameliorate internal stresses and those that minimize drought injury (Steponkus et al 1980). Investigations on mechanisms of drought resistance of ICRISAT have two objectives: 1) to establish simple field or laboratory screening methods to handle a large number of genotypes, and 2) to study which of the plant attributes or mechanisms contribute



Number of lines tested whose origin is not known = 60
Number of lines selected whose origin is not known = 7

**4.** Lines screened for drought resistance (1977 and 1978 cycles). Source: ICRISAT Sorghum Breeding annual reports 1977-78.

**Table 1. Genotypes selected for drought resistance at 2 sites and their origins. ISDRON[a], 1979 entries.[b]**

| Genotype | Origin | Selection made at |
|---|---|---|
| (NP × E65352-1)-2-1-1[c] | ICRISAT[c] | ICRISAT, India, and Sudan |
| IS-2312 | Sudan | ICRISAT, India, and Sudan |
| IS-3581 | Sudan | ICRISAT, India, and Sudan |
| 15-6 | USA[d] | ICRISAT, India |
| IS-8344 | Pakistan | ICRISAT, India |
| 11-9 | USA | ICRISAT, India |
| IS-8595 | Sudan | ICRISAT, India |
| 340 | USA | ICRISAT, India |
| IS-7525 | Nigeria | ICRISAT, India |
| IS-2321 | Sudan | Sudan |
| IS-2311 | Sudan | Sudan |
| IS-8662 | USA | Sudan |
| DJ-1195 | India | Sudan |
| M35-1 (variety check) | Rabi, India | Sudan |
| CSH6 (hybrid check) | India | Sudan |

[a] International Sorghum Drought Observation Nursery. [b] Reddy et al 1980. [c] From Karper's Nursery, Texas, USA. [d] Line derived from Nebraska population.

to resistance for a particular pattern of drought (for example, midseason stress vs postrainy season terminal stress). The mechanisms described are escape, avoidance, and tolerance (Levitt 1972).

## Drought escape

Three escape mechanisms enable crop plants to resist drought: early maturity, developmental plasticity, and remobilization to grain of stem reserves stored before anthesis (Turner 1979).

*Early maturity and remobilization of stem reserves.* In the Indian Peninsula, the replacement of traditional 130- to 180-day sorghums with early hybrids and varieties of 100-110 days duration, which mature before the rains end or before soil moisture is depleted, has resulted in a remarkable increase in sorghum production (Rao et al 1979). The character concerned (maturity) is detected visually.

Under terminal water stress during the postrainy season, early maturing sorghum genotypes such as CSH6, CSH1, and NK300 escape drought. They produce equal grain but less dry matter than late (100-110 days) cultivars such as M35-1, CSH8, and SPV86 (Table 2). The late cultivars also extract more soil water. CSH8, which has a large seed number, shows maximum remobilization of stem reserves, suggesting that retranslocation of stem reserves depends on potential sink strength.

*Developmental plasticity.* Most of the sorghums grown in SAT (especially in India) do not produce (basal) tillers. They lack the advantage of adjusting tiller number in response to drought. Many sorghum lines delay or postpone their development during stress and resume their development with the start of rain (Seetharama and Bidinger 1977). This kind of plasticity in phenology during midseason stress is useful where there is a good probability of adequate rains to

**Table 2. Genotypic differences in grain yield and dry matter production; estimates of retranslocation of stem reserves to the grain and associated seasonal water use.**

| Genotype | Days to physio-logical maturity | Grain yield (t/ha) | Dry matter production (t/ha) | | Retranslocation from stem[b] (equivalent wt) (t/ha) | Seasonal water use (mm) |
|---|---|---|---|---|---|---|
| | | | Seasonal | In GS3[a] | | |
| CSH1 | 100 | 4.06 | 9.23 | 4.36 | – | 276 |
| CSH6 | 95 | 3.16 | 8.20 | 3.02 | 0.14 | 166 |
| CSH8 | 105 | 4.05 | 9.89 | 2.79 | 1.26 | 215 |
| M35-1 | 105 | 1.94 | 10.47 | 4.51 | – | 272 |
| SPV86 | 108 | 2.95 | 11.38 | 3.23 | – | 197 |
| CS3541 | 105 | 3.18 | 8.01 | 2.42 | 0.76 | 322 |
| IS-1037 | 98 | 2.07 | 8.01 | 3.51 | – | 270 |
| CSV5 | 105 | 3.69 | 8.58 | 2.64 | 1.05 | 309 |
| V302 | 105 | 3.15 | 8.98 | 2.76 | 0.39 | 231 |
| NK300 | 88 | 4.03 | 9.44 | 5.08 | – | 264 |

[a] GS3 = grain-filling period (anthesis to physiological maturity). Values for GS3 are estimated as the difference between dry matter at physiological maturing and flowering. [b] Values represent differences between dry matter at physiological maturity and flowering.

complete an extended crop period. Sometimes even the nodal tillers produced during the recovery period contribute toward grain yield.

## Drought avoidance

Although modern cultivars can escape drought, most crops in the SAT undergo some periods of water shortage. Plants avoid low tissue water potentials by one or more quite discrete mechanisms, such as a change in rooting pattern or an adjustment in leaf area.

*Root pattern.* Drought avoidance achieved by increased root growth draws considerable interest since it does not unduly hamper the productive processes, unlike reduction in leaf area or stomatal closure. Genotypic differences in sorghum roots have been noted (Blum et al 1977a,b; Jordan et al 1979). Screening methods using nutrient culture (Jordan et al 1979) or brick chambers (ICRISAT 1976) are available. However, while these techniques are useful in screening parent lines in a breeding program, selection of segregating material may be better carried out in deep soils when rainfall is absent or meager (Wayne Jordan: Temple, Texas, pers. comm.).

*Leaf area adjustment.* Leaf area adjustment has been suggested as one of the most powerful means of avoiding stress (Passioura 1976). Blum (1979b) has shown that early sorghum genotypes not only escape drought but also avoid it because of reduced transpiration demand as a result of decreased leaf area (and high root length-leaf area ratio). Many have felt that physiologists have not given sufficient attention to the processes determining leaf area, especially in the field (Elston 1980, Kramer 1979). Because of the high sensitivity of leaf extension to change in turgor, several authors (Orshan 1954, Boyer and McPherson 1975, Karamanos 1979, Hsiao and Acevedo 1974) have suggested that leaf extension rate be used as the criterion for evaluating drought sensitivity. Culm (stem and leaf) extension rates are being used as an index of drought avoidance in the maize program at the International Maize and Wheat Improvement Center (CIMMYT) (K. S. Fischer, pers. comm.). Table 3 shows the range in genotypic variation in leaf extension rates with respect to stress. Note that CSV5 and V302, which are sensitive to water stress, show more marked reduction in extension rates than M35-1 or CSH8, which are more drought resistant.

*Other adaptations.* During the 1979 rainy season at ICRISAT, a severe drought occurred on shallow Alfisols during the boot stage. Many elite entries (which yielded more than 7 t on deep Vertisols during the same season) gave very low yields on Alfisols because under stress they failed to exsert their panicles through the boot (sheath of flag leaf). The entries can be easily screened for such a failure of stem and peduncle extension under stress and susceptible ones discarded. Further genotypes whose panicles are damaged (for example, aborted spikelets) during stress also can be eliminated.

A decrease in radiation absorption by the leaf by leaf rolling (Begg 1979) or by light reflection and a decrease in cuticular loss of water normally save only small amounts of water. But, under conditions of severe stress, gains are substantial. Sorghum shows all these adaptations (Blum 1975, Chatterton et al 1975) but the traits have been incompletely quantified.

**Table 3. Extension rates of culm (leaf + stem; Ter) and of leaf (Ler) under control (irrigated) and stress during the panicle development stage.**

| Genotype | Ter[a] (mm/h) | | Reduction (%) | Ler[a] (mm/h) | | Reduction (%) |
|---|---|---|---|---|---|---|
| | Control | Stress | | Control | Stress | |
| CSV5 | 2.42 | 1.42 | 41.3 | 2.18 | 1.23 | 43.6 |
| V302 | 2.37 | 1.53 | 35.4 | 1.76 | 1.11 | 36.9 |
| CSH8 | 2.09 | 1.79 | 14.4 | 1.74 | 1.47 | 15.5 |
| M35-1 | 2.45 | 2.28 | 6.9 | 1.95 | 1.70 | 12.8 |
| IS-12611 | 4.05 | 2.67 | 34.1 | 2.42 | 1.72 | 28.9 |
| CS3541 | 3.08 | 1.49 | 29.5 | 1.49 | 1.16 | 22.2 |
| CSH-1 | 2.55 | 1.72 | 32.6 | 1.30 | 0.88 | 32.3 |
| CSH-5 | 2.87 | 2.20 | 23.3 | 2.06 | 1.65 | 19.9 |
| Mean ± S.E. | 2.61 ± 0.22 | 1.89 ± 0.16 | 27.19 ± 4.10 | 1.86 ± 0.13 | 1.37 ± 0.11 | 26.51 ± 3.80 |
| Range | 2.08-4.06 | 1.42-2.67 | 6.9-41.3 | 1.30-2.42 | 0.88-1.72 | 12.8-43.6 |

[a] Data for period 1600 h on 31 Jan 1981 to 1530 h on 2 Feb 1981. Field RP 16A Patancheru (Seetharama, unpubl.).

Genotypes were compared for drought avoidance through short-term measurements of leaf water potential, leaf temperature, and stomatal conductance. While repeatable genotypic differences are found, there is no simple way they can be related to final yield reduction under stress (Seetharama et al, unpubl.), although these studies help in understanding the various mechanisms.

## Drought tolerance

In spite of a plant's efforts to avoid drought, low tissue water potential will occur during prolonged periods of water stress. It is necessary, under SAT conditions where chances of prolonged drought are high, to distinguish between the tolerance mechanisms that enable the protoplasm to survive and allow the plant to recover from stress after the rains (for example, heat and desiccation tolerance) and those that enable the plant to adapt to low tissue water potential (for example, osmotic adjustment) so that it can continue to grow and develop at reasonable rates (Turner 1979).

*Heat and desiccation tolerance and recovery ability.* Conditions of high temperature and evaporative demands are more conducive to drought resistance screening than milder conditions (Fig. 1).

Three hundred and sixty-four advanced selections from the drought resistance breeding project were evaluated in replicated trials at Sangareddy (20 km west of ICRISAT center) during the hot summer (Apr-May) of 1980, when the maximum daily temperature varied between 35°C and 43°C. The plots were irrigated at planting, then subjected to severe desiccation and heat stress. The leaves rolled

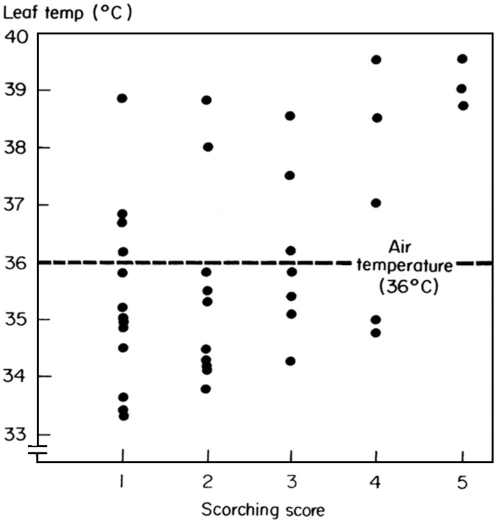
**5.** Screening of Sorghum bicolor for heat and drought resistance: genotypic differences in leaf firing. Selection D71305 (left) shows severe leaf firing: D71152 (right) has dark green leaves.

and growth practically ceased in most of the genotypes during the stress period. The cumulative effect of heat and water stress was more apparent 20 days after the onset of the monsoon, by which time a total of 60 mm of rainfall had been received. Genotypes that were severely damaged because of stress did not recover and part of or whole leaves remained white or fired (Fig. 5). In contrast, other genotypes with little fired leaf area showed varying ability to recover and resume growth (Reddy et al 1980).

Genotypes were scored on a 1-5 scale (1 = least firing). One trial had an additional treatment and received 2 more irrigations at 3-week intervals after initial establishment. The leaf and air temperatures were measured on two occasions and correlated with leaf firing. Entries receiving a score of one (least scorching) had leaves cooler than air and entries receiving a higher score (more scorching) had hotter leaves (Fig. 6). Many entries showing resistance to leaf firing were also agronomically good. Preliminary results showed good correlations (P <0.01) between scores for leaf firing and ability to recover at Sangareddy in summer (off-season) and at Anantapur (14°7'N) during the normal rainy season under natural drought.

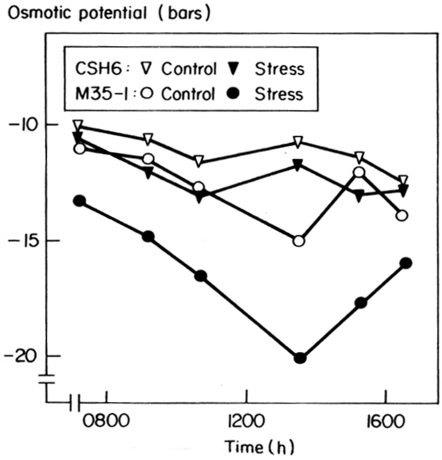
Sullivan and Ross (1979) have cited seven reports in which heat tolerance tests were used to select for drought resistance. It should be possible to screen large numbers of breeding lines and germplasm for resistance to heat and desiccation tolerance in the field during summer. Arnon (1975) and Sullivan and Ross (1979) have pointed out certain instances in which correlation between heat and desiccation tolerance was poor, but it is generally agreed that heat tests can be used to reduce the number of genotypes to a small group which then can be subjected separately to both heat and desiccation tests.

*Osmotic adjustment.* Diurnal and seasonal osmotic adjustments to water stress have been noted in sorghum (Jones and Turner 1978) and genotypic differences are known to exist (Stout and Simpson 1978). A decrease in osmotic potential



**6.** Relationship between scorching score and leaf temperature. Leaf temperature was measured with infrared thermometer during stress on 21 May 1980 between 1420 and 1440 h; scorching was scored after recovery period of 18 July 1980; score 1 = leaf firing. Each point represents one genotype.

**7.** Diurnal variations in osmotic potentials in sorghum cultivars CSH6 and M35-1. Standard error of the mean is less than 0.5 bar.



contributes to leaf expansion in sorghum during conditions of high atmospheric demand for water (Acevedo et al 1979). At ICRISAT, genotypic differences have been detected in predawn osmotic potentials even under mild stress. Postrainy season cultivars such as M35-1 and CSH8 which encounter terminal water stress have a greater capacity to decrease their osmotic potential under stress than the rainy-season type CSH6 (Fig. 7). A regression approach (Ackerson et al 1980) showed that the leaf water potential at zero turgor was 4 bars less for M35-1 than for CSH6.

## FUTURE PROSPECTS AND PROBLEMS

The first step in planning any crop improvement program for drought-prone areas is the comprehensive diagnosis of direct (a water deficit which depends upon the rainfall pattern and the soils' capacity to store and supply water between rainfall events) and indirect (attendant physical, chemical and biological, and cultural changes) factors determining the locational and temporal specificity of drought (Gotoh et al 1979, Jordan and Monk 1980). However, it must be understood that our concept of an ideal plant for a given environment cannot be more accurate than the prediction of the climate (within confidence limits) for an average year. The rabi sorghum environments in the Indian Deccan plateau under deep Vertisols can be well defined and greater progress can be expected toward bridging the gap between potential and actual yield in these environments. In contrast, great seasonal fluctuations within an adaptation zone exist in vast areas of the SAT.

The progress in producing genotypes that have the maximum flexibility to adjust to a wide range of seasonal conditions will be understandably slow. Any international or regional breeding program aiming to serve a large number of adaptation zones (such as ICRISAT) should have a broad spectrum of drought-resistant genetic material differing in maturity and plant type. The breeders in local and national programs could then evaluate the most promising progeny for their own use.

**Table 4. Constitutiveadaptation, facultative adaptation, and management practices thatconfer drought resistance: prospects in a sorghum improvement program.**

| Remarks | Examples | Existing variability | Basic information or techniques | Prospects for breeding |
|---|---|---|---|---|
| | *Constitutive adaptation* | | | |
| Mostly irreversible and lifelong | *Morphological or phenological* | | | |
| | 1. Maturity | High | High | High |
| | 2. Developmental plasticity | Meager (tillering not considered) | Scant | Moderate-low |
| | 3. Glossy leaf | High | Scant | High |
| | 4. Number, shape, and size of leaf | Moderate | Moderate-low | Moderate |
| | *Physiological* | | | |
| | 5. Desiccation tolerance | High | Moderate | High |
| | 6. Heat tolerance | High | Moderate | High |
| | 7. High growth rates | Moderate among elite breeding stocks | Moderate | Moderate |
| | 8. Low respiration | Moderate | Scant | Low |
| | 9. Recovery rate after stress | High | Moderate | High |
| | 10. Anatomical features | Low | Scant | Low |
| | 11. Root-shoot ratio | Moderately high | Scant | Low |
| | 12. Liquid phase resistance | Low | Scant | Low |
| | 13. Deep roots | Moderate | Scant | Low |

| | | | | |
|---|---|---|---|---|
| | *Facultative adaptation* | | | |
| Shorter term responses, more, dynamic, some (1-2) almost completely reversible, others (4-8) irreversible | 1. Stomatal closure | Moderate to high | Moderately high | Low |
| | 2. Leaf rolling | High | Moderate | Low |
| | 3. Increase in wax content of epidermis | Moderate | Moderate | Low-moderate |
| | 4. Leaf area increase | Moderate to high | Moderate | Moderate to high |
| | 5. Leaf senescence | High | Moderate | High |
| | 6. Remobilization of stem reserves | Moderate (up to 30%) | Moderate | High |
| | 7. Plant hormones | Low | Scant | Low-unknown |
| | 8. Osmotic adjustment | Moderate | Scant to moderate | Moderate |
| | 9. Relative increase in root growth | Moderate | Scant | Moderate |
| | *Management factors* | | | |
| Application of antitranspirants is not within means of small farmers. | 1. Time of planting | Genotype-management interactions well documented but information not enough for initiating special breeding program. | | Except in case of change in planting date where thermo-sensitivity and photoperiod sensitivity may be involved, screen only the advanced material, at least in the near future. |
| | 2. Plant population | | | |
| | 3. Row spacing | | | |
| | 4. Fertilizer application | | | |
| | 5. Tillage practices | | | |
| | 6. Use more than one variety | | | |
| | 7. Intercrop midseason correction by ratooning | | | |

## Multicriteria approach breeders' dilemma

Control of water loss from the shoot can be curtailed by one or more mechanisms (Table 4). Undoubtedly, drought escape is a first line of defense but other mechanisms should be used for any further improvement. Because crops use several of these mechanisms to varying degrees in field conditions, it is necessary to incorporate at least some of them for a high degree of drought resistance.

It is important to show that all the adaptive mechanisms that have been advocated are heritable. In sorghum, the inheritance of traits such as waxy bloom (Blum 1975) is simple, but others are expected to be governed by several genes. Some of these traits (such as net carbon dioxide exchange rate/transpiration rate 6-14% higher in lines having blooms than in bloomless ones, Chatterton et al 1975) apparently contribute little in isolation, but the collective contribution may be substantial. For example, waxiness, glossy appearance, and narrowness of leaf individually may contribute little but collectively the contribution to water economy may be considerable, especially under severe stress. Some useful traits seem to occur together in some local germplasm lines. For example, M35-1 has glossy leaves and deep roots and is heat resistant, besides being less susceptible to diseases such as charcoal rot and to shoot fly. It is advisable to thoroughly examine the value of such traits before trying to accumulate the corresponding genes in a breeding population.

At present, our understanding of metabolic traits such as osmotic adjustment and hormonal regulation is incomplete. At the beginning, screening for physiological and metabolic traits could be confined to parents used in the crossing program or in hybrid development. It should be used only to complement the more important, easier, and inexpensive techniques. In breeding, the emphasis also must be on traits that apparently have no or minimal deleterious influence on yield.

This approach poses another problem: how to bring together several of the traits, sometimes linked and sometimes mutually exclusive. Conventional breeding techniques, such as selections in single cross and backcross progenies, can be used to accumulate a few genes at a time. The population breeding method, which allows simultaneous incorporation of several genes or traits (Doggett 1977), is advocated. However, progress with such an approach is slow. Because it is generally agreed that sorghum hybrids are superior to other varieties, even under stress (Rao and Harinarayana 1969, Blum 1979a), reciprocal recurrent selection may allow concentrating a set of characters in each of two B- and R-populations. Two sorghum drought-resistant populations (NP9BR and Downes) are available for further improvement.

*Other traits closely related to drought.* Good management practice is a precondition for more efficient use of water. Physiologists and breeders are aware that genotypes interact differently with various management factors (Table 4), especially those that influence soil water extraction patterns. At ICRISAT, significant genotypic differences in response to drought at the seedling stage were found in both the germplasm and breeders' elite lines, as measured by scoring for wilting, recovery, and survival after stress. Many lines resistant to drought at the seedling stage were observed to have light-green leaves with a glossy surface. The susceptible lines generally had dark-green leaves (Maiti 1980). Currently, more germplasm is being screened for wide-scale applicability in the breeding program.

In addition, nutrient uptake, metabolism under stress, and mineral toxicity need more intensive study. Sorghum production problems such as higher incidence of *Striga,* charcoal rot, and root lodging are closely associated with drought.

## Modeling

Crop weather models are useful in quantifying the response of factors, singly or in combination, on crop growth and development. If sufficiently accurate and properly used (Passioura 1973), these models are powerful research tools in designing alternate strategies, either in plant structure or in management. Fortunately, some models of varying complexity are already available to sorghum workers: PLANTGRO (R. J. Hanks, Utah State University, Logan, pers. comm.), SORGF (Arkin et al 1976), and the model by Hodges et al (1979). Simulation models for individual plant responses, such as leaf water potential, also are available (Takami and Yukimura 1979).

The use of agroclimatic analogues in the transfer of technology using models of known areas is well established (Nix 1980). But it must be noted that the usefulness of the models will not be thoroughly appreciated until they are placed in the hands of physiologists, breeders, agronomists, soil scientists, and engineers.

## Exchange of germplasm and training

Despite locational specificity, exchange of genetic material can take place if a reasonable correspondence between sites is established (House 1980). Germplasm and breeding material can be exchanged most usefully between similar adaptation zones (especially after reaping the initial benefits of introduced exotics) on different continents. Material received from corresponding sites can be further improved according to local needs, to suit specific patterns of drought and for other traits concerned with productivity such as disease or pest resistance.

With the help of empirically established correspondence between sites and with further refinement by using models, the basic idea regarding the adaptability of a cultivar to a site can be transferred.

One of the more appropriate ways to deal with locational and temporal specificity throughout the sorghum-growing regions is by encouraging the formation of interdisciplinary teams to work in regional and national programs. Since its inception, ICRISAT has recognized the need to train more sorghum workers to tackle such problems as drought to enable them to find an appropriate solution to the kind of drought prevalent in their own countries.

## REFERENCES CITED

Acevedo, E., E. Fereres, T. C. Hsiao, and D. W. Henderson. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. Plant Physiol. 64:476-480.

Ackerson, R. C., D. R. Krieg, and F. J. M. Sung. 1980. Leaf conductance and osmoregulation of field-grown sorghum genotypes. Crop Sci. 20:10-14.

Arkin, G. G., R. L. Vanderlip, and J. T. Ritchie. 1976. A dynamic grain sorghum growth model.

Trans. ASAE. 19:622-630.

Arnon, I. 1975. Physiological principles of dryland crop production. Pages 3-145 *in* U. S. Gupta, ed. Physiological aspect of dryland farming. Oxford and IBH Publishing Co., New Delhi.

Begg, J. E. 1979. Morphological adaptations of leaves to water stress. Pages 33-42 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Bidinger, F. R., J. Mahalakshmi, B. S. Talukdar, and G. Alagarswamy. 1982. Improvement of drought resistance in pearl millet. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Blum, A. 1975. Effect of the BM gene onepicuticular wax deposition and the spectral characteristics of sorghum leaves. SABRAO J. 7:45-52.

Blum, A. 1979a. Genetic improvement ofdrought resistance in crop plants: a case for sorghum. Pages 429-445 *in* H. Mussel and R. C. Staples, eds. Stress physiology in crop plants. John Wiley and Sons, New York.

Blum, A. 1979b. Principles and methodology of selecting for drought resistance in sorghum. Monografie di Genetica Agrano. 4:205-215.

Blum, A., G. F. Arkin, and W. R. Jordan. 1977a. Sorghum root morphogenesis and growth. I. Effect of maturity genes. Crop Sci. 17:149-153.

Blum, A., W. R. Jordan, and G. F. Arkin. 1977b. Sorghum root morphogenesis and growth. II. Manifestation of heterosis. Crop Sci. 17:153-157.

Boyer, J. S., and H. G. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-22.

Chatterton, N. J., W. W. Hanna, J. B. Powell, and D. R. Lee. 1975. Photosynthesis and transpiration of bloom and bloomless sorghum. Can. J. Plant Sci. 55:541-643.

Doggett, H. 1970. Sorghum. Longmans, London. 403 p.

Doggett, H. 1977. Keynote address. International sorghum workshop, 6-13 March, 1977. ICRISAT, Hyderabad, India.

Elston, J. 1980. Climate. Paper presented at the symposium on potential productivity of field crops under different environments, 22-26 September 1980. International Rice Research Institute, Los Baños, Philippines.

Evans, L. T, 1980. Book review: stress physiology in crop plants. Field Crops Res. 3:194-196.

FAO (Food and Agriculture Organization of the United Nations). 1979. Production yearbook, Vol. 33, p. 107-108. Rome.

Fischer, R. A. 1981. Optimizing the use of water and nitrogen through breeding of crops. Plant Soil 58:249-278.

Gaff, D. F. 1980. Protoplasmic tolerance of extreme water stress. Pages 207-230 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Garrity, D. P., C. Y. Sullivan, and W. M. Ross. 1982. Altanative approaches to improving grain sorghum productivity under drought stress. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Gotoh, K., T. T. Chang, J. C. O'Toole, R. Riley, and B. R. Murty. 1979. Crop adaptation. Pages 234-261 *in* J. Sneep and A. J. T. Hendriksen, eds. Plant breeding perspectives. Centre for Agricultural Publishing and Documentation, Wageningen.

Hanks, R. J., J. Keller, V. P. Rassmussen, and D. G. Wilson. 1976. Line source sprinkler for continuous variable irrigation - crop production studies. Soil Sci. Soc. Am. J. 40:426-429.

Henzell, R. C., K. J. McCree, C. H. M. von Bavel, and K. F. Sherz. 1975. Method of screening for sorghum genotypes for stomatal sensitivity to water stress. Crop Sci. 15:516-518.

Higgins, G. M. 1978. Report on the agro-ecological zones project. Vol. 1. Methodology and results for Africa. Food and Agriculture Organization of the United Nations, Rome. 157 p.

Hodges, T., E. T. Kanemasu, and I. D. Teare. 1979. Modelling dry matter accumulation and yield of grain sorghum. Can. J. Plant Sci. 59:803-818.

House, L. R. 1980. ICRISAT sorghum improvement program: 10-year projection. ICRISAT, Patancheru P. O., India. 22 p.

Hsiao, T. C., and E. Acevedo. 1974. Plant responses to water deficits, water use efficiency, and drought resistance. Agric. Meteorol. 14:59-84.

Hurd, E. A. 1976. Plant breeding for drought resistance. Pages 317-353 *in* T. T. Kozlowski, ed. Water deficits and plant growth. Vol. 2. Academic Press, New York.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1976. Annual report 1975-1976. Hyderabad, India. p. 44.

Jones, M. M., and N. C. Turner. 1979. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Jordan, W. R., F. R. Miller, and D. E. Morris. 1979. Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci. 19:468-472.

Jordan, W. R., and R. L. Monk. 1980. Enhancement of drought resistance of sorghum. Paper to be published in the Proceedings of 35th Corn and Sorghum Research Conference, September 1980, Chicago.

Karamanos, A. J. 1979. Water stress: A challenge for the future of agriculture. Pages 415-455 *in* T. Scott, ed. Plant regulation and world agriculture. Plenum Press, New York.

Kramer, P. J. 1979. The role of physiology in crop improvement. Pages 51-62 *in* R. C. Staples and R. J. Kuhn, eds. Linking research to crop production. Plenum Press, New York.

Levitt, J. 1972. Responses of plant to environmental stresses. Academic Press, New York. 697 p.

Maiti, R. K. 1980. The role of glossy and trichome traits in sorghum crop improvement. Paper presented at the AICSIP annual workshop, 12-14 May 1980, Coimbatore.

Motha, R. P., and C. M. Sakamoto. 1979. The performance of crop yield models in drought-prone countries of Central Africa. Paper presented at the 71st Annual Meeting of the American Society of Agronomy, 5-10 August 1979, Fort Collins, Colorado.

Murthy, R. S., and S. Pandey. 1978. Delineation of agro-ecological regions of India. Commission V, 11th Congress of the International Society of Soil Science, 19-22 June 1978, Edmonton, Canada.

Nix, H. 1980. Agroclimatic analogues in transfer of technology. Pages 83-88 *in* Proceedings, international symposium on development and transfer of technology for rainfed agriculture and the SAT farmer, 28 August-I September 1979, ICRISAT, Patancheru, India.

Orshan, G. 1954. Surface reductionand its significance as hydroecological factor. J. Ecol. 42:442-444.

O'Toole, J. C., and T. T. Chang. 1978. Drought and rice improvement in perspective. IRRI Res. Pap. Ser. 14. 27 p.

Passioura, J. B. 1973. Sense and nonsense in crop simulation. J. Aust. Inst. Agric. Sci. 39:181-183.

Passioura, J. B. 1976. Physiology of grain yield in wheat growing on stored water. Aust. J. Plant Physiol. 3:559-565.

Rao, X. G. P., and G. Harinarayana. 1969. Phenotypic stability of hybrids and varieties in grain sorghum. Curr. Sci. 38:97-98:

Rao, N. G. P., M. J. Vasudeva Rao, B. S. Rana, and V. J. M. Rao. 1979. Responses to water availability and modifications for water use efficiency in tropical dryland sorghums. Paper presented at the symposiumon plantresponses to water availability, 22-24 February 1979, IARI, New Delhi, India.

Reddy, B. V. S., N. Seetharama, R. K. Maiti, F. R. Bidinger, J. M. Peacock, and L. R. House. 1980. Breeding for drought resistance in sorghum at ICRISAT. Paper presented at the AICSIP workshop, 12-14 May 1980, Coimbatore, India.

Seetharama, N., and F. R. Bidinger, 1977. Sorghum drought resistance. Paper presented at the International Sorghum Workshop, 6-13 March 1977, ICRISAT, Hyderabad, India.

Seerharama, N., and F. R. Bidinger, 1979. Initial experiments on drought-resistance screening methodology. ICRISAT Sorghum Physiology Progress Rep. 2, Patancheru, India. 67 p.

Sharma, D., and S. P. Saxena. 1979. Crop response to drought-screening techniques and breeding for resistance. Paper presented at the symposium on plant responses to water availability, 22-24 February 1979, IARI, New Delhi, India.

Steponkus, P. L., J. M. Cutler, and J. C. O'Toole. 1980. Adaptation to water stress in rice. Pages 401-418 in N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York.

Stour, D. G., and G. M. Simpson. 1978. Drought resistance of sorghum bicolor. I. Drought avoidance mechanisms related to leaf water status. Can J. Plant. Sci. 58:213-224.

Sullivan, C. Y., and W. M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. Pages 263-281 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. John Wiley and Sons. Sew York.

Takami, S., and T. Yukimura. 1979. Varietal difference in leafwater status and water use ofsorghumas affected by the stomatal sensitivity. Pages 1-24 *in* Memoirs of the College of Agriculture, Kyoto University, No. 113.

Townley-Smith, T. F., and E. A. Hurd. 1979. Testing and selecting for drought resistance in wheat. Pages 447-464 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. John Wiley and Sons, New York.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. Pages 343-372 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. John Wiley and Sons, New York.

Virmani, S. M., M. V. K. Sivakumar, and S. J. Reddy. 1980a. Climatological features of the semi-arid tropics in relation to the farming systems research program. Pages 5-16 *in* Proceedings, intertional workshop on agroclimatological research needs of the semi-arid tropics. ICRISAT, 22-24, November 1978, Hyderabad, India

Virmani, S. M., S. J. Reddy, and M. N. S. Bose. 1980b. A handbook on the rainfall climatology of West Africa: data for selected locations. Inf. Bull. 7, ICRISAT, Patancheru P. O., India.

# ALTERNATIVE APPROACHES TO IMPROVING GRAIN SORGHUM PRODUCTIVITY UNDER DROUGHT STRESS

D. P. GARRITY, C. Y. SULLIVAN, AND W. M. ROSS

The incorporation of greater drought resistance into the world's major field crops is urgently needed to increase food supplies while using less energy-intensive technology. Efforts to improve productivity of sorghum under drought stress have followed one of two paths:

- the physiological approach. Specific traits that enable the plant to better withstand drought are identified and introduced into superior genetic backgrounds.
- the performance approach. Direct selection under water stress environments is followed.

Numerous traits have been hypothesized to confer a productive advantage to sorghum in drought-stressed environments and genetic differences have been observed for several of these. However, the development of efficient screening techniques has been a major constraint to incorporating the traits into genotypes. In addition, little work has been done on the inheritance of drought resistance traits and their association with superior plant performance under drought. Without this information, there is scant basis for a selection effort.

Until individual drought-resistance traits are better understood, crop improvement programs will have to rely on selection for whole plant performance. Conventional breeding programs have resulted in significant gains in sorghum productivity for water-limited conditions. But progress has slowed.

---

The International Rice Research Institute, Los Baños, Philippines; and the Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583, USA.

Population breeding is an effective means to counter this situation. Genes for drought stress productivity can be concentrated from a broad genetic base, even though the specific traits involved are not identified. By combining population breeding with methods of creating precise stress environments in the field, such as the line source sprinkler system, and by using techniques to better characterize genotypic response to the range of environments, increasing progress is expected.

Water-deficient, semiarid agricultural lands are assuming greater importance in the production of the world food supply. When fuel resources were relatively cheap, agricultural research concentrated on increasing crop yields of these areas through such energy-intensive practices of irrigation. Economics dictated that relatively little emphasis be placed on the development of technology to increase and stabilize crop production in nonirrigated dry areas, particularly in developing countries.

The situation has changed over the last decade. Agricultural research cannot continue to rely predominantly on boosting productivity through energy-intensive practices, else the energy resources and the time needed to develop alternative methods will be lost. Improving drought resistance in the world's major field crops is an urgently needed, low-energy method for increasing the world food supply.

Today, sorghum ranks fifth among the major cereals in area sown, following wheat, rice, maize, and barley. Major production regions include the Great Plains of the United States, sub-Saharan Africa, northern China, and the Deccan Plateau of central India.

Although sorghum has maximum yield potentials similar to the other cereals, its average worldwide yields are much lower — 1,200 kg/ha compared with 1,800-2,800 kg/ha for other cereals (House 1981). These low yields reflect common exposure to extreme heat and drought stress. Sorghum frequently is grown during the warmest part of the year in areas receiving as little as 400 mm annual rainfall.

Given the relatively harsh and variable climatic conditions of most production regions, varietal yield potential seldom is approached. The need for higher and more stable yields under water stress has been given relatively strong attention in recent sorghum improvement programs. Experiences gained with sorghum may be relevant because the evidence, although inadequate, is greater than for most crops.

Efforts to improve sorghum productivity under drought stress can be differentiated into the physiological approach and the performance approach (Bidinger 1980). In the physiological approach, specific physiological or morphological adaptations that enable the plant to better withstand water stress are identified. Subsequent breeding and selection incorporates these traits into elite germplasm and new varieties.

In the performance approach, methods and criteria to make effective direct selection under stress environments are developed. This conforms more closely to conventional breeding procedures but faces the difficult requirements of defining and controlling water stress in test environments.

Drought resistance indicates the sum total of a plant's capacity to escape, avoid, tolerate, or recover from water stress. Drought resistance is quantified as a fraction: grain yield under water stress/grain yield under nonstress. Drought stress productivity indicates superiority in yield performance among genotypes in a water-limited environment.

## THE PHYSIOLOGICAL APPROACH

Specific physiological or morphological traits that exist within a crop species contribute significantly to performance under water stress. These traits can be identified and manipulated genetically.

The physiological approach has five critical stages:

1. Development of a hypothesis concerning the potential contribution of a particular trait;
2. Search for genotypic variability for the trait;
3. Development of a rapid and efficient screening method;
4. Elucidation of the mode of trait inheritance and selection of an appropriate breeding method to incorporate it into agronomically superior genotypes;
5. Documentation of a strong causal relationship between high levels of a trait and improved drought resistance.

### Hypothesis development

Hypotheses concerning traits that could confer a productive advantage to field crops under drought are numerous. In fact, the number of proposed mechanisms is constantly expanding. In some cases, hypotheses are based on biophysical criteria resulting from an understanding of plant-water relations. In others, they arise through observation of the association between a particular trait and varieties or species that seem to thrive in drought-prone conditions.

*Avoidance mechanisms.* Improvements in the ability of a crop plant to maintain a favorable water status under drought depend on either more efficient control of water loss or on greater water flow through the plant. To control water loss, numerous methods have been suggested for selection of specific stomatal characters.

Jones (1979) summarized some directions: selection for low maximum stomatal conductance to conserve soil moisture for later developmental stages; selection for a high or low threshold of stomatal closure in respect to leaf water potential; selection for a high degree of stomatal responsiveness to environmental conditions (such as vapor pressure deficit); or selection for particular levels of abscisic acid to promote better stomatal control.

Sullivan (1971) suggested selecting for a high threshold leaf water potential for stomatal closure to prevent the damaging effects of short stress periods. Selecting for gradual closure over a wide range of water potentials might be of value in maintaining photosynthesis through longer stress periods.

Selecting for a greater thickness of epicuticular wax has been proposed for greater drought avoidance through transpiration control. Blum (1975) found that greater wax deposits reduced cuticular water loss and net radiation in the sorghum canopy. Other morphological tactics to control water loss include modifications of the arrangement, shape, color, and number of leaves in the canopy.

The tactic of maintaining a favorable crop water status by continuing high water flow through a plant under drought relies on manipulating the root system to obtain more efficient soil water extraction or reduced root resistance. Root characteristics that may be important include increased rooting depth and density, reduced radial or axial resistance, and osmotic adjustment of the root system.

*Tolerance mechanisms.* In water-stress conditions severe enough to override avoidance mechanisms, the plant's ability to survive and continue carbon assimilation under low water potentials will depend on desiccation tolerance. Considerable work has been done with a method that determines desiccation tolerance as a function of cell membrane integrity under a fairly severe stress treatment (Sullivan and Ross 1979). The osmotic adjustment of shoots also may be an important tolerance mechanism.

Other traits presumably are associated with drought resistance. The effectiveness of a particular trait will be dependent on the nature of the drought stress occurring in a particular area and growing season.

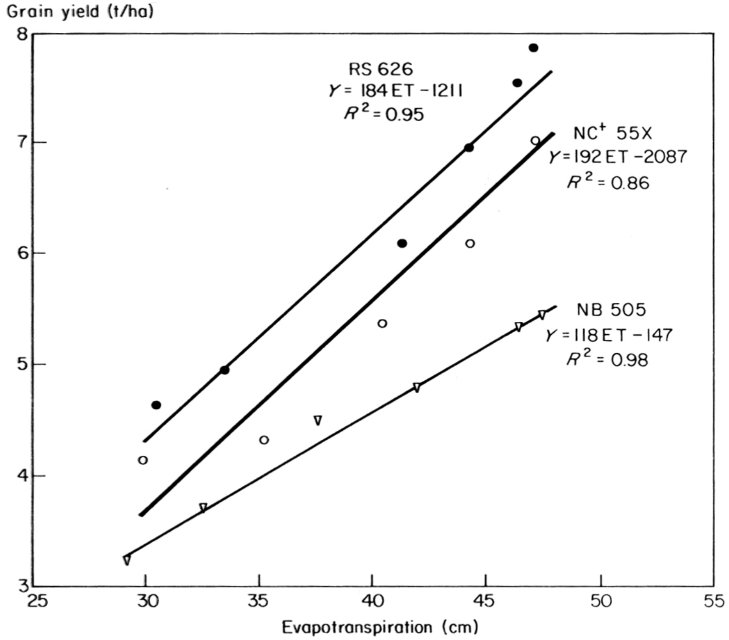
## Search for genotypic variation

Varietal differences within sorghum have been observed for a number of traits. Jordan and Miller (1980) and Sullivan and Ross (1979) reported variation in root parameters among genotypes grown in hydroponic culture in the field. Jordan et al (1979) found that, although a sample of breeding lines were similar in three root parameters, several more recently developed lines from a more diverse genetic base differed significantly from the standard lines. They concluded that there was sufficient variability in shoot and root growth characteristics to warrant further study on the genetic improvement of sorghum root systems.

Garrity et al (1981b) compared the seasonal evapotranspiration among three sorghum hybrids subjected to a series of water-stress treatments and found nearly identical values, indicating a lack of variation in gross soil moisture extraction. The highly significant differences observed in dry matter and grain yield were not attributable to differences in total water use but to differences in water-use efficiency among the genotypes (Fig. 1).

Genotypic differences in the stomatal response of young sorghum plants to reduced leaf water potentials were reported by Henzell et al (1976). They proposed a controlled environment screening method in which differential stomatal activity could be evaluated across a set of genotypes. Subsequent work by Hultquist (1973), Ackerson and Krieg (1977), Ackerson et al (1980), and Garrity et al (1980a) indicated that sorghum stomata lose nearly all sensitivity to lower leaf water potentials after the onset of the reproductive period, regardless of genotype. The stomata remain open even under low water potential. Any potential benefit of more efficient stomatal response would seem to be limited to the vegetative period.

Significant genotypic variation also has been reported for the deposition of epicuticular wax in sorghum (Blum 1978), the maintenance of leaf water potential



**1.** Relationship between evapotranspiration and grain yield for 3 sorghum hybrids. Sandhills Agricultural Laboratory, Nebraska, 1978 (from Garrity et al 1980b).

under stress (Blum 1974), and leaf tissue tolerance for heat and desiccation (Sullivan and Ross 1979).

A threshold amount of genotypic variability would be necessary to make these traits worthwhile breeding objectives, especially since considerable resources would be expended in the screening effort. Whether or not enough variability exists to make the effort worthwhile has not been convincingly established.

## Development of screening methods

A screening technique should be rapid, use only small quantities of plant materials, and be capable of screening large populations (Johnson 1980). Among the techniques now available, few fulfill these criteria. The difficulty of developing acceptable screening techniques is widely perceived as the greatest barrier to the application of the physiological approach.

## Elucidating inheritance and developing a breeding method

Although intraspecific differences in response to a hypothesized drought resistance trait may be found, the heritability of the trait must be demonstrated. There have been few studies and little information on this aspect; none to our knowledge on sorghum.

Roark and Quisenberry (1977) attempted a genetic analysis of the variability in leaf diffusive resistance within across between two diverse lines of upland cotton.

They found the trait associated with both additive and dominance variances, with a 25% narrow-sense heritability. These results imply at least a modest scope for genetic improvement.

The inheritance of heat tolerance in soybean was investigated by Martineau et al (1979) using the membrane thermostability technique (Sullivan and Ross 1979). Estimates of the heritability for heat tolerance in two populations derived from crosses between tolerant and tolerant and between tolerant and intolerant parents were comparable to those for maturity and yield. The estimated 16-18% gains indicated that substantial progress could be made toward developing heat-tolerant genotypes.

## Documentation of drought resistance association

This stage could be the most critical. Unless superior plant performance under drought can be associated convincingly with a trait, there is little basis for selection. Such evidence generally has remained elusive for traits that have been investigated in sorghum.

Several factors are responsible. The importance of a trait in contributing to improved performance is highly dependent on the intensity, duration, and timing of the stress. For example, the heat tolerance of 15 sorghum hybrids, determined by the membrane thermostability test, was strongly correlated with grain yield in a season of extremely high heat stress in Nebraska (Sullivan and Ross 1979). The relationship was not found in other tests under less extreme temperature conditions.

Another difficulty arises in proving the effects of a particular trait on yield when the genotypes involved are nonisogenic for the trait in question. Interpretation of the importance of the trait alone is then open to question.

Attempts have been made to develop isogenic lines to test hypothesized drought-resistance traits. Some interesting work has been done on awned vs awnless and pale vs normal green leaves as means of reducing canopy temperature in barley (Ferguson 1974).

However, isogenic analysis has limitations in addition to the difficulties involved in generating the isolines. The worth of a gene may be obscured by pleiotropic or compensating effects. The light-colored foliage trait in barley, for example, is associated with later maturity, complicating comparisons of light and normal leaf color (Eslick and Hockett 1974).

Physiological research on sorghum drought resistance has emphasized the hypothesis, genetic variation, and screening methods stages. The key to progress would seem to be significant breakthroughs confirming the relationship between particular traits and crop performance under drought stress.

*Analogy between disease resistance and drought resistance.* There have been a number of important successes in breeding for disease resistance in field crops, but progress in drought resistance has been difficult to measure.

Blum (1978) illustrated that yield and drought resistance could be handled as separate genetic entities in a manner similar to the way rust resistance is incorporated into wheat. A cultivar with superior potential yield may be converted into a drought-resistant one by selective incorporation of drought-resistance factors.

Such an analogy neglects important differences between the two breeding efforts.

First, in the case of most disease breeding problems, plant pathologists actually do not know what morphophysiological traits are responsible for the resistance. They screen overt visual symptoms of infection levels. Information on the causes of genetic resistance may accumulate later, but does not constitute the basis of screening. However, in the case of drought resistance, knowledge of the morphophysiological characteristics involved with resistance are the foundation for the development of relevant screening methods.

Relating morphological or physiological traits to yield performance has always proven difficult, both in dealing with drought resistance and in developing crop ideotypes for increasing yield potential under optimum conditions. There seems to be a significant qualitative difference in the process of developing screening methods for disease and drought resistance.

Second, drought resistance traits predominantly are genetically complex. The analogy would be more appropriate for efforts on a polygenic disease-resistance trait. Breeding for disease tolerance (quantitative inheritance) has had very limited success, even though convenient screening methods have been available. There are numerous examples of resistances to plant diseases that can be screened for quite rapidly even where strong phenotypic differences exist. But significant genetic improvement has not been made (J. P. Jones, pers. comm. 1981).

## THE PERFORMANCE APPROACH

The study of morphological and physiological characteristics of grain sorghum tends to confirm that drought resistance is a complex of interacting mechanisms. Until individual mechanisms can be better understood, functionally and genetically, plant improvement programs will have to rely on criteria based on whole plant response rather than on specific plant characteristics. This is the more conventional plant breeding approach.

Methods of direct selection for performance under water stress conditions face their own important drawbacks. There is a strong need for greater genetic diversity in the materials being evaluated, but prospective carriers of drought resistance from exotic sources tend to be overlooked because the desirable characters cannot be recognized. There also is scope for the development and refinement of methods of site selection and control of field environments to enable effective evaluation, analysis, and interpretation of trial results.

### Utilizing genetic diversity: population breeding

Drought resistance probably involves many genes with small effects (Hurd 1971). A broad genetic base is of fundamental importance in obtaining variation for drought-resistance characteristics, although these characteristics cannot be individually recognized. Nevertheless, the introduction and gradual accumulation of useful genes from exotic sources using conventional hybridization techniques can be a very tedious job with the massive amount of intercrossing necessary in a self-pollinated crop. The possibility of exploiting a broad germplasm base now exists for crops in which genetic male sterility has been found.

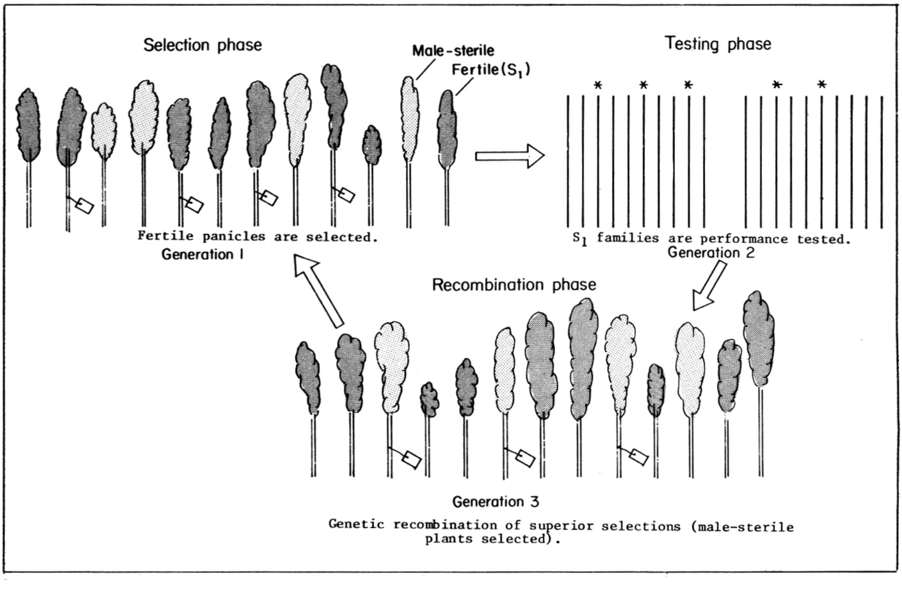
Random-mating populations of grain sorghum were initiated in Nebraska, USA, about 20 years ago (Ross et al 1971). The many improved populations form the basis of the USDA-University of Nebraska sorghum breeding program. Sorghum populations are built by first introducing genetic male sterility into a selected group of lines or varieties. These are intermated. New populations can easily be made by crossing the intermated lines onto male-sterile plants in an existing population.

Random mating is assured by retaining only those panicles which are male sterile in each generation. Plants from a male-sterile panicle are half-sibs, with a common female parent but different male parents from varying pollen sources. Several generations of random mating mixes the gene pool in a fairly thorough fashion. Then, selection begins.

One of the most effective breeding methods applied to random-mating populations has been $S_1$ family selection (Fig. 2). Male-sterile plants are selected from the population. The seed of each selected panicle constitutes an $S_1$ family, the first generation of selfing after random mating. Each $S_1$ family is comparable to the $F_2$ generation of a conventional varietal cross.

The $S_1$ families are compared in yield trials (the testing phase). Seed from the outstanding families is bulked and sown for random mating (the recombination phase). Male-sterile panicles are selected, bulked, and sown. The male-fertile ($S_1$) panicles are then identified in the following generation (the selection phase), which begins the next cycle.

Several other selection and testing methods can be applied to such populations, but the overall objective' is the same: to gradually accumulate and concentrate the



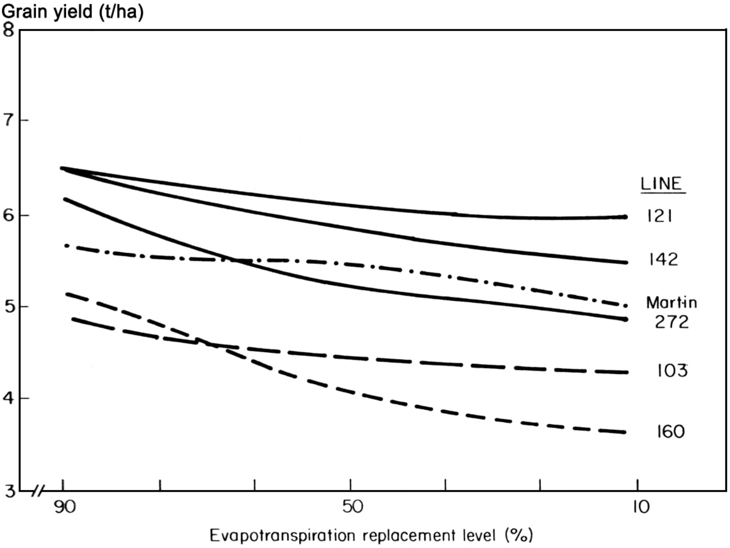
2. The three phases of the $S_1$ family selection method for improving a sorghum random-mating population.

most desirable additive genes for the traits in question. Only those individuals with superior performance are retained. They are randomly mated to make up the population in the next cycle of selection. Because of the massive numbers of crosses that occur each generation, the probability of fortuitous combinations and the breaking of strong linkages increases from that which might occur in a conventional breeding program. With each cycle, it should be possible to obtain superior genotypes in larger numbers with less effort. The ultimate objective is to use the superior lines derived from the selected population to develop outstanding $F_1$ hybrid sorghums.

## Selection and testing

Several years ago, population NP9BR[1] was chosen for studies on selection for drought resistance. NP9BR was derived from KP1BR[2], a broad-based population of 217 component lines of grain and forage sorghums from diverse sources. The antherless type of male sterility was used (Ross 1974).

The population was grown at Tucson in alternate years in cooperation with Dr. R. L. Voigt, University of Arizona, USA. In the Arizona environment of dependably near-zero summer rainfall, NP9BR was subjected to drought stress conditions under limited irrigation. Mass-selected fertile panicles ($S_1$s) were grown in Nebraska the next year for recombination. After three cycles of mass selection were completed, studies of genotypic variation for drought resistance were undertaken.



**3.** Yield response of sorghum $S_1$ families across an irrigation gradient, 1977 (from Watts et al 1980).

---

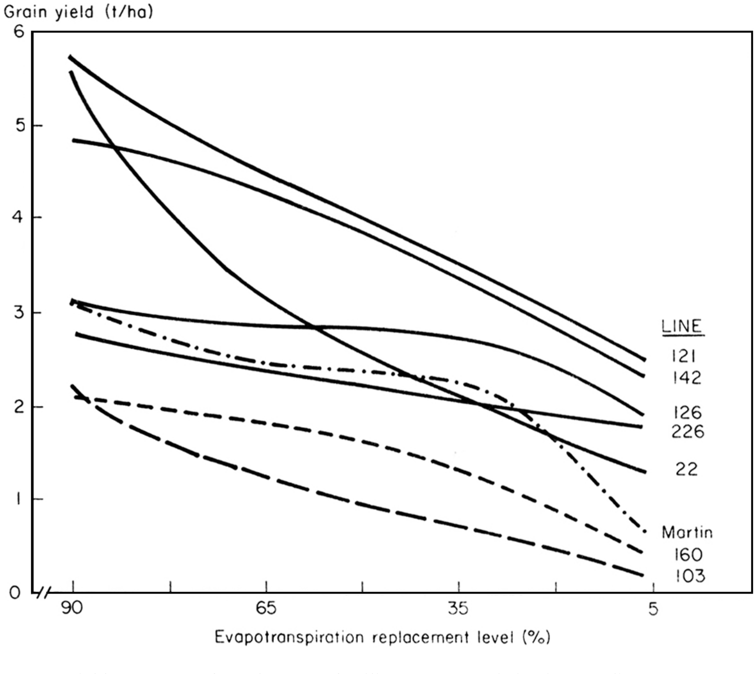
[1] The name designates Nebraska Population 9 composed of both B (sterility maintainer) and R (fertility restorer) lines. [2] Kansas Population I.

The line source sprinkler system was evaluated as a means of field testing early-generation selections from the population (Watts et al 1980). Fifty-five $S_1$ progenies were planted in individual rows perpendicular to the center sprinkler line. Irrigation was applied weekly to replace actual evapotranspiration and to maintain nonstress conditions adjacent to the sprinkler line. The rows were divided into declining levels of evapotranspiration replacement with distance from the sprinkler line. Figure 3 shows the response for 1977 of the highest- and lowest-yielding genotypes in relation to the check variety Martin. Martin was a parent of some important hybrid sorghums in the USA and was once an outstanding inbred line cultivar.

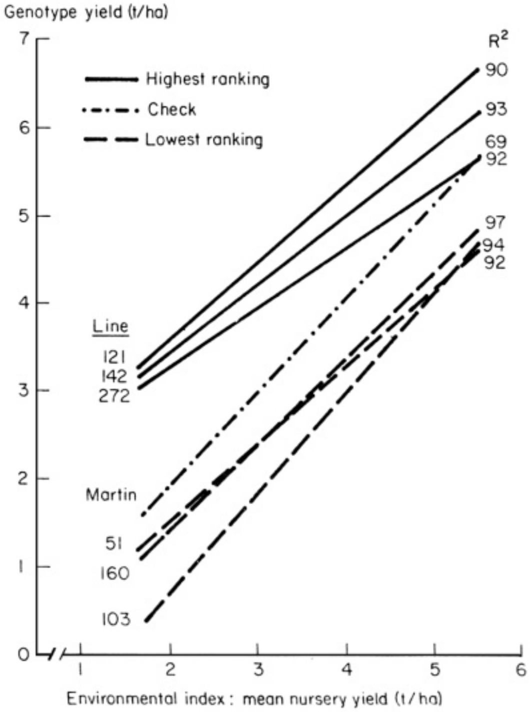
The seasonal evapotranspiration for the nonstress treatment was about 50.5 cm. No stress occurred during the vegetative stage on the dryland side of the gradient, but there were evapotranspiration deficits of about 23% during the reproductive stage and 21% during the grain-filling stage.

From the initial year's results, 20 families ($S_2$s) were selected for testing a second year. The selections were from the best performing lines in terms of yield potential and low yield reduction due to stress. Equal numbers of selections represented intermediate and high yield reduction. The nonstress seasonal evapotranspiration in 1978 was again about 50 cm, with severe evapotranspiration deficits across the gradient in all 3 growth stages: 34% during vegetative; 30% during reproductive; and 52% during grain fill.

The rankings and relative performance of the families were quite consistent over



4. Yield response of sorghum $S_2$ families across an irrigation gradient, 1978 (from Watts et al 1980).



**5.** Stability analysis of sorghum selections from NP9BR population grown on an irrigation gradient, 1977 and 1978.

the two seasons, although the stress timing and intensity differed between years (Fig. 3,4).

The 2-year data produced comparisons among genotypes from 7 environments (3 in 1977, 4 in 1978). Mean yields ranged from 1.6 to 5.5 t/ha.

The regressions ofgenotype yield on mean nursery yield were highly linear (Fig. 5). Families with the highest yield potentials (121, 142, and 272) also were found to have the lowest regression coefficients. Lower yielding families (103, 160, and 51) tended to exhibit the highest regression coefficients and the largest relative yield reductions (Watts et al 1980). There was a negative correlation (-0.45*) between mean yield potential and stability index among the 20 families. This suggests considerable scope for combining stability with good yield potential in this population and in lines derived from it. A recent evaluation of the NP9BR population in a trial involving other populations and hybrids over 16 locations showed that it had a relatively low regression coefficient and performed relatively better under low yielding environments (Table 1).

The line source appears to be quite useful as a tool to evaluate early generation sorghum selections under a set of diverse water stress environments. The amount of land area saved in creating the environments and the precision with which they can be controlled and characterized are distinct advantages of the method. Even so, the amount of seed required may be prohibitive for early generation testing on crops with fewer seeds per inflorescence than sorghum. Hanks et al (1980)

**Table 1. Mean yields and stability parameters for 7 sorghum populations and 4 $F_1$ hybrids tested in 16 U.S. environments in 1979 (from Ross and Nordquist 1980).**

| Genotype | Yield (t/ha) | Regression coefficient | Deviation M.S. |
|---|---|---|---|
| Population | | | |
| NP1BR | 4.6 | 0.89 | 24.63 |
| RP2B | 5.4 | 0.99 | 26.90 |
| NP3R | 4.7 | 0.78 | 20.95 |
| NP9BR | 4.2 | 0.72 | 24.59 |
| NP12B | 4.6 | 0.93 | 39.05 |
| NP18B | 4.7 | 0.84 | 34.16 |
| NP20BR | 5.3 | 0.98 | 10.10 |
| Mean | 4.8 | 0.88 | 25.77 |
| Hybrid | | | |
| RS610 | 6.3 | 1.45 | 25.66 |
| RS671 | 6.8 | 1.26 | 181.44 |
| Commercial 1 | 5.5 | 0.97 | 31.49 |
| Commercial 2 | 6.5 | 1.16 | 34.05 |
| Mean | 6.3 | 1.21 | 68.16 |

discussed the statistical limitations of this method.

Rapidly obtaining performance data for early generation material over a range of environmental conditions is a widely recognized practice in breeding for variable moisture conditions. Multilocational testing is an established method. Additional locations also can be produced by varying the environment at a site, as in the case of the line source system. Interpretation of the data for optimum selection value provides a major challenge.

Genotype-environment interactions have been a problem in understanding and exploiting genetic variability. These interactions have not proved tractable in biometrical analysis until recently. The discovery of a linear regression approach proved to be of great practical as well as theoretical importance. By applying the techniques suggested by Finlay and Wilkenson (1963) and later refined by Eberhart and Russell (1966) and others, genetic expression could be simply and predictably related to the environment under study.

The success of the method depends to a large extent on the condition that a very high proportion of variation in genotypic performance across environments be explained by linear regression. The conditions determining high linearity are difficult to determine and in some cases wide deviations from linearity are found (Brennan and Byth 1979). In these situations, the use of two stability parameters to characterize a genotype has been suggested—deviations from regression in addition to the regression coefficient (Eberhart and Russell 1966).

Fischez and Maurer (1978) recognized that in stability analysis the slope of the regression is highly influenced by the potential yield of a genotype. To utilize the regression coefficient as a stability parameter independent of the differences in yield potential among genotypes, the yields may be expressed on a relative basis. This relative slope is termed the drought susceptibility index. A lower drought susceptibility index was considered synonymous with higher drought resistance.

Several sorghum workers have employed stability analysis to evaluate sorghum germplasm. Kofoid et al (1978) compared the performance of four Nebraska random-mating populations with population crosses and with two $F_1$ hybrids over five environments. Mean yields ranged from 3.0 to 8.7 t/ha. The population crosses showed the greatest stability in both regression coefficient and deviations from regression, while the hybrids were the least stable.

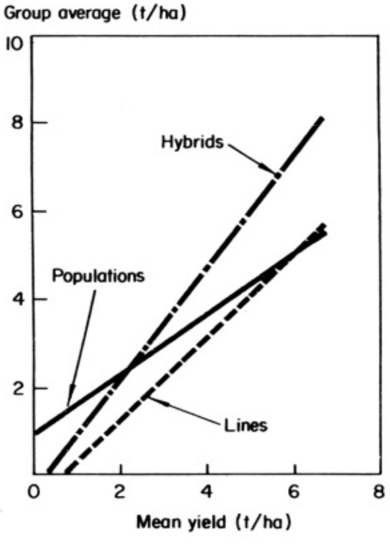
Ross and Nordquist's (1980) comparison of populations vs hybrids over 16 environments also indicated greater stability among the populations than among the hybrids. As expected, mean yield levels of the populations were lower than those of the hybrids.

Francis et al (1979) used the line source at 6 stations in Nebraska and Kansas to create 27 different testing environments. Their results showed that the hybrids had much greater yield potential in the most favorable environments but had high regression coefficients (Fig. 6). The populations were more stable and were superior under less favorable conditions (yield levels less than 2.5 t/ha).

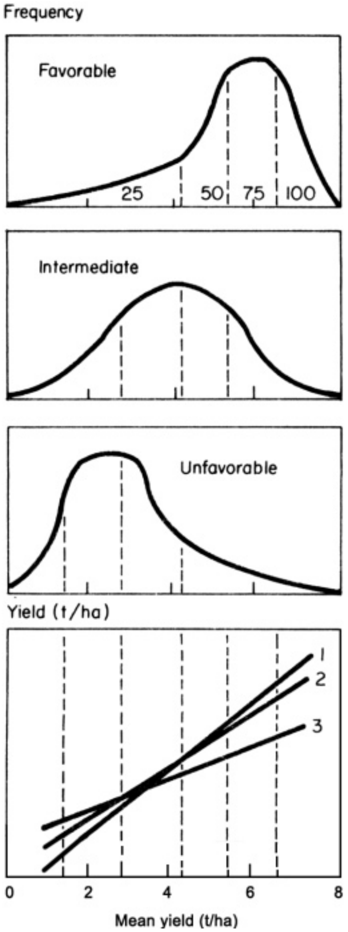
These results imply that genetic diversity makes a significant contribution to yield stability under drought. A single genotype may have individual buffering, enabling it to perform well over a wide range of environmental conditions (Allard and Bradshaw 1964). However, a genetically diverse population may have an additional property—the presence of a sufficient number of adapted genotypes to satisfy a wide range of environments. The potential utility of population buffering under environments of extreme variability needs more attention (Neeley et al 1976).

## Application of environmental characterization

Stability analysis can make genotypic comparisons across environments more simple and interpretable than was possible previously. However, there are no clear



**6.** Stability analysis of sorghum hybrids, populations, and lines grown on an irrigation gradient at 6 research stations in Nebraska and Kansas, 1978.



**7.** Interpretation of stability analysis based on the frequency distribution on mean yields in a region.

and generalizable rules for selecting the optimum genotypes from the analysis alone. A major reason for this is that, although the environmental index represents a range of environments, it contains no information on the relative frequency with which those environments occur.

One approach to environmental characterization that could be useful in interpreting stability analyses might be to construct the frequency distribution of mean yields over seasons or locations within an agricultural region. Variety trial data or even yearly farm production data for the region could be used. Genotypic performance could then be weighted in accordance with the frequency of occurrence of mean yields across the range of the environmental index represented in the stability analysis.

Figure 7 illustrates how the frequency of environments influences the choice of optimum genotype. In the region of relatively favorable environments, yields are above 5 t/ha more than 50% of the time. Genotype 1, which tends to excel in high yield situations, would be the obvious choice. It does poorly under severe stress; however, severe-stress environments are quite rare.

For the region of intermediate yields, genotypes 1 and 2, with nearly identical mean yields, will have similar long-term results. Genotype 2 would appear preferable for smaller-scale and subsistence-level farmers because of its relatively better performance in low-yielding environments.

In the region of relatively unfavorable environments with under 3 t/ha yields over 50% of the time, genotype 3, with low yield potential but stable yields under stress, would tend to be superior for risk-averse cultivators. Genotype 2 would still have the highest long-term mean yields.

The extent to which stability analysis will deliver significantly more information than mean yields alone will depend on the nature of the frequency distribution of yields for a given production region.

## EVALUATING PROGRESS

Progress toward a goal may be measured quite differently by different people. The physiologist tends to measure progress by his level of understanding of a phenomenon; the breeder, by his level of yield. It might be argued that an evaluation of progress in attacking drought resistance by the physiological approach should be confined to aspects of how far and how fast we have come toward understanding the traits involved and their potential manipulation, leaving the performance approach to be judged by improvement in yield or yield stability.

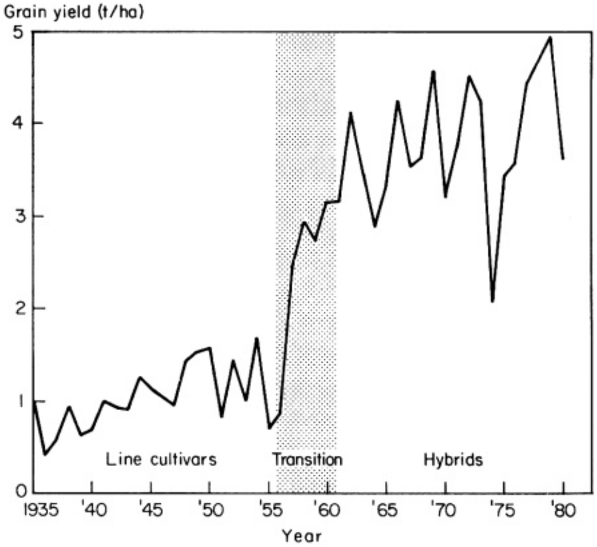
Knowledge about the water relations of the sorghum plant has grown enormously over the past 20 years. However, the capacity to pinpoint the one or two drought-resistance mechanisms most critical to improved crop performance in a given environment and to manipulate these traits genetically to our advantage has not been developed yet.

A number of difficult problems must be solved in the application of the physiological approach. Each of the five suggested stages seems critical to success. The development of screening methods and the search for genetic variability have received considerable emphasis for a number of traits. The greatest obstacle appears to be obtaining convincing evidence linking high levels of a trait to improved crop performance under drought. This is a challenging task.

Another stage for which we find relatively scant information is that of examining the inheritance of particular traits.

Measuring the progress of the performance approach by detecting yield increases under drought stress also has been elusive. The yield increases can result from other factors, including improved pest and disease resistance. However, where such effects are minimal, differences in yields between genotypes in an environment where water stress is the major yield-limiting factor may reasonably be assumed to be due to the expression of traits that are determinants of the ability to produce under water stress.

The greatest progress in the improvement of grain sorghum yields in water-limiting environments came about with the introduction of $F_1$ hybrids. In the



**8.** Historical trend in the mean yield of grain sorghum for the state of Nebraska, USA, 1935-80.

United States, hybrids were first grown on a large scale in 1956. Within a few years, they were adopted on virtually the total hectarage, resulting in a dramatic jump in average yield levels. Figure 8 shows the near doubling of Nebraska State average yields which occurred during this remarkable transition.

Yield levels tended to be substantially raised across the entire range of environments when hybrids were compared to superior inbred line cultivars, including environments of severe drought stress (Fig. 6). The higher drought-stress productivity of the hybrids does not appear to be related to drought adaptation mechanisms *per se.* Rather, it is due to greater physiological efficiency, resulting in higher biomass production and a higher harvest index (Quinby 1974). The greater efficiency is most dramatic under optimum conditions, but is expressed to advantage under stress as well. On this basis, real and significant gains have been made in sorghum improvement for water-limited conditions.

The subsequent development of new sorghum hybrids with further improvement in drought stress productivity has been more difficult. Progress has slowed. One recognized factor is the narrow genetic base of adapted material to which USA sorghum workers have confined their efforts. Population breeding has evolved as a means for making efficient use of a broad germplasm base. Random-mating populations tend to be more yield stable across environments and to outperform hybrids under more severe stress situations. This would suggest that retaining some genetic diversity in released cultivars may be of value for these environments.

The basic purpose of population breeding is to evolve inbred lines which will produce superior hybrid combinations. At present, it is too early to assess this method's effectiveness in creating hybrids of outstanding drought stress productivity. The rate of progress will depend on the relevant genetic variability of the base population and the efficiency of the procedure used.

## REFERENCES CITED

Ackerson, R. D., and D. R. Krieg. 1977. Stomatal and nonstomatal regulation of water use by cotton, corn, and sorghum. Plant Physiol. 60:850-63.

Ackerson, R. C., D. R. Krieg, and F. J. M. Sung. 1980. Leaf conductance and osmoregulation of field-grown sorghum genotypes. Crop Sci. 20:10-14.

Allard, R. W., and A. O. Bradshaw. 1964. Implications of genotype-environment interaction. Crop Sci. 4:503-508.

Bidinger, F. 1980. Breeding for drought resistance. Pages 452-454 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. New York, Wiley and Sons.

Blum, A. 1974. Genotypic responses in sorghum to drought stress. I. Response to soil moisture stress. Crop Sci. 14:361-364.

Blum, A. 1975. Effect of the *bm* gene onepicuticular wax deposition and the spectral characteristics of sorghum leaves. SABRAO J. 7:45-52.

Blum, A. 1978. Genetic improvement of drought resistance in crop plants. A case for sorghum. Pages 429-446 *in* H. W. Mussell and R. C. Staples, eds. Stress physiology in crop plants. New York: Wiley.

Brennan, P. S., and D. E. Byth. 1979. Genotype x environment interactions for wheat yields and selection for widely adapted wheat genotypes. Aust. J. Agric. Res. 30:221-232.

Eberhart, S. A., and W. A. Russell. 1966. Stability parameters for comparing varieties. Crop Sci. 6:36-40.

Eslick, R. F., and E. A. Hockett. 1974. Genetic engineering as a key to water-use efficiency. Agric. Meteorol. 14:13-24.

Ferguson, H. 1974. Use of variety isogenes in plant water-use efficiency studies. Agric. Meteorol. 14:25-30.

Finlay, K. VU., and G. N. Wilkenson. 1963. The analysis ofadaptation in a plant-breeding program. Aust. J. Agric. Res. 14:742-754.

Fischer, R. A., and R. Maurer. 1978. Drought stress resistance inspringwheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:897-912.

Francis, C. A., J. F. Rajewski, C. Jimenez, and R. V. Mathews. 1979. Grain sorghum adaptation and yield stability in the Great Plains. Agron. Abstracts. p. 101.

Garrity, D. P., C. Y. Sullivan, and D. G. Watts. 1980a. Changes in grain sorghum stomatal response and photosynthesis under moisture stress over a growing season. (submitted to Crop Science)

Garrity, D. P., D. G. Watts, and C. Y. Sullivan. 1980b. Moisture deficit and grain sorghum performance. II. Crop evapotranspiration relationships. (submitted to Agronomy Journal)

Hanks, R. J., D. V. Sesson, R. L. Hurst, and K. G. Hubbard. 1980. Statistical analysis of results from irrigation experiments using the line source sprinkler system. Soil Sci. Soc. Am. J. 44:886-888.

Henzell, R. G., K. J. McCree, C. H. M. van Bavel, and K. F. Scherrz. 1975. Method for screening sorghum genotypes for stomatal sensitivity to water deficits. Crop Sci. 15:516-18.

Henzell, R. G., K. J. McCree, C. H. M. van Bavel, and K. F. Schertz. 1976. Sorghum genotype variation in stomatal sensitivity to leaf water deficits. Crop Sci. 16:660-62.

House, L. B. 1981. A guide to sorghum breeding. ICRISAT, Hyderabad, India. 238 p.

Huitquist, J. H. 1973. Physiologic and morphologic investigations of grain sorghum (*Sorghum bicolor* L. Moench). Ph D dissertation, Univ. of Nebraska, Lincoln, Nebraska, USA.

Hurd, E. A. 1971. Can we breed for drought resistance. Pages 77-88 *in* Drought injury and resistance in crops. Crop Science Society of America, Madison, Wisconsin.

Johnson, D. A. 1980. Improvement of perennial herbaceous plants for drought-stressed western rangelands. *In* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley, New York.

Jones, H. G. 1979. Stomatal behavior and breeding for drought resistance. Pages 407-428 *in* H. W. Mussell and R. C. Staples, eds. Stress physiology in crop plants, Wiley, New York.

Jordan, W. R., E. R. Miller, and D. E. Morris. 1979. Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci. 19:468-472.

Jordan, W. R., and F. R. Miller. 1980. Genetic variability in sorghum root systems - Implications for drought tolerance. *In* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley, New York.

Kofoid, K. O., W. M. Ross, and R. F. Mumm. 1978. Yield stability of sorghum random-mating populations. Crop Sci. 18:677-679.

Martineau, J. R., J. H. Williams, and J. C. Specht. 1979. Temperature tolerance in soybeans. II. Evaluation of segregating populations for membrane thermostability. Crop Sci. 19:79-81.

Neeley, D., W. McProud, and J. Yohe. 1976. Diversity by breeding: genetic variability on the farmer's field. Paper presented at conference on Risk and Uncertainty in Agricultural Development, CIMMYT, Mexico.

Quinby, J. Roy. 1974. Sorghum improvement and the genetics of growth. Texas A and M University Press: College Station.

Roark, B., and J. E. Quisenberry. 1977. Environmental and genetic components of stomatal behavior in two genotypes of upland cotton. Plant Physiol. 59:354-56.

Ross, W. M., C. O. Gardner, and P. T. Nordquist. 1971. Population breeding in sorghum. Pages 93-98 in Grain Sorghum Research and Utilization Conference, Lubbock, Texas.

Ross, W. M. 1974. Use of population breeding in sorghum — problems and progress. Pages 30-43 *in* Proc. 28th Annual Corn and Sorghum Research Conference, American Seed Trade Ass'n, Chicago.

Ross, W. M., and P. T. Nordquist. 1980. Yield and yield stability of seven sorghum random-mating populations. Sorghum Newsletter 23. (forthcoming)

Sullivan, C. Y. 1971. Techniques for measuring plant drought stress. Pages 1-18 *in* Drought injury and resistance *in* crops. Crop Sci. Soc. of Amer., Spec. Publ. 2, Madison, Wisconsin.

Sullivan, C. Y., and W. M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. Pages 263-282 *in* H. W. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley, New York.

Watts, D. G., J. R. Gilley, and C. Y. Sullivan. 1980. Management of irrigation agriculture with a limited water supply. Final Project Report, Agricultural Engineering Dep., University of Nebraska, Lincoln. 168 p.

# IMPROVEMENT OF DROUGHT RESISTANCE IN PEARL MILLET

F. R. BIDINGER, V. MAHALAKSHMI, B. S. TALUKDAR, AND G. ALAGARSWAMY

Pearl millet is grown almost exclusively in arid and semiarid tropical areas characterized by high growing season temperatures, low and frequently erratic rainfall, and shallow or sandy soils. Inadequate moisture is the major limitation to production in most of the areas. The crop appears to adapt to these conditions by a combination of short-duration important developmental periods and considerable development plasticity to maximize its use of short periods of favorable moisture. Little is known of its possible physiological adaptations to stress, although the limited information available suggests a significant heat tolerance.

Efforts to improve performance under drought stress have centered on the development of field and analysis techniques to assess drought resistance as a factor independent of or complementary to yield potential and drought escape in determining cultivar performance under stress. Direct selection for yield ability in a controlled, off-season stress nursery is being evaluated as a breeding tactic for improvement of pearl millet's adaptation to stress. Progress in combining adaptation to at least certain types of stresses and better yield potential is the goal.

Pearl millet *Pennisetum americanum* (L.) Leeke and rice stand at opposite ends of the spectrum of major tropical cereals. Almost entirely a rainfed crop, pearl millet is grown in sandy and often shallow soils in areas of 200-800 mm of rainfall/year. It is entirely a subsistence crop, generally grown without fertilizer or chemical protection. Relatively little research has been done on pearl millet and many farmers grow traditional land race cultivars.

Like rice, pearl millet is the main source of calories and protein for the people

---

Pearl Millet Improvement Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, P.O. 502 324, India.

who depend on it. Most are in arid and semiarid areas where no other major cereal is as well adapted. The ever-present risk of drought in these areas makes yielding ability under drought conditions a major objective for millet improvement programs. Progress in realizing this objective is limited by the general lack of methods to improve drought resistance in crop plants and by the specific lack of knowledge of responses to drought of the millet crop itself.

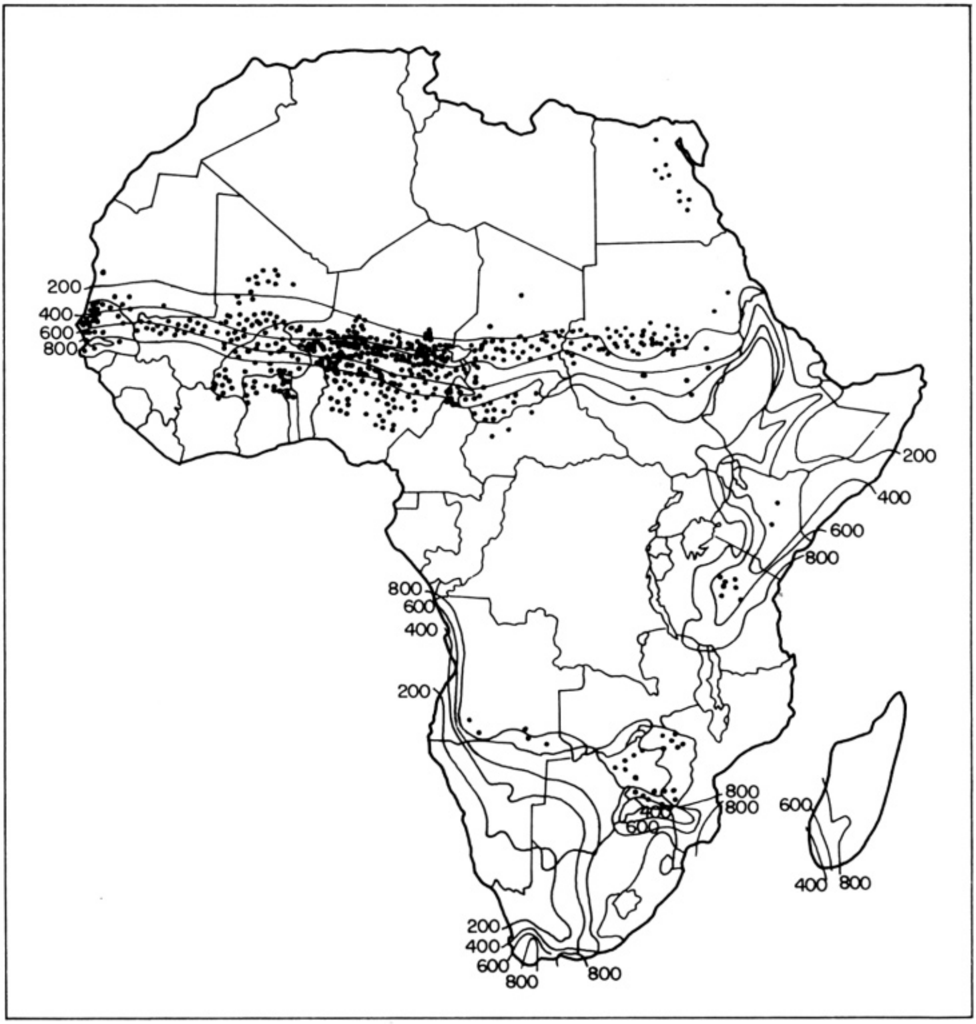
## ECOLOGICAL DESCRIPTION OF MILLET GROWING AREAS

More than 95% of the world's millet crop is grown in Africa and South Asia, principally in the Sahelian-Sudanian zones of West Africa and in the semiarid regions east and southeast of the Thar desert in India. The areas of adaptation of the species are clearly defined by the mean annual rainfall isohyets of 200-600 mm in both continents (Fig. 1, 2). These zones are generally characterized by short rainy seasons (2-4 mo), high mean temperatures, high potential evapotranspiration rates, and shallow, sandy soils (Cocheme and Franquin 1967, Kowal and Kassam 1978).

Inter- and intraseasonal variability in available soil moisture is the major hazard to pearl millet production. Rainfall is erratic as well as low and the water-holding capacity of soils is typically low to moderate, limiting the possibilities of buffering rainfall fluctuations with stored soil moisture. To illustrate these conditions, two locations in important millet-growing areas were chosen: Jodhpur in Rajasthan state, northwestern India, and Bambey in Senegal, West Africa. Bambey has a slightly longer rainy season (defined by Virmani et al 1978 as the period during which the ratio of rainfall to potential evapotranspiration exceeds 0.33) and a greater mean weekly total than Jodhpur (Table 1). Average weekly rainfall during the rainy season exceeds potential evapotranspiration at Bambey and the probability of receiving at least 20 mm/week (about 2/3 of the average weekly potential evapotranspiration) is high (Fig. 3). At Jodhpur, mean weekly rainfall is less than the mean potential evapotranspiration and the probability of receiving at least 20 mm of rainfall/week during the rainy season does not exceed 50%.

To illustrate annual rainfall variation, data for 3 individual years were used to calculate the ratio of actual evapotranspiration to open pan evaporation (ET:$E_0$). Data were calculated on a weekly basis for a millet crop growing in the two locations using a standard soil water balance model (Reddy, unpubl.) and appropriate climate and soils input data (Table 1). Sowing and flowering dates are those of the local cultivar from the International Pearl Millet Adaptation Trials for those years and locations.

Rainfall and the ET:$E_0$ were good for the first several weeks of the season at Jodhpur in all 3 years (Fig. 4). (ET-$E_0$ ratios depend mainly on soil evaporation in the early stages; a low ratio at early stages is not indicative of crop stress.) Dry periods occurred at weeks 6 and 7 in 1977 and weeks 4 and 5 and weeks 9-11 in 1978 (ET-$E_0$ ratios below 0.7 are indicators of probable crop stress by 30-40 days after emergence). Although total rainfall was above normal, 1979 was particularly dry. Most of the total seasonal rainfall occurred in 2 weeks in the early part of the season. Soil moisture and predicted ET:$E_0$ values during flowering and grain

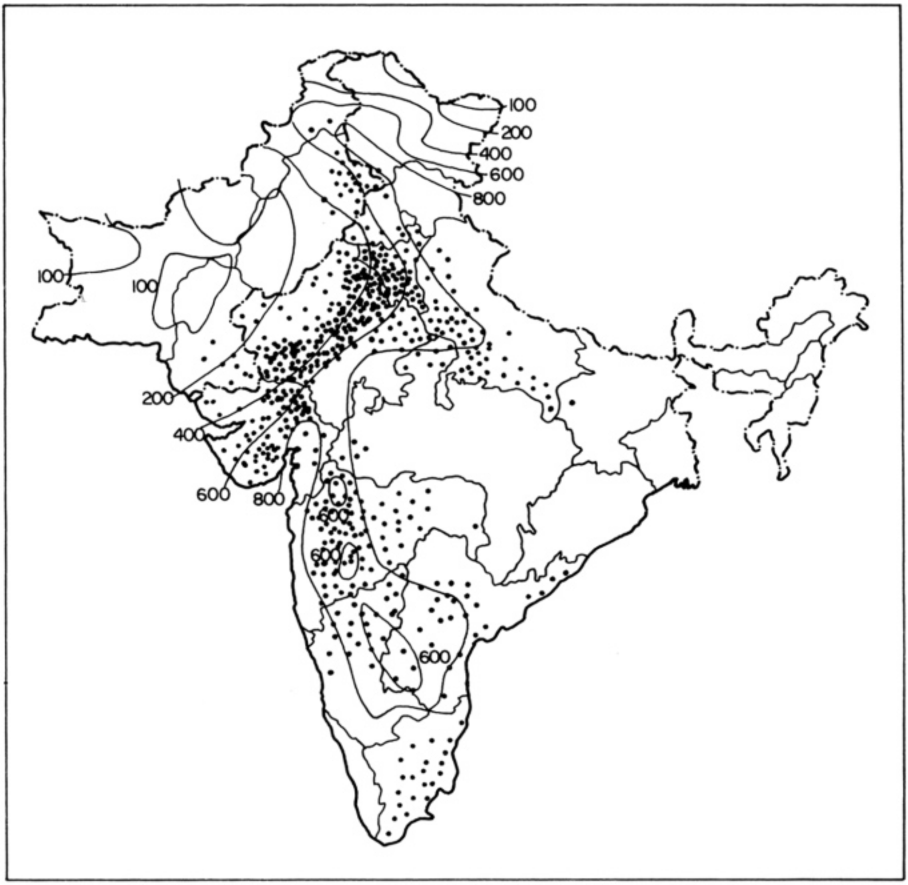


**1.** African area planted to pearl millet in 1978 in relation to the mean annual rainfall isohyets. One dot equals 20,000 ha.

filling were very low.

There was a dry period in the middle of the 1977 season at Bambey. There was little rain in weeks 2-5, but rainfall and ET:$E_0$ ratios were good during flowering and grain filling (Fig. 5). Rainfall in 1978 was well distributed throughout the season. In 1979, as in 1977, there were good sowing rains, followed by a dry period of several weeks after sowing. Rainfall thereafter was regular, but amounts in some weeks were small and several short dry periods occurred during the remainder of the season.

To the degree that these years are typical, it is clear that drought stress is a regular and frequently severe hazard to millet production.



**2.** South Asian area planted to pearl millet in 1978 in relation to the mean annual rainfall isohyets. One dot = 20,000 ha.

## ADAPTATION TO MOISTURE STRESS

The concentration of pearl millet in rainfall zones of less than 600 mm/year testifies to the relative adaptation of the crop both to low average rainfall and to high annual variability in rainfall. Rachie and Majmudar (1980) suggested that this adaptation might be due more to a combination of short duration and heat tolerance than to specific (physiological) drought resistance mechanisms. There is evidence that several developmental and morphological features of pearl millet are important in its ability to produce a grain yield in a variable moisture situation. But too little is known of the possible physiological adaptation mechanisms to drought to evaluate their importance.

### Developmental plasticity: adaptation to a variable moisture environment

An important component of the adaptation of millet to its environment is the

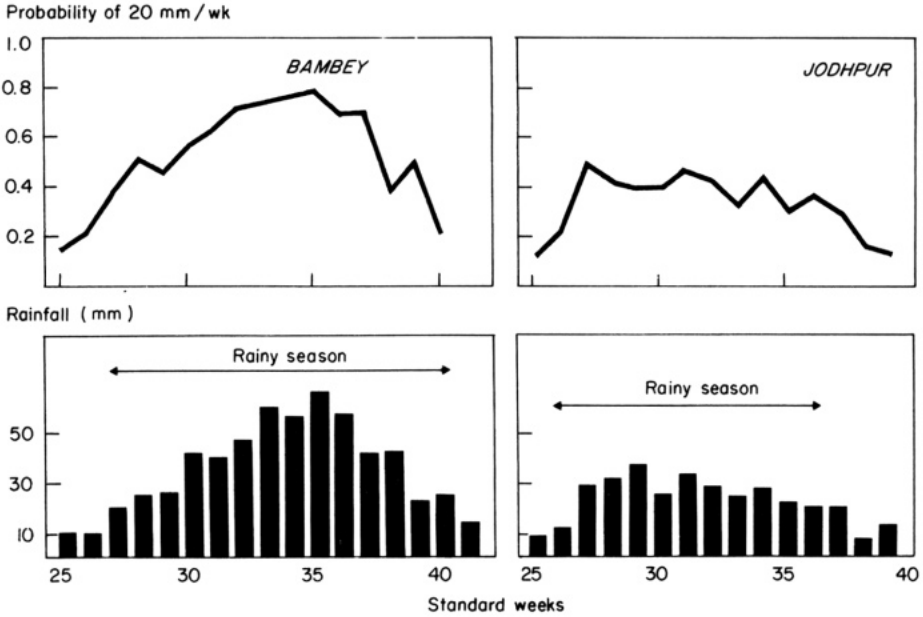
**Table 1. Rainfall and soil data for Barnbey, Senegal, and for Jodhpur, India.**

| | Bambey[a] | Jodhpur[b] |
|---|---|---|
| Latitude | 14° 42' N | 26° 18' N |
| Annual rainfall (mm) | 650 | 383 |
| CV of mean rainfall (%) | 25 | 57 |
| Rainy season[c] | | |
| Duration (wk) | 14 | 11 |
| Total rainfall (mm) | 582 | 297 |
| Mean weekly rainfall (mm) | 42 | 27 |
| Mean weekly PET (mm) | 31 | 39 |
| Soil data | | |
| Coarse sand (%) | 20–25 | 19–20 |
| Fine sand (%) | 65–75 | 66–71 |
| Silt (%) | 0–3 | 3–5 |
| Clay (%) | 2–5 | 6–9 |
| Field capacity (%) | 6–10 | 7–10 |
| Wilting point (%) | 1.5-4 | 2–5 |
| Depth[d] (cm) | 150 | 60–90 |
| Available soil water[e] (mm) | 90 | 60 |

[a] ICRISAT Agroclimatology Program (unpubl.) and Dancette (1970).
[b] Virmani et al 1978, ICRISAT Agroclimatology Program (unpubl.), All India Coordinated Research Project for Dryland Agriculture (unpubl.).
[c] Defined as the period during which the ratio of rainfall to potential evapotranspiration (PET) > 0.33.
[d] Soil depth at Bambey exceeds200 cm; 150 cm is estimate of actual wetted soil profile. Soil depth at Jodhpur is actual depth.
[e] Estimates used in calculating soil water balances in Figure 3, 4.

combination of short reproductive and grain-filling periods with a variable length of vegetative phase which generally determines the total season length. Short-duration cultivars (70-75 days to maturity) require about 20 days from emergence to floral initiation, 25 days from initiation to flowering, and 25 days for grain filling (G. Alagarswamy unpubl.). Variation in development of longer-duration cultivars is generally in the vegetative period because floral initiation is controlled by photoperiod (Kowal and Kassam 1978, Norman and Begg 1968). This has allowed an evolutionary adjustment of time of flowering to local moisture patterns (even where planting dates vary because the arrival of sowing rains varies), while keeping the duration of the important reproductive and grain filling periods short. Because drought stress during the vegetative period damages yields less than drought in later stages (Lahiri and Kharabanda 1965, Lahiri and Kumar 1966), an extension of this period results in only a marginal increase in the risk of drought injury relative to an extension of the reproductive or grain filling periods.

Many millet cultivars also interrupt development when exposed to severe stress during the late vegetative or early reproductive stages, resuming development only when moisture is again available. Flowering under these conditions may be noticeably delayed (Fig. 6), providing an escape mechanism from stress if conditions after the stress period favor continued crop growth. This has been a useful



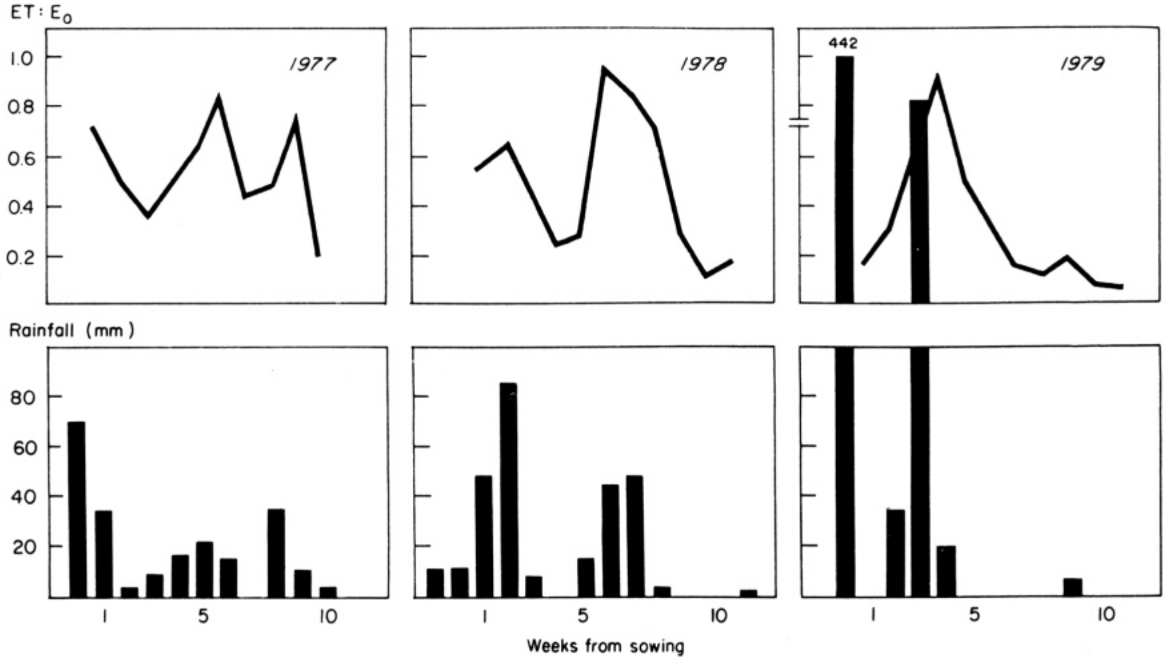
**3.** Mean weekly rainfall and the probability of receiving 20 mm/week for Bambey, Senegal and Jodhpur, India. Standard week 25 begins 18 June; see text for definition of the rainy season.

mechanism in drought screening trials at ICRISAT, in which a stress period is applied from approximately panicle initiation to flowering, after which sufficient irrigation is provided to complete development. Lines with this ability to suspend development often perform well in these conditions.

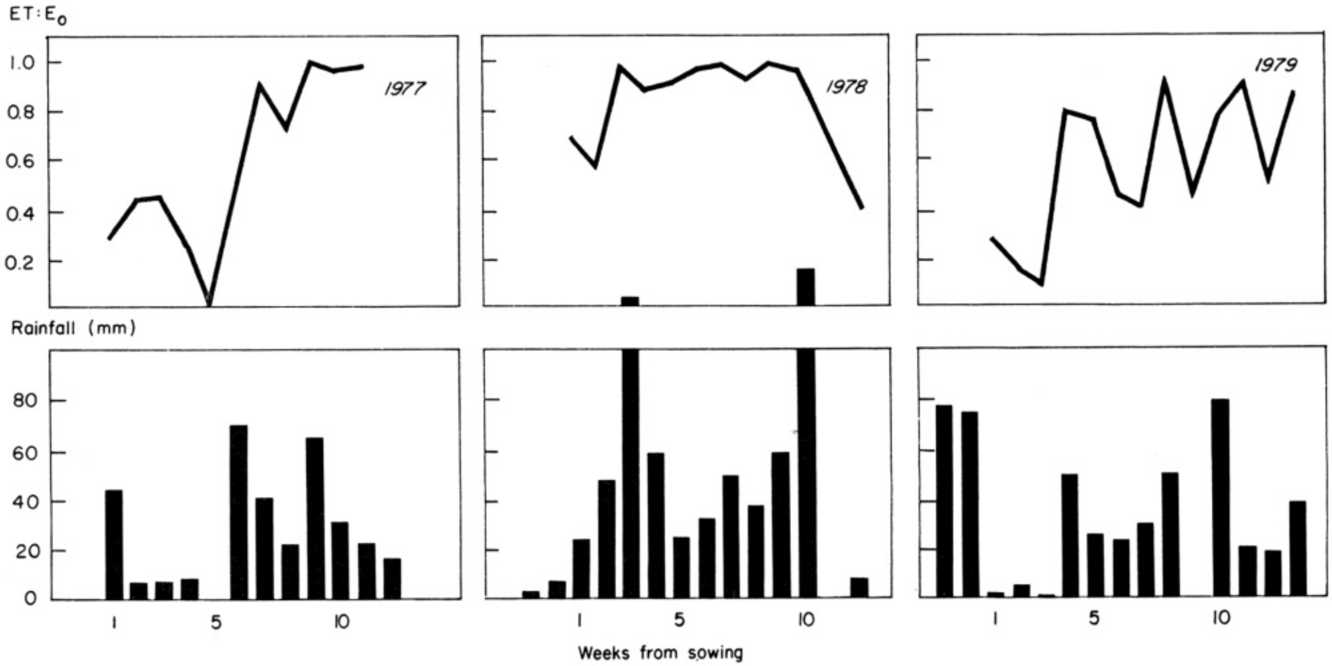
Pearl millet also has the ability to respond to moisture after a stress period during the reproductive or early grain filling periods. This ability shows in stimulation of secondary tillers that would not have developed or would not have completed development under normal conditions. Most land race cultivars (and many improved ones) have an asynchronous tillering habit (Raymond 1968) that maintains a potential for regrowth if drought affects the main stem and primary tillers. In some cases, final head numbers, crop growth, and grain yield may not differ from those of a nonstressed comparison crop, provided sufficient moisture is available after the stress period to complete development of the secondary basal tillers (Fig. 7, G. Alagarswamy, unpubl.).

Under intermittent drought conditions, certain land race materials will produce several flushes of heads from small tillers formed in the upper nodes of the primary tillers as well as from secondary basal tillers. These nodal tillers form only 2–3 leaves and a small head, but do so in a very short period of time, 10–20 days to flowering (Nanda and Chinoy 1958). The presence and productivity of the nodal tillers has strong negative relationship to grain set and grain growth in the head of the parent shoot. When these are poor (for example, when the parent shoot flowers during a period of severe stress), the nodal tillers may compensate to a significant degree.

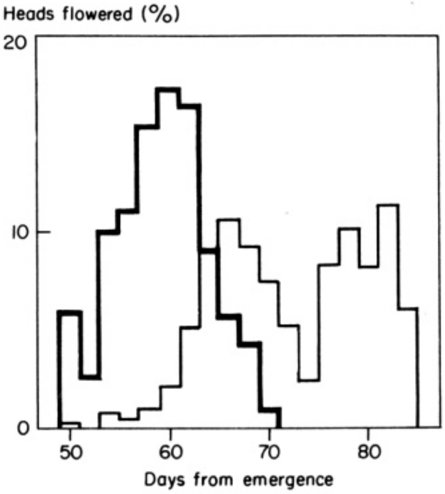
In addition to the developmental plasticity to utilize short or intermittent



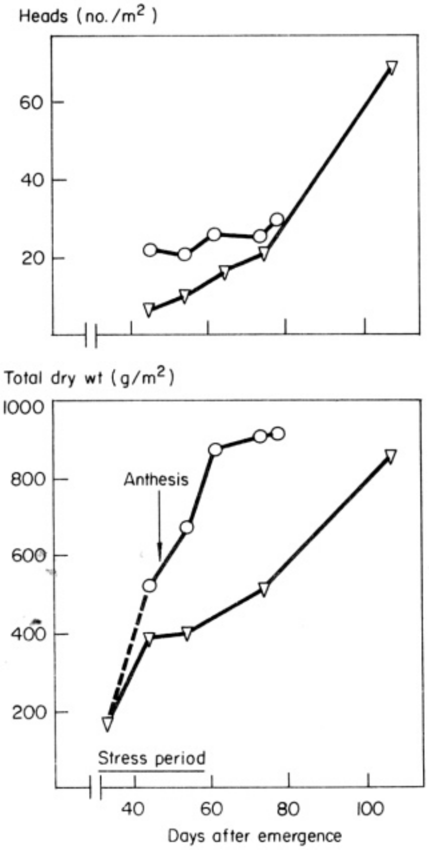
**4.** Weekly rainfall and predicted weekly ratios of actual evapotranspiration to pan evaporation ($ET{:}E_0$) during the 1977 to 1979 cropping seasons for Jodhpur, India.



**5.** Weekly rainfall and predicted weekly ratios of actual evapotranspiration to pan evaporation (*ET:E$_o$*) during the 1977 to 1979 cropping seasons for Bambey, Senegal.



**6.** Frequency distribution of days to flowering (individual heads) of cultivar BD763 in irrigated-control (bold line) and midseason stress (fine line) treatments. The stress treatment was terminated on the 45th day from emergence. n = 298 for the control and 359 for stress treatments.



**7.** Total dry weight and head numbers per unit area for cultivar ICH 118 under irrigation (O) and midseason-drought stress (O) treatments. The stress period was imposed from about 30 to 62 days after emergence.

periods of favorable moisture, pearl millet also has a capacity for high rates of crop growth and for efficient conversion of intercepted radiation to dry matter (Begg 1965). This presumably permits the crop to maximize growth during favorable periods.

## Physiological adaptive features: adaptation to drought and heat stress

*Control of water loss and internal water status.* From the limited information available, pearl millet appears to have several mechanisms for the control of internal water status. Stomatal conductance has been shown to be sensitive both to rates of canopy transpiration and to differences in vapor pressure between the leaf and the atmosphere under adequate soil moisture levels (Squire 1979, Black and Squire 1979). Over a range of saturation deficits from 1.3 to 2.6 kPa (at a constant irradiance), Black and Squire (1979) measured a twofold to threefold variation in stomatal conductance.

There is also evidence of variation in internal resistance to water transport in the crop where soil moisture levels are adequate, since bulk leaf water potentials were found to vary only slightly (3 bars) over a threefold range of estimated leaf transpiration rates (ICRISAT 1980).

Both of these mechanisms have value for adaptation to atmospheric stress conditions (high radiation, high temperature, and low humidity) rather than for edaphic stress conditions. Presumably the mechanisms permit maximization of carbon dioxide uptake consistent with the maintenance of a nonstress internal water status in such conditions.

Under conditions of inadequate soil water availability, the response to low saturation deficits was not observed (Squire 1979). Leaf water potentials were found to be linearly dependent on transpiration rates (ICRISAT 1980). Stomatal conductance was either dependent on radiation (Squire 1979) or, in a more severe stress case, on threshold leaf water potential (ICRISAT 1980). Under such conditions, millet appears to behave similarly to other cereal crops and its advantage, if any, is in its greater heat tolerance when transpirational cooling is lost with stomatal closure.

Little is known about the contribution of other possible mechanisms to drought resistance in pearl millet. Measurement of osmotic potentials under stress conditions do not suggest that osmotic adjustment is important in the crop (Henson, Mahalakshmi, Bidinger, and Alagarswamy, unpubl.). Studies on abscisic acid accumulation under stress have indicated considerable genetic variation in this response, but its relationship to drought resistance is yet to be determined (Austin et al, this vol). Work in Australia has indicated the capacity for deep rooting in forage cultivars (Begg et al 1964, Wetselaar and Norman 1960). However, depth of root penetration may be influenced by extended vegetative periods and high rates of dry matter production in forage types. Studies on shorter duration grain types have suggested relatively shallow rooting (Gregory, this vol).

*High temperature adaptation.* Again from limited evidence, pearl millet appears to have both a relatively high temperature optimum and a significant tolerance for heat stress beyond the optimum. Temperature optimum (leaf temperature) for photosynthesis of intact leaves was reported to be 35-40° C with rates greater than

75% of maximum at temperatures as high as 45°C (McPhearson and Slatyer 1973). For oxygen evolution of isolated chloroplast, rates at 43°C were similar to those at 25°C (Sullivan et al 1977). This range exceeds that which would be experienced by normally transpiring leaves (which would be below air temperatures) and extends well into the range of temperatures experienced by leaves with loss of transpirational cooling.

More appropriate to these conditions are direct measurements of the heat tolerance indicated by electrolyte leakage from the cells of heat-treated leaf discs (Sullivan et al 1977). The pearl millet cultivars tested had a relatively low degree of injury (< 20% after treatment at 48° C for 1 hour) compared to sorghum (30-38% injury under the same conditions). In contrast, estimates of drought tolerance using a similar technique (a period of desiccation of the leaf discs rather than heat treatment) suggested that pearl millet was less tolerant than sorghum of the direct effect of drought stress on a cellular level (Sullivan 1972).

Present knowledge suggests that pearl millet is adapted to its environment largely by means of an opportunistic strategy:

1. Short duration of basic developmental stages plus the capacity for high growth rates under favorable conditions allows the crop to maximize periods of favorable moisture.
2. Considerable plasticity in development and the possibility for rapid regrowth following the end of a stress period allow the crop to adjust to intermittent periods of favorable and unfavorable conditions.
3. Adaptation to atmospheric stress through effective control of water loss, through resistance to water movement, and through a high temperature optimum for photosynthesis results in a very efficient use of a high temperature, high radiation, low humidity environment, provided that sufficient soil water is present.
4. Survival of periods of combined edaphic and atmospheric stress by the suspension of development and by tolerance for heat stress when transpirational cooling is lost.

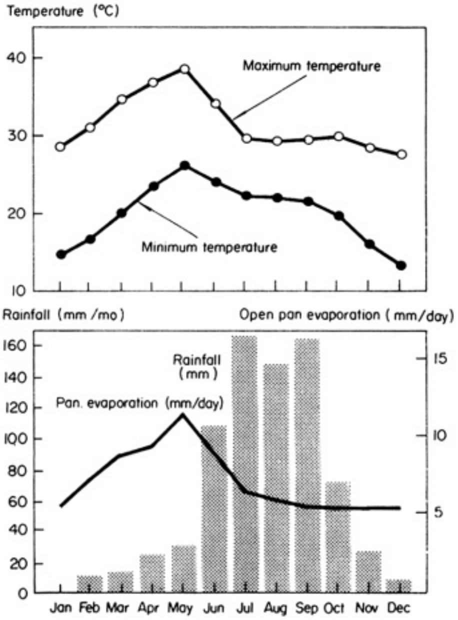
## IMPROVEMENT OF DROUGHT RESISTANCE

The ICRISAT program is the basis for this discussion as it is the only one of which we are aware that has published reports of research specifically on the improvement of drought resistance in pearl millet. Drought stress occurs naturally in most millet breeding programs. Thus, segregating materials are routinely selected and advanced materials evaluated in such conditions. But performance under drought conditions, rather than drought resistance itself, is the selection criterion.

### Factors affecting performance under drought stress

Measured grain yields (the simplest definition of performance) in a given stress condition are influenced by three factors: 1) the basic yield potential of the cultivar, 2) the developmental pattern of the cultivar (which may allow it to partially or totally escape the effects of that stress), and 3) the drought resistance or susceptibility of the cultivar.

We illustrate this with data from three years of replicated trials of advanced



**8.** Monthly mean rainfall, open pan evaporation, and maximum and minimum temperatures at Hyderabad, India. The summer season (Feb-May) is used for drought resistance work.

breeding materials from ICRISAT. The trials are conducted every year during the rainfree summer season (Feb-May) when atmospheric conditions favor severe stress. Maximum temperatures range from 33 to 40° C, open pan evaporation rates reach 8-11 mm/day, and daily radiation averages 500-600 1x (Fig. 8). Controlled irrigation is used to create two standard stress treatments, from panicle initiation to flowering (midseason stress) and from flowering to maturity (terminal stress). Varieties in these trials vary in maturity (Table 2) and the onset and termination of the stress treatments are aimed at average dates of floral initiation and flowering. Grain yields from these two treatments are compared with those from a fully irrigated control treatment, which provides an estimate of the yield potential of the material under the climatic conditions of the summer season.

The influence of both yield potential and phenology (days to flowering) on stress treatment yields is clear under these conditions (Fig. 9). When these two effects are combined into a single regression equation, we can explain 40-60% of the observed yield variation under stress conditions (Table 3). This knowledge is useful, but it does not provide a basis for attempting to specifically improve cultivar performance under drought stress. Improvement in yield potential may result in some improvement in performance under stress (Fig. 9), but breeding for drought escape (phenology) is of use only where stress occurs in regular, predictable patterns. In a variable rainfall environment, a cultivar that escapes stress one year may be seriously affected the next year if the timing of the stress differs.

On the other hand, about half of the variability in yield under stress conditions is apparently due to specific cultivar × stress interaction. If it were possible to identify the factors contributing to this interaction and to specifically incorporate these into otherwise good cultivars (or to select against those responsible for poor performance), progress might be more rapid. But the utilization of specific

**Table 2. Mean yields, days to flowering, and drought indices from Advanced Screen 1979. Hyderabad, India.**[a]

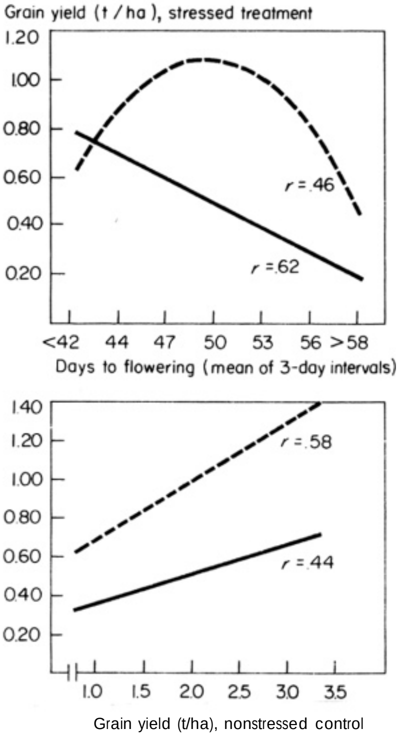
| | Control | | Midseason stress | | Flowering stress | |
|---|---|---|---|---|---|---|
| Pedigree | Yield (t/ha) | Days to flowering | Yield (t/ha) | Drought index | Yield (t/ha) | Drought index |
| LC-Cx75 | 4.0 | 49 | 3.1 | – 0.6 | 1.6 | 0.4 |
| 7224 | 4.0 | 55 | 3.8 | 1.0 | 1.2 | – 0.7 |
| SSC-Cx75 | 3.8 | 49 | 3.4 | 0.8 | 1.7 | 1.5 |
| 700490/GNS-1 | 3.5 | 54 | 3.0 | – 0.3 | 0.9 | – 1.5 |
| RF-Ax76 | 3.6 | 47 | 2.8 | – 0.3 | 1.7 | 1.3 |
| ICMS 7703 | 3.6 | 49 | 3.0 | – 0.0 | 1.3 | – 0.7 |
| Mali NNK | 3.5 | 50 | 2.3 | – 1.7 | 1.2 | – 0.6 |
| A-836/GNS-1 | 3.5 | 52 | 2.5 | – 1.4 | 1.2 | – 0.4 |
| 1CI-7504 | 3.2 | 50 | 3.1 | 0.8 | 1.0 | – 1.5 |
| IP-1964 | 3.1 | 50 | 2.8 | 0.2 | 1.5 | 1.9 |
| 700250-25 | 3.0 | 52 | 3.4 | 1.7 | 1.2 | 0.8 |
| J-1197 | 3.0 | 51 | 2.5 | – 0.4 | 1.3 | 0.8 |
| 7203 | 2.9 | 51 | 2.7 | 0.1 | 1.1 | 0.3 |
| Serere 4A | 2.9 | 48 | 2.2 | 0.2 | 1.2 | – 0.3 |
| BK-560-230 | 2.9 | 43 | 2.1 | 0.0 | 1.2 | – 0.8 |
| 700516 | 2.9 | 57 | 2.7 | 1.2 | 0.7 | – 0.0 |
| B-816//J-1623/WG2 | 2.8 | 56 | 2.1 | – 0.6 | 0.8 | – 0.3 |
| Serere-39 | 2.7 | 58 | 1.8 | – 1.1 | 0.7 | 0.1 |
| 112 HK Nain | 2.6 | 50 | 2.1 | – 0.7 | 1.0 | – 0.5 |
| 700441 | 2.6 | 50 | 2.1 | – 0.5 | 1.1 | 0.2 |
| J-1623/J-1644-1 | 2.6 | 49 | 2.0 | – 1.1 | 0.8 | – 1.6 |
| Cassady | 2.4 | 47 | 2.0 | 0.2 | 1.2 | 0.2 |
| J-1150 | 2.3 | 54 | 2.6 | 0.9 | 1.1 | – 1.6 |
| BJ-104 | 2.3 | 42 | 1.7 | – 0.1 | 1.2 | 0.3 |
| CD-67-13 | 2.3 | 55 | 2.1 | – 0.2 | 0.6 | – 0.7 |
| SE% | 14.9 | 3.4 | 12.5 | | 27.5 | |
| CD at 5% | 0.64 | 2.5 | 0.45 | | 0.45 | |

[a] Net plot size: 4.5 $m^2$. Replications: 4.

physiological or morphological characteristics as selection criteria is possible only 1) where evidence is clear that incorporation of these characteristics into breeding materials will improve their yield performance under stress and 2) where there are simple efficient techniques for selecting for these characters on the scale necessary for a breeding program. For most physiological and many morphological characteristics, one or both conditions (usually the first) are lacking (Bidinger 1980).

This is clearly the case with pearl millet. Little research is available on drought resistance mechanisms and there is no solid evidence that breeding for those mechanisms will produce cultivars with higher or more stable yields under stress. In the absence of such evidence the expenditure of the manpower and resources necessary to breed for such mechanisms is not justifiable.

Therefore we are concentrating on 1) the identification of lines with probable resistance to stress and 2) determining if initial selection for performance under specific, repeatable stress conditions, followed by direct evaluation of resistance,



**9.** Grain yields in midseason (----) and terminal (——) stress treatments in relation to days to flowering and grain yield in the nonstressed control treatment.

**Table 3. Summary of the variation in stress yields explained by yield potential and by drought escape. 1977-79 Advanced Screens.**

| Year | Entries (no.) | Days to flowering | Percentage variation explained ($r^2$) | |
|---|---|---|---|---|
| | | | Midseason stress[a] f(yc, bl, $bl^2$) | Terminal stress[a] f(yc, bl) |
| 1977 | 40 | 38-61 | 49 | 44 |
| 1978 | 64 | 39-60 | 42 | 55 |
| 1979 | 25 | 42-58 | 67 | 61 |

[a] f = function of, yc = yield potential measured in nonstressed conditions, bl = days to flowering.

will be useful as a means of identifying lines with drought resistance characteristics.

## Identification of resistance to drought stress

In the ICRISAT program, drought resistance or susceptibility is identified with variation in grain yield under stress which is not explained by yield potential and drought escape. This is done by applying regression equations of the type shown in Table 4 to data sets from groups of lines or cultivars tested together in the previously described controlled stress treatments. This procedure establishes the

**Table 4. Regression equations used to develop stress indices for lines in the Advanced Screen.**[a]

| | |
|---|---|
| Midseason stress | $\hat{y}_s = a + b_1(Y_c) + b_2\,(bl) - b_3\,(bl^2)$ |
| Terminal stress | $\hat{y}_s = a + b_1(Y_c) - b_2\,(bl)$ |
| Drought index | $\dfrac{Y_s - \hat{y}_s}{\text{Std. error of } \hat{y}_s}$ |

[a] $\hat{y}_s$ = regression estimates of stress yield, $Y_8$ = measured stress yield, $Y_c$ = nonstress control yield, and bl = days to flowering.

general effects of yield potential and drought escape for the entire cultivar set. These regressions are then applied to individual cultivars and the residuals for each individual cultivar (the difference between the measured yield under stress and the yield predicted) are calculated. These residuals, divided by the standard error of the regression estimates, are termed the *stress indices* for the test varieties. Table 4 shows the procedure for calculating stress index.

The sign of the index indicates resistance (positive sign — measured yield exceeding predicted yield) or susceptibility (negative sign — measured yield less than predicted yield). The magnitude of the index indicates the degree of the response. Because the residual includes experimental error as well as specific cultivar × stress interaction, we focus attention only on those cultivars with indices of less than –1.3 or more than +1.3. These represent the upper and lower 10% of the normal distribution of the indices. Thus there is a reasonable probability ($p \geqslant .2.80$) that the effects are real and not random.

For advanced breeding lines screened for drought resistance, program scientists use the drought index as one of several pieces of information (including various disease scores and yield test results) to make decisions on the advancement of individual lines. Table 2 shows one such data set, the 1979 Advanced Screen. Several entries illustrate the type of responses commonly observed: LC-Cx75 (an ICRISAT experimental line) yielded well in both stress treatments, but mainly on the strength of its yield potential (yield in the control treatment) because its stress index for both treatments was near 0. The selection 7000250-25 (from Nigerian material) and IP1964 yielded relatively well in the midseason and terminal stress treatments. respectively, but more on the strength of a resistant response because the yield potential of both was only average. BJ104 (a standard Indian hybrid) yielded poorly in the midseason stress, due largely to a low yield potential in the summer season, but did relatively well in the terminal stress, mainly because early flowering allowed escape from stress. Finally, the line derived from the cross J-162315-1644-1 performed poorly in both stress situations because of an apparent susceptibility to both stress treatments.

## Breeding for drought resistance

The definition of stress resistance or susceptibility used to evaluate advanced materials is not useful as a selection criterion in the early segregating generations of a breeding program. Seed, space, and labor requirements do not allow replicated tests with control plots to identify lines with high positive stress indices in $F_3/S_1$ generations. Also, doubts about the effectiveness of selection for yield in early generations apply equally to any yield-based estimate of drought resistance or susceptibility. Therefore, we are investigating the alternative approach of selection for performance under well-defined stress conditions as a means of identifying lines with resistance to stress or with a combination of resistance and yield potential.

To test this approach, we are using the midseason controlled-stress treatment described above (panicle initiation to flowering) as a selection environment. This has two advantages: 1) Selection conditions are repeatable to a reasonable degree in an off-season nursery and therefore initial selection and subsequent evaluations are for response to the same conditions. This should avoid some problems of selection in a variable, natural-stress environment; and 2) Because this is a known stress environment, selection for escape rather than resistance can be minimized by avoiding disproportionate selection in those maturity groups that favor escape. In addition, the environmental conditions of the summer season maximize the selection pressure for segregating lines least affected by stress or best able to recover rapidly from it. In a sense, this procedure is analogous to a managed disease-screening nursery in which a severe disease pressure can be placed on test materials to maximize the expression of resistance and in which selected lines can be retested to verify their responses.

The disadvantages of this approach are that lines are exposed only to a single stress treatment and are selected in an off-season environment. The latter objection is partially covered by evaluating (but not advancing) selected $F_3/S_1$ lines in the normal season before their reselection in the following dry season.

This system involves visual selection in the first generation ($F_2/S_0$). Beginning with the $F_3/S_1$ generations, however, grain yield is also measured and used for selection along with visual scores of the lines both at the end of the stress period and after recovery. Particular emphasis is on the ability to recover rapidly from the stress exposure principally through tiller regrowth, as this appears to be the character for which major variability exists.

We emphasize that this approach is still experimental. Direct selection in controlled stress conditions has not been shown to be the most effective procedure for identifying lines with either good performance or resistance under naturally occurring stress conditions. Nor is it clear that selection for performance in early generations is the most efficient way to identify lines with stress resistance. To answer these questions, parallel selection in the same crosses and populations under selection in stress conditions is being carried out in both the normal crop season (to represent the current breeding practice) and in a nonstressed summer season planting (to separate possible effects of selection for adaptation to summer-season environmental conditions from selection for adaptation to drought stress). Final evaluation will be a comparison of the performance of the products of each of the three selection environments, over all three environments, and in several naturally occurring stress environments. Performance analysis in each stress environment will be in terms of yield potential, escape, and resistance to determine if stress exposure during selection has influenced the relative contribution of each factor to final performance. The $F_3/S_1$ selection generation has just been harvested. Final comparisons of finished products will be available in several years.

## PROSPECTS FOR IMPROVEMENT IN DROUGHT RESISTANCE

The most promising short-term approach for improving the drought resistance of pearl millet is probably the exploitation of differences in developmental patterns and in rates of recovery after a stress period. These include such responses as 1) delay in development during severe stress, 2) degree of asynchrony in tiller development which allows some tillers to escape a stress period that damages others, and 3) rapid release and growth of secondary tillers after stress damage to the main tillers. Pearl millet has considerable genetic variation for these characteristics and they can be easily selected for in a managed stress nursery, where stress occurrence can be timed to maximize the value of the responses. Additional experiments on these mechanisms should be done, particularly on the specificity of these responses to the timing and duration of stress. We are now selecting indirectly for these responses, because lines selected on the basis of yield performance under stress are often lines with one or more of these responses.

Selection for specific physiological response mechanisms of drought resistance is a future, rather than a current, possibility. Research to identify these mechanisms and to determine if using them as selection criteria will improve cultivar performance under stress has not yet been done.

The possibility of exploiting avoidance mechanisms in pearl millet seems limited. Because of the nature of rainfall, soils, and potential evapotranspiration in many arid and semiarid environments, the amount of water available in soils (relative to potential rates of water use) will be small. Therefore, plant mechanisms to exploit these will be of limited usefulness. Tolerance mechanisms may be more useful in pearl millet in these circumstances (the earlier discussion of heat tolerance in the crop supports this). But tolerance mechanisms are generally better known in theory than in practice in crop plants.

Millet has an additional, somewhat different, factor that may prove an advantage in the improvement of its drought resistance: there are fewer competing priorities in millet improvement than in other major tropical cereals. Disease and insect problems in millet, while present, are generally less extensive and perhaps less serious than in maize, rice, and sorghum. Yield potential is also less of an actual limitation to yield at the *farmer level* than in the case of other cereals and, hence, high yield potential may be a lower priority in pearl millet. Part of this is because of the generally low input levels under which the crop is grown (a factor that may change with time), but also because factors such as drought often do not permit millet to fully express its yield potential. We hope these factors will allow millet breeders to concentrate relatively more of their inputs on drought resistance.

In summary, if relatively simple and reliable methods can be developed for improvement in drought resistance, the opportunity for at least modest improvements should be good. But there will clearly be years and environments without enough rainfall for a crop — and no amount of research will change that. Hope-fully, improvement of yields in the average years (which do include stress periods) will allow farmers to better withstand the poor years.

Dr. Larry Robertson and M. N. S. Bose of ICRISAT provided the figures showing the distribution of pearl millet relative to mean annual rainfall. S. J. Reddy, ICRISAT, provided climatic data for Table 1. D. S. Raju, K. V. Hanumantha Rao, G. D. Prasada Rao, and N. R. Sharma contributed to the field research.

## REFERENCES CITED

Austin, R. B., I. E. Henson, and S. A. Quarrie. 1982. Abscisic acid and drought resistance in wheat, millet, and rice. *In* International Rice Research Institute. Drought resistance in crops, with emphasis on rice. Los Baños, Philippines.

Begg, J. E., J. F. Bierhujzen, E. R. Lemon, D. K. Misra, R. O. Slatyer, and W. R. Stern. 1964. Diurnal energy and water exchange in bulrush millet in an area of high solar radiation. Agric. Meteorol. 1:294-312.

Begg, J. R. 1965. The growth and development of a crop of bulrush millet (*Pennisetum typhoides* S. and H.). J. Agric. Sci. 65:341-349.

Bidinger, F. R. 1980. Breeding for drought resistance. Pages 452-454 *in* N. C. Turner and P. J. Kramer, eds. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York.

Black, C. A., and G. R. Squire. 1979. Effects of atmospheric saturation deficit on the stomatal conductance of pearl millet (*Penniserum ryphoides* S. and H.) and groundnut (*Arachis hypogea,* L.). J. Exp. Bot. 30:935-945.

Cocheme, J., and P. Franquin. 1967. A study of the agroclimatology of the semi-arid areas south of the Sahara in West Africa. FAO/UNESCO/WMO interagency project on climatology. FAO, Rome.

Dancette, C. 1970. Determination au champ de la capacite de retention apres irrigation dans un sol sableux du Senegal. L'Agron. Trop. 25:225-240.

International Crops Research Institute for the Semi-Arid Tropics. 1980. Annual report for 1978-1979. Hyderabad, India. pp. 69-71.

Kowal, J. M., and A. H. Kassam. 1978. Agricultural Ecology of Savanna. Oxford University Press, Oxford. 403 pp.

Lahiri, A. N., and B. C. Kharabanda. 1965. Studies on plant water relationships: effects of moisture deficit at various developmental stages of bulrush millet. Proc. Nat'l Int. Sci. India B. 31:14-23.

Lahiri, A. N., and V. Kumar. 1966. Studies on plant water relationships. III. Further studies on the drought mediated alterations in the performance of bulrush millet. Proc. Nat'l Inst. Sci. India B. 32:116-129.

McPhearson, H. G., and R. O. Slatyer. 1973. Mechanisms regulating photosynthesis in *Penniserum typhoides.* Aust. J. Biol. Sci. 26329-339.

Nanda, K. K., and J. J. Chinoy. 1958. Lateral bud development in "Pearl Millet" (*Penniserum typhoides* Stapf and Hubb.) in relation to its flowering. Curr. Sci. 27:141-143.

Norman, M. J. T., and J. E. Begg. 1968. Bulrush millet [*Pennisetum typhoides* (Burm.) S. and H.] at Katherine, Northern Territory: A review. J. Aust. Inst. Agric. Sci. 34:59-68.

Rachie, K. O., and J. V. Majmudar. 1980. Pearl millet. Pennsylvania State University Press, University Park, Pa. 307 pp.

Raymond, C. 1968. Pour une meilleure connaissance de la croissance et du development des mils Penniserum. L' Agron. Trop. 23:844-863.

Reddy, S. J. 1981. A simple method of estimating soil water balance. Agric. Meteorol. (in press)

Squire, G. R. 1979. The response of stomata of pearl millet (*Penniserum typhoides,* S. and H.) to atmospheric humidity. J. Exp. Bot. 30:925-933.

Sullivan, C. Y., N. V. Narcio, and J. D. Eastin. 1977. Plant responses to high temperatures. Pages 301-317 *in* A. Mohamed, R. Aksel, and R. C. Von Borstel, eds. Genetic diversity in plants. Plenum Publishing Corp., New York.

Sullivan, C. Y. 1972. Mechanisms of heat and drought tolerance in grain sorghum and methods of measurement. Pages 247-269 *in* N. G. P. Rao and L. R. House, eds. Sorghum in the seventies. Oxford and IBH, New Delhi.

Virmani, S. M., M. V. K. Sivakumar, and S. J. Reddy. 1978. Rainfall probability estimates for selected locations of semi-arid India. Research report I, International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India.

Wetselaar, R., and M. J. T. Norman. 1960. Recovery of available soil nitrogen by annual fodder crops at Katherine, Northern Territory. Aust. J. Agric. Res. 11:693-704.

# BREEDING AND SELECTION FOR DROUGHT RESISTANCE IN TROPICAL MAIZE

K. S. FISCHER, E. C. JOHNSON,
AND G. O. EDMEADES

Throughout the lowland wet tropics, periodic nonprotracted drought caused by irregular rainfall distribution is responsible for sizable reductions in maize yields, particularly when reduced water availability coincides with flowering. Such a drought cannot be escaped by genotype maturity or by planting date. Other species are not necessarily better adapted. Improving the resistance of maize to drought at flowering could enhance productivity and minimize farmers' risks.

When sorghum and maize under drought are compared, sorghum appears to maintain photosynthesis and growth at lower water potentials and seems to have more developmental plasticity than maize. Increasing the dry matter available for ear development around flowering may help reduce the detrimental effects of drought at flowering in maize.

The drought resistance of one lowland tropical maize population is being improved at CIMMYT in a full sib recurrent selection program using a drought selection index based on grain yield under stress and no stress, leaf elongation rate, interval between anthesis and silking, canopy temperature, and leaf area loss during grain filling. After three cycles of recurrent selection, the crop shows a significant increase in yield under severe drought conditions. Improvement is about 8%/cycle.

Other morphophysiological traits also are being evaluated for

---

Maize physiologist and maize breeder, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, Mexico 6, D. F.; and maize agronomist/physiologist, Crops Research Institute, P.O. Box 3785, Kumasi, Ghana.

> effectiveness in drought response. Selections for reduced tassel, leaf, and height may improve yields under severe stress conditions.

Throughout the tropics, periodic drought caused by irregular rainfall distribution and accentuated by soils with low water-holding capacities causes sizable reductions in maize yields (Wolf et al 1974). Estimates show that drought may account for an average 15% production loss in tropical areas, even when total rainfall is reasonably high. The probability of yield loss due to drought influences the use of fertilizer and other inputs. Drought is probably responsible for a much higher economic loss than has been thought.

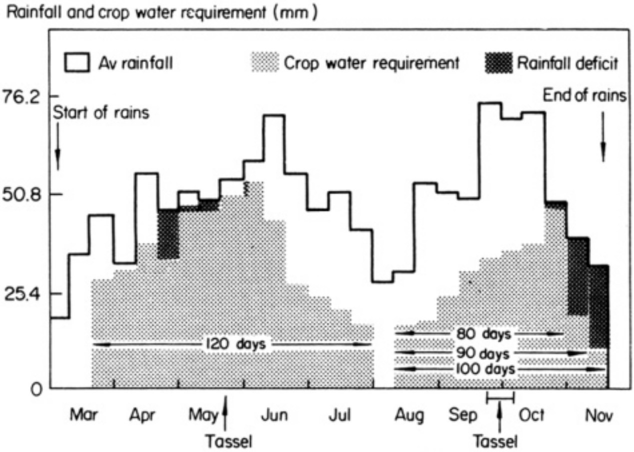
From greenhouse experiments, field trials, and historical analysis of on-farm yield data, agronomists and meteorologists have concluded that drought occurring around flowering has a major effect on grain yield. Water deficits lasting 1-2 days during tasseling or pollination can cause as much as a 22% reduction in yield (Robins and Domingo 1953), while stress during the grain-filling stage (McPherson and Boyer 1977) and vegetative stage (Denmead and Shaw 1960) may not have any pronounced effect.

The most effective means of reducing the effects of' drought on maize would be to manipulate genotype maturity and planting date to escape periods of low moisture availability. Kassam et al (1975) give an example for maize grown at Ibadan, Nigeria, where total rainfall is about 1,140 mm spread in a bimodal pattern from March to November. The first season has sufficient moisture for a 120-day maize crop, while in the second season there is only sufficient moisture to support a crop of 80- to 90-day-maturity maizes. Plant breeding programs should aim at providing high-yielding genotypes with a range of maturities to best fit the season as determined by moisture availability.

But large areas of the tropics are affected by drought occurring in the middle of the main summer maize-growing season. Total rainfall for the crop season may be adequate, but a drop in the number of days with rain, particularly around the critical flowering stage of the crop, may cause a large reduction in yield. The first season at Ibadan (Fig. 1) illustrates this form of drought. Although total moisture is adequate, the difference between crop water requirement and water availability is narrow, particularly in the period just before flowering. When water stress occurs at this time, there may be a sizable reduction in grain yield.

Mosino and Garcia (1968) suggest that summer drought may affect over 7 million hectares of rainfed maize in Mexico, including most of the lowland tropical area where total annual rainfall is greater than 1,000 mm. In El Salvador, although monthly rainfall may average 300 mm, the summer drought known as canicula may be responsible for reducing yields by 20%. This summer drought is cited as the most frequent source of crop loss, more damaging than insects, lodging, and excess water (Walker 1980).

Since drought may occur at any time during the growing season, it cannot be consistently avoided through the manipulation of either genotype maturity or



**1.** Rainfall and crop water requirement for maize grown at Ibadan, Nigeria (from Kassam et al 1975).

planting date. Maize may even be the cereal best adapted to the mid–crop drought, since high humidity and rain at harvest could be harmful to an alternative crop such as sorghum. To minimize the risk of yield loss, farmers now stagger their plantings of maize, plant maizes of different maturities, or intercrop different species. Improved agronomic practices such as better weed control and provision of more surface mulch (minimum tillage) will also have a substantial benefit. However, there is an opportunity to stabilize grain yields by breeding for improved drought resistance in maize.

In situations where the duration of adequate moisture is limited, yields should be stabilized through the use of genotypes and planting arrangements that escape stress. In situations where moisture availability can be predicted to be inadequate to sustain maize, alternate crop species should be grown or additional moisture should be provided. However, improved practices such as better weed control and minimum tillage will substantially affect yield under drought.

## SOME PHYSIOLOGICAL FACTORS

Drought resistance in an agricultural sense refers to the ability of a species to produce its economic product with limited available water. Drought resistance in an evolutionary sense refers to the ability of a species to survive. It is likely that mechanisms responsible for survival differ from those responsible for maximum economic production. That the survival of maize has always relied on the intervention of man reduces the probability that maize has evolved strong mechanisms for survival under moisture stress (Qualset 1979).

The mechanisms involved in drought resistance have been classified by Levitt (1972) into drought escape, drought avoidance, and drought tolerance. But

O'Toole and Chang (1979) note that these mechanisms are viewed too often in terms of either/or, with the implication that a choice is necessary, rather than in terms of and/or.

Drought escape, with the aim to completely preclude drought from interacting with crop growth and yield, is probably the most successful form of resistance. However, it usually is imparted through early maturity of genotype. The usual negative association of yield and earliness is a separate issue and will not be discussed here. Selection for drought resistance will imply selection for avoidance or tolerance mechanisms or both.

Tolerance is the ability of a plant to perform despite low plant water status. Avoidance is the ability of a plant to maintain relatively high plant water status despite a shortage of moisture in the environment (O'Toole and Chang 1979, Fischer and Sanchez 1979).

A multiplicity of factors and factor interactions affect productivity under limiting moisture. Although information explaining the physiological basis for drought resistance continues to grow, it is difficult to relate a general pattern or a major association of a trait or traits to a breeding program (Fischer and Wood 1979). One approach to studying the usefulness of a factor for crop improvement is to develop isogenic lines or to make divergent selections for the character being considered. This approach, while time-consuming (Moss et al 1974), may be necessary to unravel the complexity of drought-resistant mechanisms. To determine which factors are likely to be of consequence, it is useful to compare two species (such as maize and sorghum) which differ markedly in drought resistance but which otherwise are somewhat adapted to similar environments. The information provided will be influenced by the genotype (genotypes) chosen to represent each species, since traits vary considerably within each species.

## Sorghum and maize, and drought resistance

Under tropical conditions in Nigeria, Kassam (1976) obtained water use efficiencies of 3.95 mg dry matter/g water produced for maize and 3.70 mg dry matter/g water for sorghum. Ludlow (1976) reported values of 2.86 mg dry matter/g water for maize and 3.28 mg dry matter/g water for sorghum. Under well-watered conditions, water use efficiency of the two crops probably is similar.

A number of studies have compared maize and sorghum under drought, with some conflicting evidence. Characters examined in terms of drought avoidance, tolerance mechanisms, and other factors are listed in Table 1, with their probable importance in explaining the differences between the two crops.

Martin (1930) suggested that the drought resistance of sorghum was due in part to a greater number of secondary roots which result in greater water absorption. However, Sanchez-Diaz et al (1969) obtained similar water uptake rates in maize and sorghum growing in similar containers where the soil was fully exploited by the roots. Hsiao et al (1976) summarized work which compared the rooting patterns of maize and sorghum grown in a deep clay loam soil. Based on this evidence and other reports, they suggested that the differences in root systems are minor and insufficient to explain the observed differences in grain yield when crops are grown with limited moisture supplies. A comparison of root profiles of

**Table 1. A comparison of drought resistance mechanisms in sorghum and maize and their relative importance in explaining differences in productivity under nonprotracted moisture stress.**

| Character | Level of importance | References |
|---|---|---|
| Drought avoidance | | |
| Root density | High-low | Martin (1930), Sanchez-Diaz et al (1969) |
| Root exploration | Low | Hsiao et al (1976), O'Toole and Chang (1980) |
| Root osmotic potential | High | Martin (1930), Sullivan and Blum (1970) |
| Cuticular resistance | High-low | Martin (1930), Yoshida and de los Reyes (1976) |
| Stomatal resistance | Low | Beadle et al (1973), Boyer (1970), Sanchez-Diaz and Kramer (1971) |
| Leaf size and rolling | Low | Martin (1930) |
| Development plasticity | High- | Whiteman and Wilson (1965), Eastin (1980), Sullivan and Blum (1970) |
| Drought tolerance | | |
| High critical [a] potential | High | Sanchez-Diaz and Kramer (1971), Boyer (1970), Newman et al (1974), Ludlow (1976) |
| Osmoregulation | High | Jurgens et al 1978, Stout and Simpson (1977), Jones and Turner (1978) |
| Desiccation and heat tolerance | Low | Sullivan and Blum (1970) |

[a] For example, water potential at zero turgor.

the two crops by O'Toole and Chang (1979) supports this view.

Martin et al (1931) measured differences in osmotic pressure of the sap from stalks, crowns, and roots of sorghum and maize. The values were -12 to -15 atmospheres for sorghum and -9 to -11 atmospheres for maize. This difference aided sorghum in resisting desiccation, enabling it to extract more moisture from the soil during moisture stress.

Martin (1930) also suggested that the waxy nature of sorghum leaves could be important in increasing its cuticular resistance. Yet Yoshida and de los Reyes (1976) obtained cuticular resistance of 116 sec/cm for sorghum and 112 sec/cm for maize. Maize stomata are more sensitive and begin to close at a higher water potential than those of sorghum (Beadle et al 1973, Boyer 1970a, Sanchez-Diaz and Kramer 1971). Upon release of stress conditions, sorghum stomata recover their prestress behavior more quickly (Iljin 1957). In maize, only stomata on newly developed leaves function normally (Glover 1959). The stomata of sorghum are about two-thirds the length of those of maize and there are almost 50% more of them on the upper or the lower leaf surfaces (Martin 1930).

Small groups of motor cells at intervals on the upper surface of maize leaves lose water rapidly and cause the leaf to roll. These cells are more numerous in sorghum and occur in a single row along each side of the midrib, causing more rapid and complete sorghum leaf folding than maize leaf folding (Martin 1930).

Sorghum has more developmental plasticity than maize and is able to avoid the effects of moisture stress at a critical stage of plant development. Whiteman and Wilson (1965) found that inflorescence development in sorghum could be suspended during stress and resume development after rewatering. Moisture stress during various stages of panicle development in sorghum causes a reduction in grain number, but even under severe stress plants will exsert partial panicles (Eastin 1980). In contrast, stress initially reduces ear size in maize, then reduces the number of ear-bearing plants (increased barrenness). This may be a special feature of maize associated with its botanical arrangement, with the female inflorescence on a side tiller of the main stem. Individual sorghum grains also have a greater capacity to compensate for a reduction in grain number (Fischer and Wilson 1975, Fischer and Palmer 1980). The ability of sorghum to form panicle-bearing tillers allows the possibility of recovery upon relief of water stress.

The species also differ in drought tolerance. In a controlled environment study, Neumann et al (1974) measured critical leaf water potentials (water potential at zero turgor) of −8.1 to −9.6 bars for maize and −11.2 to −13.8 bars for sorghum. Field data are −16 bars for maize and −21 bars for sorghum. Sorghum tolerates higher internal water deficits before stomata close and can continue photosynthesis at lower water potentials (Boyer 1970a, Beadle et al 1973).

Neumann et al (1974) found a small but sustained rate of water content loss from full turgidity to wilting, and afterward, the less of total water content was similar in both species. However, Boyer (1970a) found that sorghum had a smaller reduction in leaf water content than maize for the same change in water potential. Ludlow (1976) obtained values of 58% relative water content for maize and 81% for sorghum at leaf water potentials of −15 bars.

Stout and Simpson (1978) and Turner et al (1978) suggest that the osmoregulation brought about in sorghum by age and stress is an important factor in determining the critical potential. Jones and Turner (1978) measured a lowering of leaf water potential from 8 to 10 bars after prestress treatments in sorghum. Ludlow (1976) showed large differences in the critical potential of crops, depending on the environment to which the plants were adapted. Jurgens et al (1978) reported no adjustment of critical leaf potential in maize during the grain-filling period. The extent to which differences in osmoregulation are important in explaining differences between maize and sorghum has been reasonably well studied.

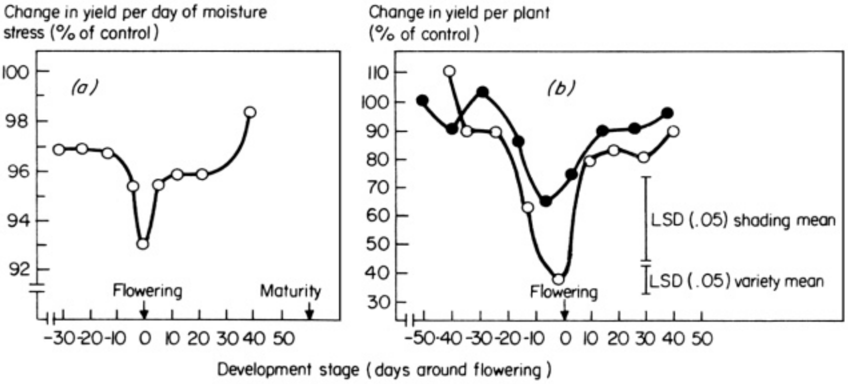
Evidence conflicts on differences in heat or desiccation tolerance of the leaf or intact plants between the two species. This may be due in part to the genotypes used in the comparisons (Sullivan and Blum 1970). The earlier closure of maize stomata under moisture stress may have acted as a selection pressure (evolutionary sense) for heat tolerance.

Two features of the comparison of sorghum and maize may be of considerable relevance to studies on drought resistance of maize, particularly for a nonprotracted form of drought—the ability to maintain photosynthesis and growth at lower water potentials and the developmental plasticity of both the main stem and tiller. Understanding the factors controlling ear development and barrenness of maize grown under moisture Stress should prove useful in developing drought resistance.

## Dry matter production and distribution under stress

Shaw (1977) has estimated the sensitivity of various developmental stages to water stress (Fig. 2). The critical period brackets flowering and coincides with the time of maximum crop transpiration (Downey 1971, Andre et al 1978).

The pattern of yield reduction because of drought stress is similar to the effects of reduced radiation (Fig. 2) shown by Fischer and Palmer (1980) and Prine (1971). Tollenaar (1977), reviewing the control of grain yield in maize, concluded that the intercepted irradiance per plant during flowering is the dominant factor



**2.** Effect of (a) a single day of moisture stress (from Shaw 1977) and (b) 11 days with 54% shading of the crop at different stages of development on grain yield (Fischer and Palmer 1980). Note different scales of Y axis in (a) and (b).

determining grain number. Maintenance of photosynthesis during flowering is critical to yield. Castleberry and Lerette (1979) suggest that the drought resistance of some corn belt/Michoacan 21 hybrids is due to lower stomata sensitivity to water stress.

The partitioning of dry matter to the developing ear and factors affecting spikelet fertility control grain number. Fischer and Palmer (1980) viewed a number of morphophysiological traits that may affect grain number under nonstress conditions. Some of them may be relevant under nonprotracted drought stress. Dow (1981) concluded that the drought resistance of a number of hybrids could best be related to a smaller leaf area and a shorter interval from midanthesis to midsilking. He suggested that leaf development in the leafier genotypes may have been at the expense of growth of the developing ear.

Hybrids with heavier tassels also have longer anthesis to silking intervals (Daynard 1968) and lower grain yield under density stress (Buren et al 1974). Careful removal of the male inflorescence before flowering in tropical maize grown under stress levels of nitrogen, water, and density increased grain yield by 9.5, 21.0, and 17.9% respectively (Poey et al 1977).

Johnson and Fischer (1979) reported that selection for reduced plant height increased grain yield under nonstress conditions. Fischer and Palmer (1980) attributed some of that increase in yield to less dry matter in the stem at flowering and to more dry matter available for ear development. However, nonstructural carbohydrates stored in the stem and elsewhere can be mobilized for grain filling at a later stage, particularly if current assimilation is less than grain demand (Jurgens et al 1978, Wilson and Allison 1978).

The interval between anthesis and silking increases under most stress conditions, including drought and high density. Delay in silk development may be related to a decline in nitrate reductase (Hsiao and Acevedo 1974), to a reduction in current assimilate supply (Dow 1981), or to other factors. A number of authors (Jensen 1971, Duvick 1977) have advocated selection for reduced interval between silking and anthesis under population density stress to get better performance under moisture stress. Genotypes with a tendency toward prolificacy (two ears) also have better population tolerance (Buren et al 1974). Hallauer and Troyer (1972) concluded that the prolific character contributes to the reduction of the genotype by environment interaction through its ability to adjust to environmental stresses, including drought.

Dow (1981) concluded that hybrids resistant to density stress were also more drought resistant. However, he warned that while selection for a decrease in the anthesis to silking interval under high density and nonmoisture stress conditions would improve drought resistance, other parameters conferring drought resistance could be lost or selected against.

## BREEDING STRATEGIES AND GENETIC VARIATION

Blum (1979) describes two major breeding philosophies aimed at improving a genotype's response to stress:

- The first, very common approach accepts that a superior-yielding variety at the potential level will also yield relatively well under subpotential levels. Drought resistance may be present in such a variety, expressed as an unidentified component of stability in performance over various environments. During the breeding process, yield and stability in performance are handled as one complex. Accumulation of environmentally stable yield genes equates with better performance under stress situations.

- A second approach to breeding for yield performance in a stress environment maintains that potential yield is irrelevant (Blum 1979). Varieties must be selected, developed, and tested under the relevant conditions.

## Improved yield potential and stability

This approach has been successful in sorghum (Blum 1979), wheat (Worrall et al 1980), and maize (Russell 1974, Duvick 1977). In wheat, improved yields of CIMMYT-derived genotypes over a wide range of conditions are attributed mainly to an increase in yield potential, an increase in environmental stability, and a small change in genotype response to environmental conditions (Worrall et al 1980). It appears that some traits, such as improved harvest index of short straw wheats, have sufficiently strong positive effects on yield under all conditions to give them obvious superiority over traditional varieties or collections, even under dry conditions, despite any specific drought-resistant mechanisms the latter group may possess (Fischer and Wall 1976). However, subsequent work by Fischer and Wood (1979) did not indicate a relationship between harvest index under irrigation and grain yield under drought.

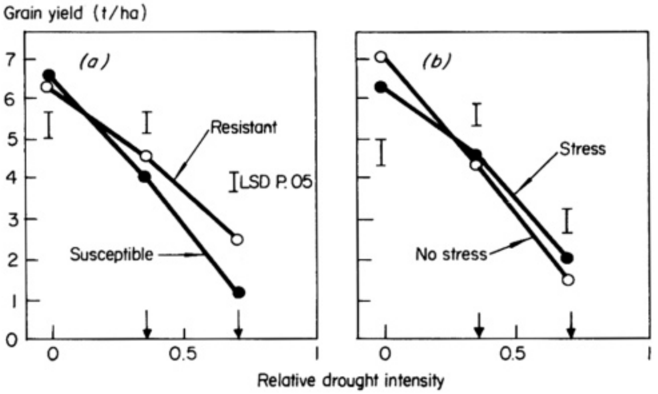
Gains in maize yields due to breeding in the US corn belt from 1920 to 1970 indicate an increase in yield potential. There is considerable improvement at the lower-yielding environments in the more recent commercial hybrids (Table 2) (Russell 1974). The improved performance at the higher stress environments (in this case probably due to moisture availability) might be due to better stalk and root quality from initial selection under high plant density and to extensive testing of germplasm for yield stability (Russell 1974).

While there is considerable scope for the improvement of yield potential, in view of the lack of sound information on specific drought characters, a breeding strategy based on selection under well-watered conditions may very likely be the most efficient for bringing about rapid progress. This system has the advantage that heritabilities for yield are high under optimal growing conditions (Johnson and Frey 1967).

Testing over a large number of sites with varying moisture availabilities, although expensive, should enable the elimination of those genotypes which may have yield-negative traits under moisture stress. Separation of the effects of drought escape and identification of traits specifically favoring performance under these drought conditions could also facilitate selection. For international crop improvement centers such as CIMMYT, testing over a wide geographic range also provides a vehicle to introduce improved germplasm to national programs.

## Breeding for specific stress conditions

There are a few examples of population improvement in maize based on selection



**3.** Yield versus drought intensity for experimental varieties selected from Tuxpeño population for drought resistance and susceptibility and grain yield without stress and with stress. Tlaltizapan, 1976.

under a specific condition. One mass selection study was done in Colombia for the rainy season (600 mm) and dry season (300 mm) separately and in combination (Arboleda-Rivera and Compton 1974). The selection criterion was grain yield. Three cycles of selection during the rainy season increased yield by 10.5%/cycle in the wet season but by only 0.8% in the dry season. Three cycles of selection during the dry season increased yield by 2.5%/cycle in the dry season and by 7.6% in the rainy season. Another study in Mexico involved mass selection for a number of cycles under irrigated or rainfed conditions or both (Muñoz 1975). Testing of the synthetic derived from these selections showed similar performance at the high, rainfall, high-yielding site, but a greater yield from the selection made under stress at the low-rainfall, low-yielding site. However, in a lowland tropical maize population, Edmeades and Fischer (1977) found no difference in the performance of two experimental varieties derived from selection for yield under irrigated and water stress treatments when they were grown under moisture stress (Fig. 3).

An alternate approach to these two strategies is to improve drought resistance in those materials that already have high yield potential. As yield potential becomes relatively difficult to improve, breeding programs might focus more attention on identifying specific drought resistance mechanisms. Finlay and Wilkinson (1963) suggested that both yield potential and yield stability across environments could be independently manipulated in a barley breeding program. Russell (1974) clearly demonstrated the importance of improved yield potential in improving maize yields over a wide range of environments. However, his analysis of the performance of some of the more recently developed maize hybrids demonstrates differences in yield at higher stress environments because of factors other than yield potential (Table 2). Edmeades and Fischer (1977) used a drought selection index based on grain yield under both no stress and stress treatments and on other characters associated with drought resistance. They demonstrated considerable

**Table 2. Change in yield potential and yield and stability of yield over a number of locations in representative maize materials of the corn belt (US) from 1930 onward (from Russell 1974).**

| Approximate year of release | Maize type | Grain yield (t/ha) | | Regression slope |
|---|---|---|---|---|
| | | Mean across locations | Max yield | |
| – | Open-pollinated | 5.48 | 7.05 | 1.16 |
| 1930 | Double-cross hybrid | 5.78 | 8.03 | 1.26 |
| 1940 | Double-cross hybrid | 6.58 | 8.68 | 1.01 |
| 1950 | Double-cross hybrid | 6.75 | 9.08 | 1.03 |
| 1960 | Double-cross hybrid | 7.31 | 10.15 | 1.27 |
| 1970 | Single-cross hybrid (public line) | 8.37 | 10.87 | 1.06 |
| 1970 | Single cross hybrid (commercial line) | 8.07 | 9.30 | 0.63 |

variability within a high-yielding tropical population. An experimental variety formed from families selected for drought resistance yielded significantly more grain under moisture stress than did a divergent drought susceptible selection (Fig. 3).

Selection must be for increasing or at least maintaining yield potential and for improving drought-resistant traits. It is likely that such traits in maize will be multigenic and at a low gene frequency level in any given population. Their frequency should be increased through recurrent selection programs. Accumulation of the frequency of genes for one or two drought-resistant traits while maintaining yield may lead to an indirect improvement in yield under stress. The effectiveness of recurrent selection for a trait associated with grain yield in maize is demonstrated by Johnson and Fischer (1979), where reduced plant height was the primary selection criterion, yet grain yield was increased substantially. It is interesting to speculate as to the effect on yield under stress if a similar study involving selection for a trait associated with drought tolerance were done. To do so for improved drought resistance depends on an understanding of drought-resistance mechanisms relative to the ecology for which the material is being developed and the rapid identification of such mechanisms in large breeding nurseries. At the same time, materials should be evaluated under favorable conditions to maintain or improve yield potential.

A few races of maize under the influence of natural selection in various parts of the tropics have developed drought avoidance or tolerance mechanisms, or both. Palacios de la Rosa (1959) described Michoacan 21 as having a distinct response to drought and frost. This mechanism was called latente. The collection maintained itself under drought without flowering, recovered remarkably on rewatering, was more resistant to permanent wilting at the seedling stage, and transpired more than other lines under irrigation and less under stress because of stomatal closure (Munoz 1975). This response may be partly due to high abscisic acid levels (Larque-Saavedra and Wain 1974). But the latente trait has proven difficult to transfer to higher yielding, agronomically desirable germplasm, particularly in the wetland tropics. However, workers at DeKalb have successfully used Michoacan 21 as a source of genes for the improvement of drought resistance of hybrids for the US corn belt (Castleberry and Lerette 1980). The latente trait did not appear to be simply inherited and the development of drought-resistant hybrids required the selection of inbred lines under controlled moisture conditions for yield and other traits associated with drought resistance.

Many morphological and physiological characters have been suggested for modification to enhance either drought avoidance or tolerance (Moss et al 1974, Parker 1968). A number of screening methods have been used to compare the responses of different genotypes of maize to drought. While some of these methods appear useful to a plant breeding program, there is a paucity of evidence of their use in a population improvement program (Qualset 1979). In almost all cases cited, the screening of lines was the end product of the breeding program. There are too few reported programs in which selected materials have been recombined and further tested. In many cases, the results obtained in laboratory tests have not been evaluated in the field.

Hurd (1976) has reviewed numerous accounts where plant water stress decreased with increased width, depth, and branching of roots. There may be some ecological condition where reduced root growth, particularly early in the crop cycle, is an advantage (Passioura 1972). Nass and Zuber (1971) measured differences in total root volume and weight of nodal roots at two growth stages before flowering of 40 maize genotypes. The characters correlated with measured resistance to root pulling at maturity. Differences in root volume in maize genotypes also have been recorded by Musick et al (1965) and Thompson (1968). Spencer (1940) noted large differences in the rate of development of lateral roots and in the ratio of top dry weight to root dry weight of seedlings between inbred lines of maize. Muleba (International Maize and Wheat Improvement Centre, Mexico, pers. comm.) selected families for superior root weight and length and recombined them to form experimental varieties. Evaluation of the experimental varieties under water stress conditions in the field showed that selection for larger root weight was useful in increasing grain yield under mild water stress. Selection for increased root length was superior under severe stress.

The rate of leaf elongation has been shown to be sensitive to changes in leaf water potential (Boyer 1970b, Watts 1974) and soil water supply (Acevedo et al 1971). Boyer and McPherson (1975) suggested that the rate of cell elongation in seedlings could be used to screen for drought tolerance in cereals. Edmeades and Fischer (1977) used leaf elongation rates to screen maize progenies for drought resistance under field stress conditions.

There has been a considerable breeding effort to modify stomatal response and reduce water loss by transpiration. A number of workers in other crops have successfully reduced transpiration per unit leaf area (Jones 1979). Selection has been for the frequency and anatomical structure of the stomata and for measured stomatal conductance (Wilson 1975). Infrared thermometry has been used to screen large numbers of genotypes for canopy temperature that can be related to stomatal conductance (Jackson et al 1977, Kretchmer et al 1980).

Williams et al (1967) compared inbreds and hybrids for drought resistance by 1) the percentage of seedlings that recovered from 6-hour exposure to 52°C (heat tolerance), 2) germination percentage of seeds exposed to a mannitol solution of 15 atmospheres, and 3) percentage recovery of seedlings watered 14 days after reaching wilting. The ratings were tested by correlation analysis with field evaluations based on the ratio of grain yield under stress to yield under full irrigation. The results suggest that data from these procedures are correlated with field data. As such, any of them could aid a breeding program.

Other workers have used similar techniques. Hunter et al (1936), Tatum (1954), and Kilen and Andrew (1969) showed that the relative differences in response of inbred lines to high temperature coincided with observations of leaf firing in the field. Muñoz (1975) conducted three cycles of mass pollination (mass selection) of seedlings that showed good recovery upon rewatering after initially beingstressed to the wilting point.

Kilen and Andrew (1969) found that a chlorophyll stability index of heat tolerance for inbred lines of maize correlated with ratings of leaf firing in the field.

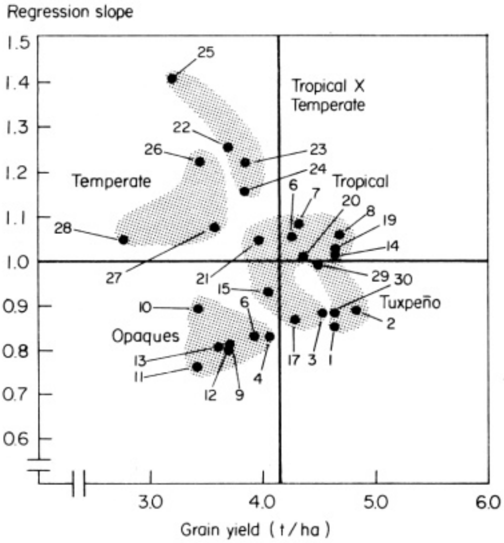
Screening of seeds or seedlings in solutions of different osmotic potential was used as early as 1930 with limited results (Ashton 1948). Parmar and Moore (1968) modified this technique for maize by using polyethylene glycol solutions. Johnson and Asay (1978) demonstrated the effectiveness of this osmoticum in differentiating between lines of crested wheat grass.

Abscisic acid has been found important in drought resistance. Larque-Saavedra and Wain (1974) measured almost five times higher levels of *in vivo* free abscisic acid in a drought-resistant line (Michoacan 21-latente) under no stress conditions and three times higher under stress conditions than in two European varieties. There are no examples of screening a larger number of maize genotypes under field conditions for this trait in maize.

Screening certain amino acids that increase dramatically under stress has been suggested as a means of evaluating drought resistance. One of these, proline, was implicated as useful for drought screening (Singh et al 1972). But this method has been questioned recently (Hanson et al 1977). Work with betaine suggests that it may be a valid indicator of the cumulative stress experienced by plants and, if so, discarding genotypes with high betaine content might be effective in selecting for drought tolerance. Pinter et al (1978) reported that free asparagine and proline contents of maize plant tissue subjected to drought correlated positively with drought resistance estimated from the difference in grain yield under stress and no stress conditions.

## THE EXPERIENCE AT CIMMYT

The objectives of CIMMYT's Maize Program are to increase the realized yield and yield potential of a number of adapted maize populations and to improve their yield stability. The breeding and selection system used is described by Johnson (1974) and Vasal et al (1978). Limited work to assess the feasibility of selecting more directly for drought resistance in tropical maize began in 1976. The objectives are to demonstrate the feasibility of improving, using recurrent selection, the performance of a tropical population exposed to a particular type of drought. This



**4.** Analysis of adaptation by grain yield and regression slope and by cluster analysis (genotypes in each shaded area have a more similar response than those excluded) for an international experimental variety trial grown only at rainfed sites. CIMMYT, 1974.

work was aimed particularly at improving resistance to drought occurring at the critical flowering phase of plant development. It did not seek to do this through mechanisms of escape.

## Choice of germplasm

Data from the 1973 Experimental Variety Trials (CIMMYT 1974) were used to identify a population with high, stable yields. Only rainfed sites were used. The mean yield of each site significantly correlated with rainfall during the growing season (*r* = 0.74), suggesting that yield was to some extent influenced by moisture availability. The data were analyzed for yield stability by regression analysis (Finlay and Wilkinson 1963) and for similarity of response by cluster analysis (Mungomery et al 1974). The results are shown in Figure 4. Within the group of tropical germplasm entries, those with a preponderance of the Tuxpeño race had a slope less than 1.0 and a higher than average mean yield across all sites. The Tuxpeno race was described by Wellhausen (1956) as one of the most important modern productive agricultural races in both the US and Mexico. Because this race is found in areas that sometimes experience limited rainfall during the summer season, where it is likely to have some natural adaptation to moisture stress, it was decided to use this germplasm as a basis for population improvement for drought.

## Development of suitable selection criteria

The emphasis of this work was on field screening. At Tlaltizapan (Morelos), Mexico, there is no appreciable rainfall from October through April and plantings in November are completely dependent on applied water. The site is at 900-m elevation with mean temperatures of about 28° C maximum and 15° C minimum.

The soil is calcareous Vertisol 1.8-2.0 m deep.

The response of eight maize genotypes (including Tuxpeno) of diverse genetic backgrounds to simulated drought conditions at this site was used to develop relevant selection criteria. Two treatments were used: 1) drought stress began at floral initiation and continued to flowering (to span the critical preflowering-flowering stage), and 2) drought stress began before flowering and continued to grain maturity. These treatments reduced grain yield. Fischer and Wood (1979) defined an index of drought intensity as one minus the ratio of the mean yield under stress to yield under no stress. Using this index, drought intensities were 0.48 for the stress from floral initiation to flowering and 0.47 for the stress from 10 days preflowering to grain maturity.

Although the stress intensity was similar, the yield components affected by the stress differed. In the early stress, grain numbers were reduced by 45% but, because of rewatering after flowering, final grain size was not affected. Stress from 10 days before flowering through maturity reduced grain number by 33% and grain size by 20%.

The response of the genotypes to drought was assessed by a drought index based on yield under both fully irrigated and stressed conditions. (The drought index for a genotype is the ratio of its yield under stress to yield under no stress, relative to the ratio of the mean yield of all genotypes under stress to yield under no stress. A drought index > 1.0 suggests relative drought resistance and an index < 1.0 suggests relative drought susceptibility.) There were differences between genotypes in both yield potential and drought index. Tuxpeno had both the highest yield potential and the highest drought index score. The ranking of genotypes by drought index was independent of plant height and maturity measured under nonstress conditions, suggesting that the observed differences in drought index were not due to escape mechanisms. Yield under no stress correlated with drought index (data not shown).

Leaf water potential and stomatal resistance were measured at various stages of crop development and at different times during the day. There were significant differences between genotypes in leaf water potential measured at 1200 hours the day of flowering (Table 3). However, differences in drought index correlated ($r$ = 0.76*) with maximum leaf water potential measured at 0600 hours but not with minimum water potential taken at 1200 hours (Table 4). There were significant differences between genotypes in stomatal resistance measured at 0900 and 1300 hours at flowering (Table 3). Stomatal resistance, particularly when measured in the middle of the day, negatively correlated with drought index (Table 4).

Leaf water potential and stomatal resistance also were measured during grain filling in the stress treatment from 10 days before flowering to grain maturity. The drought index for this treatment correlated negatively with stomatal resistance ($r$ = -0.72) measured during the middle of the day (Table 4).

The capacity of genotypes to restore maximum water potential during the night (before sunrise) and the ability to maintain open stomata during the day appears to be associated with better performance under a particular stress at this site. While it was suggested that differences in root morphology may explain some of the differential response, no observations of roots were made. Profiles of soil moisture,

**Table3. Drought index based on grain yield in stress and no stress treatments, and leaf water potential and stomatal resistance measured at various times of the day at flowering for 8 maize genotypes subjected to water stress from floral initiation onward. Tlaltizapan, Mexico, 1975.**

| Genotype | Drought index | Leaf water potential (bars) | | Stomatal resistance (s/cm) | |
|---|---|---|---|---|---|
| | | 0600 h | 1200 h | 0900 h | 1300 h |
| Tuxpeño-1 | 1.43 | –2.16 | –14.7 | 5.40 | 3.60 |
| Pioneer 3369 | 1.17 | –2.11 | –14.3 | 7.41 | 4.07 |
| Pepitilla | 1.09 | –2.60 | –16.0 | 7.74 | 5.25 |
| Mezcla amarilla | 0.75 | –3.21 | –14.7 | 8.28 | 4.83 |
| Super enanos | 0.93 | –2.54 | –14.6 | 9.03 | 4.58 |
| Amarillo del Bajio | 0.87 | –2.76 | –14.7 | 8.64 | 4.25 |
| (Mix. I-Col. Gpo. I) –ETO Blanco | 0.90 | –2.95 | –15.3 | 8.34 | 4.57 |
| Early tropical composite | 0.98 | –2.13 | –17.0 | 8.57 | 3.75 |
| LSD (P.05) | – | n.s. | – 1.7 | 2.07 | 0.30 |

**Table 4. Correlation between a drought index based on grain yield under no stress at either floral initiation to flowering or during grain filling, and leaf waterpotential end stomatal resistance measured at various times. Data for 8 genotypes grown at Tlaltizapan, Mexico, 1975.**

| Trait | Time of measurement | | Correlation (r) |
|---|---|---|---|
| Leaf water potential | Flowering | –0600 h | 0.76* |
| | | –1200 h | 0.08 |
| | Grain filling | –0600 h | 0.26 |
| | | –1200 h | –0.22 |
| Stomatal resistance | Flowering | –0900 h | –0.51 |
| | | –1300 h | –0.89* |
| | Grain filling | –1000 h | –0.72* |
| | | –1300 h | –0.52 |

taken every 30 cm to a depth of 180 cm, did not indicate differences in water extraction.

Two morphological traits—the interval between pollen shed and silking under stress (flower delay) and the rate of stem elongation under stress — were measured. Stem elongation was positively correlated ($r = 0.84$) and flower delay negatively correlated ($r = –0.56$) with the drought index. Both traits would appear useful for selection. Subsequent work used a measure of the rate of elongation of a newly exposed leaf rather than that of the stem. Differences in leaf area duration were not measured in this study. However, if the supply of assimilates during grain filling is important to performance under drought (as is suggested by the correlation of drought index and stomatal resistance), then duration of active leaf area may be an important criterion explaining genetic differences.

This initial work resulted in the development of a selection index for use in screening large numbers of segregating families. It is based on grain yield under irrigation and drought, flowering delay, leaf area loss during grain filling, and relative rate of leaf elongation. The correlations of these characters with grain yield under stress and no stress conditions are shown in Table 5.

## Intrapopulation variation

Using these criteria, 85 full-sib families (the progeny from a cross of two known parents) of Tuxpeño population were screened under the same moisture regime. A profile of the soil moisture available at flowering and at maturity in the severe stress treatment was reported elsewhere (CIMMYT 1981). Analysis of yield indicated a significant genotype by stress interaction. However, there was a large increase in the coefficient of variation in the stress treatment.

Experimental varieties based on families selected for yield under irrigation, yield under drought, and the divergent selection for resistance and susceptibility, based on the selection index, were formed and grown under similar moisture regimes.

The grain yields of the experimental varieties under stress and nonstress treatments are shown in Figure 3. The interaction of variety by water stress level was

**Table 5. Coefficients of linear correlations ( *r* ) between grain yield and other characters used to select drought-resistant families in Tuxpeño when grown under no stress and stress conditions. Tlaltizapan, Mexico, 1979.** [a]

| Variable | Grain yield (no stress) | Grain yield (stress) |
|---|---|---|
| Grain yield (stress) | 0.17* | 1.00** |
| Relative leaf elongated rate | 0.06 | –0.39** |
| Interval between anthesis and silking (stress) | 0.04 | –0.36** |
| Leaf tissue death (stress) | –0.15 | –0.48** |
| Leaf canopy temperature at: | | |
| 7 days before flowering | – | –0.56** |
| at flowering | – | –0.73** |
| grain filling | – | –0.65** |
| Total dry matter (no stress) | 0.64** | 0.25 |
| Harvest index (no stress) | 0.07 | –0.01 |

[a] In = 250.

insignificant. However, F values for preplanned comparisons among varieties indicate no significant differences under the no stress (irrigated) treatment but under stress the selection for resistance (based on all criteria) was significantly superior to the selection for yield under irrigation and to the selection for susceptibility.

These studies suggested that 1) there is genetic variation within a tropical maize population for performance under these specific drought situations and 2) the inclusion of plant characters in addition to yield enhances identification of the drought-resistant families.

A recurrent population improvement program based on these findings is now in the fourth cycle of selection. In addition to the characters described, during the last cycle of selection canopy temperature measured with an infrared meter also was used for screening. In the stress treatment, family canopy temperature measured before and at flowering were negatively correlated with their grain yield (*r* = 0.56* and –0.73*, respectively) (Table 5). Leaf extension rate, leaf temperature, and flower delay can be measured before flowering. Combined, they may sufficiently predict most of the variation in yield at maturity. If so, they are particularly important in a breeding program, since an evaluation trial and crossing block can be conducted at the same time. In Mexico, where CIMMYT has access during the summer season to an alternate dry site at Obregon (Sonora), two planting cycles of selection and recombination can be obtained in each year. These characters can be readily measured in CIMMYT's International Progeny Evaluation Trials, enhancing the selection for yield stability.

There has been no attempt in this work to incorporate laboratory screening techniques in the selection process. Since some of the techniques may have merit for selection for specific drought mechanisms and since they are relatively quick and easy, compared to field evaluation, they could be useful in the breeding program for prescreening a larger number of families before field evaluation.

An evaluation after three cycles of recurrent selection for drought resistance in

**Table 6. Effect of selection for various characters in Tuxpeño on yield and barrenness under severe stress conditions. Tlaltizapan, Mexico, 1981.**

| Character | Cycle | Grain yield (t/ha) | Ears (no./100 plants) | Yield change (%/cycle) |
|---|---|---|---|---|
| Reduced height | 6 | 1.16 | 58 | |
| | 12 | 1.34 | 79 | 5.2 |
| | 15 | 1.47 | 84 | 3.2 |
| | 18 | 1.74** | 76 | 6.1 |
| Reduced tassel | 0 | 1.40 | 60 | |
| | 6 | 1.80* | 78 | 4.8 |
| Reduced leaf | 0 | 1.40 | 60 | |
| | 5 | 1.56 | 78 | 2.3 |
| Drought resistance | 0 | 1.30 | 67 | |
| | 3 | 1.60 | 76 | 7.7 |
| | E.V.[a] | 1.76** | 85 | 11.8 |
| CV 23% | | | | |

[a] Experimental variety (4% selection pressure). *Significance by preplanned F-test with original cycle.

Tuxpeño currently is being conducted. In addition, various cycles of selection for morphological traits of reduced height, tassel size, and leaf size are being evaluated. Plantings were arranged so that all genotypes flowered at the same date to reduce effects due to escape. A preliminary analysis of yield under severe stress is shown in Table 6. The F values for preplanned comparisons showed that selection for drought resistance had higher grain yields. The rate of improvement (with 30% family selection pressure) was about 6%/cycle. Most of this yield increase was due to an increase in ears per plant (Table 6).

The mechanisms of drought resistance that may have been altered through selection have not yet been fully analyzed. However, a preliminary examination of the amount of total dry matter at flowering and its distribution to various plant parrs is shown in Table 7. For both the original cycle and the selection experimental variety, there was a 14% reduction in total dry matter due to the stress

**Table 7. Dry matter at flowering of various plant parts of 2 drought-resistant selections of Tuxpeño grown under stress and no stress. Tlaltizapan, Mexico, 1981.**

| Plant part | Yield ($g/m^2$) | | | | | |
|---|---|---|---|---|---|---|
| | Cycle 0 | | | Cycle 3 | | |
| Change (%) | No stress | Stress | Change | (%) | No stress | Stress |
| Stem | 500 | 406 | –18.8 | 460 | 397 | –13.6 |
| Leaf | 300 | 269 | –10.2 | 278 | 247 | –11.2 |
| Tassel | 65 | 64 | –1.0 | 61 | 56 | –17.3* |
| Husk | 60 | 43 | –27.0 | 44 | 50 | +13.6* |
| Ear | 8 | 5 | –37.5 | 6 | 7 | +20.2 |
| Total | 934 | 788 | –15.6 | 850 | 753 | –13.7 |

treatment. However, there were differences in the distribution of dry matter to various plant parts. In the original cycle, tassel weight was similar in the no-stress and stress treatments. In the drought selection, there was a significant reduction in tassel weight due to stress. Husk and ear dry matter were reduced by the stress in the original cycle but increased in weight in the drought selection (Table 7).

The selection for reduced tassel size in Tuxpeño increased yield under stress (Table 6). Selection for reduced plant height also enhanced performance under drought (Table 6). This agrees with the findings for no stress conditions (Johnson and Fischer 1979).

These genotypes selected from the same tropical population (Tuxpeño) now provide useful research materials to investigate the mechanism of drought resistance for this ecological site. This understanding is necessary to extrapolate this experience to other drought areas. Further testing of these materials in other locations also will facilitate understanding drought resistance mechanisms in tropical maize.

## REFERENCES CITED

Acevedo, E., T. C. Hsiao, and D. W. Henderson. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.

Andre, M., D. Massimono, and A. Daguenet. 1978. Daily patterns under the life cycle of a maize crop. 1. Photosynthesis, transpiration, respiration. Physiol. Plant. 43:397-403.

Arboleda-Rivera, F., and W. A. Compton. 1974. Differential response of maize (*Zea mays* L.) to mass selection in diverse selection environments. Theor. Appl. Genet. 44:77-81.

Ashton, T. 1948. Technique for breeding for drought resistance in crops. Comm. Bureaux of Plant Breeding. Tech. Comm. 14. Cambridge, England.

Beadle, C. L., K. R. Stevenson, H. H. Neumann, G. W. Thurtell, and K. W. King. 1973. Diffuse resistance, transpiration, and photosynthesis in single leaves of corn and sorghum in relation to leaf water potential. Can. J. Plant Sci. 53:537-544.

Blum, A. 1979. Genetic improvement of drought resistance in crop plants: a case for sorghum. Pages 429-445 *in* H. Mussell and R. S. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Boyer, J. S. 1970a. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybeans. Plant Physiol. 46:816-820.

Boyer, J. S. 1970b. Leaf elongation and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiol. 46:233-235.

Boyer, J. S., and H. G. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23.

Buren, L. L., J. J. Mock, and I. C. Anderson. 1974. Morphological and physiological traits in maize associated with tolerance to high plant density. Crop Sci. 14:426-429.

Castleberry, R. M., and R. J. Lerette. 1979. Latente, a new type of drought tolerance. In Ann. Corn Sorghum Res. Conf. 35:46-56.

CIMMYT (International Maize and Wheat Improvement Centre). 1974. Results of International Variety Trial 13. El Batan, Mexico.

CIMMYT (International Maize and Wheat Improvement Centre). 1981. CIMMYT report on maize improvement 1978-79. CIMMYT, Mexico.

Daynard, T. B. 1968. Relationships of certain phenotypic characteristics to population-tolerance in corn. Ph D thesis, University of Guelph, Ontario, Canada.

Denmead, O. T., and R. H. Shaw. 1960. The effects of soil moisture stress at different stages of growth on the development and yield of corn. Agron. J. 52:272-274.

Dow, E. W. 1981. Resistance to drought and density stress in Canadian and European maize (*Zea mays* L.) hybrids. MS thesis, University of Guelph, Ontario, Canada.

Downey, L. A. 1971. Water use by maize at three plant densities. Exp. Agric. 7:161-169.

Duvick, A. N. 1977. Genetic rates of gain in hybrid maize yields during the past 40 years. Maydica 22: 187-196.

Eastin, J. D. 1980. Sorghum development and yield. Paper presented at the symposium on Potential Productivity of Field Crops Under Different Environments. International Rice Research Institute, Los Baños, Laguna, Philippines.

Edmeades, G., and K. S. Fischer. 1977. Performance of tropical maize synthetics selected under simulated drought. Agron. Abstr. p. 42.

Finlay, K. W., and G. N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Aut. J. Agric. Res. 14:742-754.

Fischer, K. S., and G. L. Wilson. 1975. Studies of grain production in *sorghum bicolor* (L. Moench). III. The relative importance of assimilate supply, grain growth capacity and transport system. Aust. J. Agric. Res. 26:11-23.

Fischer, K. S., and A. F. E. Palmer. 1980. Yield efficiency in tropical maize. Paper presented at the symposium on Potential Productivity of Field Crops Under Different Environments. International Rice Research Institute, Los Baños, Laguna, Philippines.

Fischer, R. A., and P. C. Wall. 1976. Wheat breeding in Mexico and yield increases. J. Aust. Inst. Agric. Sci. 42:139-148.

Fisher, R. A,, and M. Sanchez. 1979. Drought resistance in spring wheat cultivars. II. Effects on plant water relations. Aust. J. Agric. Res. 30:801-814.

Fischer, R. A., and J. T. Wood. 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. Aust. J. Agric. Res. 30:1001-1020.

Glover, J. 1959. The apparent behaviour of maize and sorghum stomata during and after drought. J. Agric. Sci. (London) 153:412-416.

Hallauer, A. R., and A. F. Troyer. 1972. Prolific corn hybrids and minimizing risk of stress. In Ann. Corn Sorghum Res. Conf. 27:140-157.

Hanson, A. D., C. E. Nelson, and E. H. Everson. 1977. Evaluation of free proline accumulation as an index of drought resistance using two contrasting barley cultivars. Crop Sci. 17:720-726.

Hsiao, T. C., E. Fereres, E. Acevedo, and D. W. Henderson. 1976. Water stress and dynamics of growth and yield of crop plants. Ecol. Stud., Anal. Synthesis 19:281-305.

Hunter, J. W., H. H. Laude, and A. M. Brunson. 1936. A method for studying resistance to drought injury in inbred lines of maize. J. Am. Soc. Agron. 28:690-698.

Hurd, E. A. 1976. Plant breeding for drought resistance. Pages 317-353 *in* T. T. Kozlowski, ed. Water deficits and plant growth. Academic Press, New York.

Iljin, W. S. 1957. Drought resistance in plants and physiological processes. Ann. Rev. Plant Physiol. 8:257-274.

Jackson, K. D., K. J. Reginato, and S. B. Idso. 1977. Wheat canopy temperature; a practical tool for evaluating water requirements. Water Res. 13:651-656.

Jensen, S. D. 1971. Breeding for drought and heat tolerance in corn. *In* Ann. Corn Sorghum Res. Conf. 26:198-208.

Johnson, D. A., and K. H. Asay. 1978. A technique for assessing seedling emergence under drought Stress. Crop Sci. 18:520-522.

Johnson, E. C. 1974. Maize improvement. *In* Proc. World Wide Maize Improvement in the 70's and the role of CIMMYT. CIMMYT, Mexico.

Johnson, E. C. and K. S. Fischer. 1979. Ideas for the improvement of efficiency of maize varieties. Proc. XXV Ann. Meeting of the Central America Cooperative Program for the Improvement of Food Crops (PCCMCA), Tegucigalpa, Honduras.

Johnson. G. R., and K. J. Frey. 1967. Heritabilities of quantitative attributes of oats (Avena sp.) at varying levels of environmental stress. Crop Sci. 7:43-46.

Jones, H. G. 1979. Stomatal behaviour and breeding for drought resistance. Pages 408-427 *in* H. Mussell and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Jones, M. M., and N. C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Plant Physiol. 61:122-126.

Jurgens, S. K., R. K. Johnson, and J. S. Boyer. 1978. Dry matter production and translocation in maize subjected to drought during grain fill. Agron. J. 70:678-682.

Kassam, A. H. 1976. Crops of the West African semi-arid tropics. International Crops Research Institute for the Semi-Arid Tropics. India.

Kassam, A. H., J. Kowal, M. Dagg, and M. N. Harrison. 1975. Maize in West Africa and its potential in Savanna areas. World Crop 27:73-78.

Kilen, T. C., and R. H. Andrew, 1969. Measurement of drought resistance in corn. Agron. J. 61:669-672.

Kretchmer, P. J., D. R. Laing, and S. Zuluaga. 1980. Uso del termometro infraroio para la seleccion por tolerancia a sequia en *Phaseolus vulgars,* L. Proc. XXIII. PCCMCA. Guatemala City, Guatemala.

Larque-Saavedra, A., and R. L. Wain. 1974. Abscisic acid levels in relation to drought tolerance in varieties of *Zea mays* L. Nature 251:716-717.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York.

Ludlow, M. M. 1976. Ecophysiology of $C_4$ grasses. Ecol. Stud. Anal. Synthesis 19:364-386.

McPherson, H. G., and J. S. Boyer. 1977. Regulation of grain yield by photosynthesis in maize subjected to a water deficiency. Agron. J. 69:714-718.

Martin, J. H. 1930. The comparative drought resistance of sorghum and corn. Agron. J. 22:993-1003.

Martin, J. H., J. A. Harris, and I. D. Jones. 1931. Freezing point depression and specific conductivity of sorghum tissue fluids. J. Agr. Res. 42:57-69.

Mosino, A. P., and E. Garcia. 1968. Evaluacion de la sequia intraestival en la Republica Mexicana. C.P.E.N.A. Chapingo, Mexico.

Moss, D. N., J. T. Woolley, and J. F. Stone. 1974. Plant modification formoreefficient water use: The challenge. Agric. Meteorol. 14:311-320.

Mungomery, V. E., R. Shorter, and D. E. Byth. 1974. Genotype x environmental adaptation. I. Pattern analysis - application to soya bean populations. Aust. J. Agric. Res. 25:59-72.

Muñoz, O. A. 1975. Relaciones agua-planta bajo sequia, en varios sinteticos de maiz resistentes a sequia y heladas. Tesis de doctor en Ciencias, Colegio de Postgraduados, ENA. Chapingo, Mexico.

Musick, G. J., M. L. Fairchild, V. L. Ferguson, and M. S. Zuber. 1965. Amethod for measuring root volume in corn (Zea mays L.) Crop Sci. 5:601-602.

Nass, H. G., and M. S. Zuber. 1971. Correlation of corn (*Zea mays* L. ) roots early in development to mature root development. Crop Sci. 11:655-658.

Neumann, H. H., G. W. Thurtell, and K. R. Stevenson. 1974. Leaf water content and potential in corn, sorghum, soybean and sunflower. Can. J. Plant Sci. 54:185-195.

O'Toole, J. C., and T. T. Chang, 1979. Drought resistance in cereals: Rice a case study. Pages 373-405 *in* H. Mussell, and R. C. Staples, eds. Stress physiology in crop plants. Wiley Interscience, New York.

Palacios de la Rosa, G. 1959. Variedades e hibridos de maiz latente y tolerantes a la sequia y a las heladas. Mexico. Agr. 1076:38-39.

Parker, J. 1968. Drought resistance mechanisms. Pages 195-234 *in* T. T. Kozlowski, ed. Water deficits and plant growth. Academic Press, New York.

Parmar, M. T., and R. P. Moore. 1968. Carbowax 6000, mannitol and sodium chloride for stimulating drought conditions in germination studies of corn (*Zea mays* L. ) of strong and weak vigor. Agron. J. 60:1192-195.

Passioura, J. B. 1972. The effects of root geometry on the yield of wheat growing on stored moisture. Aut. J. Agric. Res. 23:745-752.

Pinter, L., L. Kalman, and C. Palfi. 1978. Determination of drought resistance in different genotype hybrids of maize (*Zea mays* L.) by field trials and biochemical test. Maydica 23:121-127.

Poey, F. R., J. E. Grajeda, O. J. Fernandez, and F. Soto. 1977. Effect of detasseling on maize grain yield components. Agron. Abstr. p. 44.

Prine, G. M. 1971. A critical period of ear development in maize. Crop Sci. 11:782-786.

Qualset, C. O. 1979. Breeding for drought resistance in maize. Proc. SAFGRAD/International Institute for Tropical Maize Workshop. Ougadougou, Upper Volta.

Robins, J. S., and L. E. Domingo. 1953. Some effects of severe soil moisture deficits at specific stages in corn. Agron. J. 45:618-621.

Russell, W. A. 1974. Comparative performance for maize hybrids representing different eras of maize breeding. In Ann. Corn Sorghum Res. Conf. 29:91-101.

Sanchez-Diaz, M., M. Moreyard, F. Gonzalez-Fernaldez. 1969. Physiological responses of sorghum and maize (corn) leaves to water stress. I. Transpiration and leaf elongation responses [in Spanish, English summary]. An. Edafol. Agrobiol., Tomo 28.

Sanchez-Diaz, M. F., and P. J. Kramer. 1971. Behaviour of corn and sorghum under water stress and during recovery. Plant Physiol. 48:613-616.

Shaw, R. H. 1977. Climatic requirement. Pages 591-623 *in* G. F. Sprague, ed. Corn and corn improvement. Am. Soc. Agron. 18.

Singh, T. N., D. Aspinall, and L. Paleg. 1972. Proline accumulation and varietal adaptability to drought in barley: A potential metabolic measure of drought resistance. Nature New Biology 236: 188-189.

Spencer, J. T. 1940. A comparative study of a seasonal root development of some inbred lines and hybrids of maize. J. Agric. Res. 61:521-538.

Stout, D. G., and G. M. Simpson. 1978. Drought resistanceof sorghum bicolor. 1. Drought avoidance mechanisms related to leaf water status. Can. J. Plant Sci. 58:211-224.

Sullivan, C. Y., and A. Blum. 1970. Drought and heat tolerance of corn and sorghum. In Ann. Corn Sorghum Res. Conf. 25:55-66.

Tatum, L. A. 1954. Breeding for drought and heat tolerance. *In* Ann. Corn Sorghum Res. Conf. 9:22-28.

Thompson, D. L. 1968. Field evaluation of corn root clumps. Agron. J. 60:170-172.

Tollenaar, M. 1977. Sink-source relationships during reproductive development in maize. A review Maydica 22. 49-75.

Turner, N. C. 1974. Stomatal response to light and water under field conditions. Pages 423-432 *in* R. L. Bieleski, A. R. Ferguson, and M. M. Creswell, eds. Mechanisms of regulation of plant growth. Bull. 12, Royal Society of New Zealand, Wellington.

Turner, N. C., J. E. Begg, and M. L. Tonnet. 1978. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its Influence on the water potential at which stomata close. Aust. J. Plant Physiol. 5:197-208.

Vasal, S. K., A. Ortega, and S. Pandey. 1978. Population improvement and varietal development in CIMMYT's maize program. In Proceedings of 15th annual meeting of Caribbean Food Crops Society.

Walker, S. T. 1980. Decision making by farmers and by the national agricultural research program on the adoption and development of maize varieties in El Salvador. Ph D thesis, Stanford University.

Watts, W. R. 1974. Leaf extension in *Zea mays*. III. Field measurements of leaf extension in response to temperature and leaf water potential. J. Exp. Bot. 25:1085-1096.

Wellhausen, E. J. 1956. Improving American corn with exotic germplasm. In Ann. Corn Sorghum Res. Conf. 11:85-96.

Whiteman, P. C., and G. L. Wilson. 1965. Effects of water stress on the reproductive development of *Sorghum vulgare*. Pers. Univ. Queensl. Pap., Dep. Bot. 4:233-239.

Williams, T. V., R. S. Snell, and J. F. Ellis. 1967. Methods of measuring drought tolerance in corn. Crop Sci. 7:179-181.

Wilson, D. 1975. Leaf growth, stomatal diffusion resistances and photosynthesis during droughting of *Lolium perenne* populations selected for contrasting stomatal length and frequency. Ann. Appl. Biol. 79:67-82.

Wilson, J. H. H., and J. C. S. Allison. 1978. Effects of water stress on the growth of maize (*Zea mays* L.). Rhod. J. Agric. Res. 16:175-192.

Wolf, J. M., G. Levine, G. C. Naderman, and E. Gonzalez E. 1974. Adverse soil-water conditions and corn production in Central Brazil. Page 47 *in* Abstracts of the 66th annual meeting of the American Society of Agronomy, Chicago.

Worrall, W. D., N. H. Scott, A. R. Klatt, and S. Rajaram. 1980. Performance of CIMMYT wheat germplasm in optimum and sub-optimum production environments. Paper presented at International Wheat Conference, Madrid, Spain.

Yoshida, S., and E. de los Reyes. 1976. Leafcuticular resistance of rice varieties. Soil Sci. Plant Nutr. 22:95-98.

# WORKING GROUP REPORTS

During the early part of the symposium, scientists from diverse drought-prone environments all over the world presented papers and research reports. In order to utilize the experience and collective knowledge of all participants, the last part of the symposium was devoted to panel discussions and working group sessions.

The working groups focused on pertinent problems currently constraining efforts to increase drought resistance in rice. The sessions were designed to allow all participants to join the discussions and to fully explore possible solutions before submitting recommendations.

Each working group included plant breeders, plant physiologists, agronomists, and soil scientists.

**Working group I** addressed these questions:

1. Based on current information, is plant breeding an effective means of improving yield in drought-prone rainfed rice areas?
2. What specific breeding techniques and methods presented in the symposium show promise for direct application in breeding increased drought resistance into dryland and wetland rice varieties?
3. What research priorities would improve breeding methods and strategies for incorporating greater drought resistance into rainfed rice varieties?

## Recommendations I

**1.** The development of improved rice varieties has resulted in higher yields, particularly in irrigated rice-growing regions and to a lesser extent in dryland regions. Some examples of rainfed dryland varieties with improved yields and farmer acceptance are N22 and IET1444 (RPCB2B849) in India, OS6 in West Africa, C22 in the Philippines. IR36 and Mashuri are extensively grown in some Asian rainfed wetland rice regions. In many rainfed rice-growing areas, however, improved cultivars have not been well-accepted.

It may be expected that, given more emphasis, breeding will be effective in producing improved varieties for rainfed rice-growing regions. But in evaluating the effectiveness of plant breeding programs, the criteria should not be only improved yield per unit area. Farmer acceptance, the ultimate measure of plant breeding success, depends on such factors as grain quality as well. Also, future breeding objectives for rainfed rice varieties must be evaluated within the totality of the growing system. This includes management and cultural practices, particularly for blast resistance. It is likely that further improvements by breeding for rainfed regions will be slower than for irrigated regions because of the major limitations imposed by water, nitrogen, and weeds.

**2.** To effectively select for improved rice yields in different rainfed systems, locations that are representative of the major rainfed regions must be identified. Priority should be given to regions of more abundant rainfall where improved varieties would be more readily accepted and have the greatest impact. Only when such locations are used will it be possible to carry out effective breeding programs. This should mean the development of new regional centers and/or the upgrading of existing centers for the breeding and testing of yield for the drought-prone regions.

Each center should be responsible for the breeding and development of improved varieties for its region. Breeding activities at these centers should include not only crossing desirable parents and making selections, but also:

a. screening for appropriate drought resistance traits from both rainfed and irrigated rice that may be identified for that region, as well as for other necessary attributes such as disease and pest resistance.
b. evaluating and testing under field conditions as well as optimal conditions of $F_3$ and $F_4$ lines.
c. increasing seed and advanced lines distribution to
    - off-station locations for further evaluation and testing, and
    - other major rice testing centers.
d. collaborating with IRRI and other centers for exchange of populations, lines, and data.
e. interchanging and evaluating of good yielding, drought-resistant lines from other centers and growing international observation and yield nurseries.

For continued improvement of rainfed rice, breeding methods and techniques already practiced by breeders, such as the pedigree method and its various modifications, will continue to be effective. More consideration could be given to:

a. use of backcross breeding methods using currently adapted, locally preferred varieties as the recurrent parent and introducing desirable traits that may be deficient.
b. use of genetic male sterility for the creation of more diverse gene pools.
c. possible modification of phenology to coincide with predictable climatic events, such as the period of maximum water availability.
d. detection or development, or both, of stable yielding varieties responsive to variable, seasonal rainfed environments.

**3.** Improved breeding methodologies and strategies should result from the judicious selection of suitable breeding and testing sites. Other areas for rice improvement include:

a. identification of a target yield level where selection for yield is maximized.
b. cooperation among researchers in many disciplines in tailoring rainfed rice to new cropping systems and management practices.
c. use of wide crosses to increase the available genetic variability and to examine problems associated with such crosses.
d. evaluation of early generation selection and testing of lines for their relation to final

crop yield.

e. study of the genetics of yield positive traits under drought that can be screened effectively. Develop contrasting lines to properly test the specific influence of a trait.
f. evaluation of the use of techniques such as single seed descent and anther culture to hasten generation turnover.
g. evaluation of the use of hybrids in rainfed regions.
h. use of mutation breeding to alter maturity, plant stature, and certain quality traits if adequate variability is unavailable in the current gene pool.
i. improvement of techniques of cell culture and gene transfer and manipulation in rice and related species.

The development of new breeding methodologies and strategies ultimately will depend on cooperative and innovative research efforts.

*Working Group I Participants*

P. B. Escuro (*chairman*)
R. Richards (*reporter*)
S. Yoshida (*co-reporter*)
K. Fischer
K. S. Murty
F. Reyniers
M. A. Hamid
R. B. Austin
D. Chaudhary
U Aung Khin
R. Lasso Guevarra
H. K. Mohanty
Nopporn Supapoj
E. T. Rasco, Jr.
Soetjipto Partohardjono
Tay Chan Yong
S. O. Fagade

**Working Group II** addressed these questions:

1. Given the diverse spectrum of ecological conditions for rainfed rice and the known genotypic variation, what is a realistic estimate of currently attainable yield in various dryland and wetland rainfed rice conditions?
2. How can the role of an individual physiological trait or complex of traits be evaluated in terms of the whole plant or crop response to drought?
3. What physiological components currently show the greatest potential for incorporation into more drought-resistant rainfed rices?
4. What research priorities are important in terms of the physiological bases of drought resistance in rice?

**Recommendations II**

1. The diversity of conditions is great. By drastically oversimplifying, we may assume that in many (perhaps the majority) areas, drought-affected crops still have available water in the soil at depths below 20-50 cm. If the root system of the crop could be changed so that it could collect that water, the effects of drought would be much reduced, perhaps even eliminated. As a gross generalization, we may argue that the attainable yield in drought-prone areas is that which occurs during a good season. If the problems of drought were reduced, farmers might be encouraged to apply more fertilizer to the crops. This might increase the attainable yield further (see table).

| | *Speculative yield increases (t/ha)* | | |
|---|---|---|---|
| | *Current* | *No drought* | *Higher inputs* |
| Dryland | 1.0 | 2 | 3 |
| Wetland | 1.8 | 3 | 4.5 |

2. The step from a physiological or morphological trait to yield is large. In trying to relate

traits to yield, it is helpful to organize along the lines of a yield component analysis:

a) $Y$ = grains/$m^2$ (N) × wt/grain, or

b) $Y$ = water transpired × water-use efficiency (physiological) × harvest index (*HI*), or

c) $Y$ = water used (ET + drainage, etc.) × *WUE* (hydrological) × *HI*.

a. In general, a large $N$ is of paramount importance in producing a high $Y$. Catastrophic environmental effects on $N$ must be avoided. Possible catastrophies are:

- (i) Water stress at flowering, which may result in failure of pollination. Selection for early flowering (i.e. early in the day) may minimize this problem.
- (ii) Sterility due to desiccation of the panicle. This appears to be due largely to a very low epidermal resistance to water loss from the panicle. Selection for waxiness, for thick glumes, or for hairiness may improve matters. Alternately, direct selection for high epidermal resistance using a porometer may be worthwhile.

b. $Y = T \times WUE$ (physiological) $\times HI$

Equations (b) and (c) are used most appropriately in conjunction with simple water-balance models such as those recommended by other working groups.

Improving $T$ would increase yield. The problem is, how? The ability of the root system to extract deep water is critical. There are three requirements: first, deep penetration; second, adequate root density at depth; and third, adequate longitudinal conductance in the main roots. Routine selection for these characters is impossible. But can they be used in selecting parents? Aeroponics gives a coarse estimate of potential rooting depth but is too tricky for use in many areas. Growth of roots in long pots may be useful in selecting parents with a large ratio of deep roots to shoot. The use of the neutron probe in small plots (1 $m^2$) may be tricky in some areas. The tensiometer may be used to determine rooting depth in nonshrinking soils. But generally, methodology is an immense problem and needs a great deal of discussion.

In some areas there may be problems of flood cycles that may damage existing roots, requiring a new batch of roots to colonize the subsoil.

3. While these characters seem strong candidates for improving yield under drought, the rigorous evaluation of their worth requires the production of isogenic lines or populations. Even then, the case may not be proved because of possible complications from pleiotropic effects. It would be a mistake to assume that using such characters in breeding programs must await thorough evaluation. Where there is a strong prima facie case for the worth of a character, it should be included in a breeding-related testing program. In evaluating such characters, it is important to test in environments in which their worth can be expressed.
4. Item (2) considers characters important in drought resistance and immediately usable in breeding. In the longer term, there is a need to study such underlying physiological mechanisms of drought resistance as:
    - (i) osmotic adjustment,
    - (ii) hormonal relationships,
    - (iii) the complex of characters associated with maintenance of tissue viability at low internal plant water status,
    - (iv) the recovery of leaf and root growth after drought relief,
    - (v) the translocation of stem reserves during postflowering drought, which might improve the harvest index, and
    - (vi) the influence of nitrogen status on the physiological efficiency of water use.

Each breeder in his own location may work with only a few adaptive features. Better understanding and appreciation by individual breeders of the total complexity of drought resistance and the dynamics of plant-environment interactions is needed. Physiologists should work closely with breeders in predicting the most useful avenues for further improvement.

*Working Group II Participants*

J. Passioura *(chairman)*
N. Seetharama *(reporter)*
T. T. Chang *(co-reporter)*
P. J. Gregory
T. C. Hsiao
M. Jacquot
K. Goli
A. R. Gomosta
N. I. Hashmi
Chairerg Maneephong
R. C. Chaudhary
G. Kuo
T. Masajo
B. S. Naidu
S. Ono
G. Kamakrishnayya
Suvit Pushpavesa
A. Bueno

**Working Group III** discussed items fundamental both to plant breeding and to agricultural resource management:

1. The role of agronomic practices and environmental modification as complementary research efforts to breeding for drought resistance in rice under diverse hydrological conditions.
2. Research on management of water resources and the physical aspects of water use requires interdisciplinary research teams. How can such teams be organized to study the soil-plant-atmosphere continuum and be encourged to support both genetic improvement and environmental modification to increase yields in rainfed rice?
3. What are the research priorities in water management relevant to rainfed rice environments?

## Recommendations III

This report should be read in the context that items critically necessary for enhanced production of rice under drought conditions are emphasized.

**1.** Rice breeding and production research should be concentrated at locations where soil, climate, and physiography have been adequately classified. If this is not possible, sites should be classified. At a minimum, soil characterization should include:
   a. water content profile at field capacity,
   b. water content profile at end of drought,
   c. visual examination of profile from a soil pit, and
   d. location of the trial on a soil map of the region.

Additional soil determinations are pH, water content versus soil matric potential, bulk density, mineral toxicity symptoms, texture infiltration rate, and nutrient availability.

At a minimum, climate characterization should include the frequency, duration, and intensity of drought during the test period compared to long-term averages for the site. These should be reported with respect to the phenological stages of the test variety or species. The drought characterization must be expressed in terms of the hydrologic balance of the site. This needs a long-term data base, including minimum daily rainfall and pan evaporation rates. Preferably, weather records also should include maximum and minimum temperature, dew point or wet and dry bulb temperatures, solar radiation, sunshine hours and wind speed.

Soil, climate, and physiographic data not previously supplied should be included when any plant performance data are transmitted to other locations of the rice drought network. Soil and crop management research is a parallel effort but often must be location specific. General areas for research in drought-prone environments, in order of priority, are:

   a. moisture conservation. Techniques that should be explored on dryland sites are mulching, weed control, tillage, land preparation, contouring, and water harvesting. All these measures are also pertinent on wetland sites, along with research on puddling and bunding.

b. crop management. Measures to be studied are row spacing, plant population, stand establishment, and timing of crop phenological stages to climatic variances.

c. nutrient management. Nitrogen, phosphorus, zinc, potassium, calcium, and magnesium are the most common nutrient deficiencies, in order of priority. In general, these alter production in drought-prone areas through enhanced leaf area or enhanced root growth. Increased leaf area may be beneficial or detrimental, depending on the hydrologic balance and plant timing.

d. cropping systems. Intercropping and cropping sequences appropriate for the available rice germplasm should be investigated.

e. elemental toxicity. Aluminum toxicity affects the size and activity of the root system, thereby affecting the plant's ability to extract water and nutrients. Although selection of varieties for tolerance for toxic levels of aluminum is the preferred method for evading effects of aluminum toxicity, research on soil amendments to reduce aluminum activity using resistant varieties should be conducted. Iron and manganese toxicity may affect the rate of leaf area development, thus the hydrologic balance.

f. deep subsoil barriers. Compacted soil, bentonite, or asphalt.

**2.** The minimum team for a single country effort is considered to be a plant breeder and an agronomist/soil scientist. The plant breeder would be charged with developing suitable varieties and the agronomist/soil scientist with developing a management package for adapted higher-yielding varieties.

At the International Rice Research Institute, the team should consist of a plant breeder, an agronomist, a soil scientist, a crop physiologist, an agroclimatologist, a plant protection specialist, and a socioeconomist.

The chances for success of this major research center team can be increased if:

- members of the team are located in physical proximity, in the same building;
- members have some research projects in close cooperation with each other;
- each member has a part of the program in which he has the leading role; and
- a team manager has been clearly designated.

To make rapid and significant progress in developing genetic materials and production practices to overcome specific constraints to production in drought-prone areas, there should be a formalized structure to exchange information and plant material between national and IRRI teams. We recommend the establishment of a network on rice production in drought-prone areas. This network would be based on the principles successfully used in the International Rice Testing Program and in the Cropping Systems Network.

*Working Group III Participants*

B. P. Ghildyal (*chairman*)
H. Taylor (*reporter*)
I. Gunawardena (*co-reporter*)
P. L. Steponkus
N. C. Turner
S. K. De Datta
A. M. Fagi
S. Hasegawa
M. A. Choudhury
U O. Kyaw
D. M. Maurya
P. R. Maurya
E. Pacardo
S. A. Risopoulos
D. de Souza
S. Takami
Truong Binh

**Working Group IV** discussed a paramount problem of those attempting to improve drought resistance in crop species:

- As research scientists engaged in crop improvement for drought resistance, how do we assess progress toward that goal? How do we measure our success, or lack of success, in breeding new varieties for this particular environmental stress?

In addition, the group was asked to review the state of the art in rice improvement for drought resistance and to recommend future research to evaluate various theories.

## Recommendations IV

To measure progress in breeding for drought resistance:

1. A breeding program for improving drought-resistant rice cultivars must be directed toward a defined target area.
2. The target area should be characterized primarily by the rice water regime (pluvial, phreatic, or fluxial) and the expected plant water stress periods in terms of frequencies, intensities, and the plant growth stages at which they occur. A description of the range of variability within the target area is required. A second-stage advanced description of the rice water regime environment should be developed by the water balance model (Angus and Zandstra 1980). Additional descriptors, such as soil type, depth, fertility, biological or additional biophysical stress, and the existing level of management technology, are required.
3. Evaluation of progress in plant breeding towards the target area should be performed within the target area.
4. Varietal improvement for drought resistance may be performed according to the breeder's concepts, utilizing various plant physiological responses in field, greenhouse, growth chamber, or laboratory facilities. However, evaluation of progress should be performed in terms of yield and stability of yield performance. Evaluation of stability in yield performance is recommended through the use of the Finlay and Wilkinson (and Eberhart and Russell) regression model. Stability is evaluated by both the coefficient of regression and its standard deviation for each tested genotype. Upon analysis, attempts should be made to determine the extent to which variation in the environmental index was affected by the water regime.
5. Data for yield evaluation would be obtained from a designated array of testing sites within the target area. Sufficient data sets should be obtained for use in the stability analysis, either through the number of test sites or the number of test years. A smaller network of test sites is recommended, with capabilities developed to perform exact collection of data, instead of a larger network of rather empirical and less precise data collection.
6. Possibilities should be explored for developing unorthodox regional testing procedures to reveal plant performance reactions to drought stress. Such procedures might include setting up line source sprinkler irrigation gradients or topographical (hydrological) gradients at testing sites.
7. Evaluation of breeding materials at each test site should use proper controls (check cultivars).
8. Common routine environmental and management data for each test site should be obtained. Additional data considered most important include:
   a. Yield components for each entry.
   b. One set of yield performance data under potential high yield conditions.
   c. Seasonal water regime in terms of precipitation and ground water levels. Efforts should be made to develop a means for describing the crop water balance at each test.
   d. Drought stress occurrences as they occur should be described by standardized visual scores of leaf rolling and firing in each entry.
   e. Confounding environmental and management factors that may have depressed yield should be described (e.g. unwarranted changes in management or nutrient deficiencies).

9. Some specific drought resistance attributes that do not require yield testing may be evaluated by the proper standardized testing procedures (e.g. seedling tolerance for desiccation and tolerance for panicle blasting due to water stress at flowering).
10. The final assessment of progress in breeding for resistance to drought stress should be judged by farmer acceptance.

    Drought-resistant cultivars may be developed and released with restrictions upon their areas of adaptation or recommended environments. Such cultivars may be relatively deficient in terms of yield performance under optimum environmental conditions.

## Proposed research

1. Develop a water balance model for use in describing target areas and individual test sites within a target area.
2. Develop a novel, unorthodox approach and design for regional testing in the context of genetic adaptation to drought-prone environments (e.g. line source sprinkler irrigation gradients at various sites). Consideration should be given to the most suitable test sites in this context, even if an occasional test may occur in a nonrice growing region.
3. Attempt to assess the environmentally determined yield ceiling for each target area.

*Working Group IV Participants*

A. Blum *(chairman)*
H. Nix *(reporter)*
D. V. Seshu *(co-reporter)*
D. J. Greenland
F. Bidinger
A. O. Abifarin
W. R. Coffman
A. Fukui
D. Garrity
Chaluay Boonwite
L. Hernandez Aragon
D. G. Kanter
F. Marquez
B. da Silveira Pinheiro
S. C. Prasad
D. del Rosario
V. S. Tomar
Kaung Zan
I. Domingo

# CLOSING REMARKS

About 140 million hectares of rice are planted each year, but only 19 million (14%) are dryland — 11 million hectares in Asia, 5.5 million in Latin America, and 2.5 million in Africa. All dryland rice areas are subject to drought, which is likely to occur at any stage of crop growth. In the less favored areas in which dryland rice is produced, drought is likely to be more severe — intensified in its effects because of shallow soil depth and such factors as aluminum toxicity, iron deficiency, and blast incidence. In the more favored areas, drought is likely to be less severe — a lack of rain can be ameliorated by large reserves of water, either stored in the soil or available from a water table near the surface.

In the great estuarine areas of Asia, 52 million hectares of alluvial soils are mostly dry-seeded prior to the start of the monsoon rains. If the rains start late, early drought may severely retard or damage the crop. As the rains develop, the rice land is flooded to a greater or lesser depth. The floodwaters usually support the crop to maturity.

The estuarine areas support more than 500 million people. An additional 50-60 million live in the dryland rice areas. For both groups, drought is always a major threat. In the shallow flooded areas (about 55 million hectares), an early finish to the rains may mean drought at flowering time — a real disaster, similar to the one that occurred in 1979 in South Asia. Eastern India, Bangladesh, Burma, and Thailand were all severely affected.

By growing shorter-duration varieties such as IR36 and by hastening turnaround time, two crops can often be obtained in areas where only one was produced before. The possibilities of drought when the first crop is sown and when the second crop is harvested are inevitably increased.

Thus the drought resistance components — escape, avoidance, and recovery — are needed, not only for varieties grown in the dryland rice areas but also for those grown in the extensive shallow or intermediate flooded rainfed areas of South and Southeast Asia.

I hope our discussions this week have helped to dispel some ideas expressed at the start of the meeting — that drought resistance is a mirage. Maybe it is still a vision, but it is a vision for which to strive, and which we may expect to realize.

I have spoken of rice as our principal focus. But drought resistance also is important for other crops. As more attention already has been given to these crops, our expectation was that it would be valuable to bring together researchers with experience in breeding and selecting for drought-resistant varieties of wheat, sorghum, maize, and millet to share their knowledge. We have learned from all of you who have come to IRRI this week and we appreciate the time you gave to share your experiences and wisdom and to work with us in helping develop our program directions. We hope that you have benefited, too.

The results of the meeting are contained in the reports of the working groups. I will not attempt to summarize them. However, I will echo the comment made earlier by Ken Fischer: “The breeders are right again, even if for the wrong reasons.” While we are accumulating a great deal of information on the physiological basis of drought resistance, we have yet to sufficiently link these characteristics to yield. The breeder, selecting for yield and an array of other characteristics, is making progress, if slowly, without too much attention to specific drought resistance characteristics. As R. A. Richards stressed, not a single variety based on an analytical approach to drought resistance has been released.

In practical terms, we need experiments to determine the amount of grain produced per unit of water used and to examine how this differs between varieties. Experiments need to be done in a range of climatic, hydrologic, and soil conditions. Collecting the necessary information will require collaborative work between organizations if a sufficiently broad spectrum of environments is to be examined.

As we move forward, we need to define our environments more specifically in order to recognize the plant physiological traits relevant to those environments. It will be important for breeders to be supported and assisted by physiologists as well as by different types of environmental scientists.

But we should not worry too much if the partnership between breeder and physiologist is rather casual. Short-term advances will come from each breeder’s conceptions. The long-term payoffs — 10 years from now — will come if each breeder pays attention to what physiologists offer and uses that, too.

D. J. Greenland
Deputy director general

# PARTICIPANTS

**A. O. Abifarin**
West Africa Rice Development Association
(WARDA)
P. O. Box 1019, Monrovia, Liberia

**R. B. Austin**
Plant Breeding Institute
Maris Lane, Trumpington,
Cambridge CB2 2LQ, England

**F. Bidinger**
International Crops Research Institute for the
Semi-Arid Tropics (ICRISAT)
1–11-256 Begumpet
Hyderabad-500016, A. P., India

**Truong Binh**
Institut de Recherches Agronomiques
Tropicales et des Cultures Vivrieres (IRAT).
B. P. 635, Bouaké, Ivory Coast

**A. Blum**
Agricultural Research Organization
The Volcani Center
P. O. B. 6
Bet Dagan, Israel

**A. Bueno**
Bureau of Plant Industry.
Maligaya Rice Research &
Training Center (MRRTC),
Muñoz, Nueva Ecija, Philippines

**Chaluay Boonwite**
Klong Luang Rice Experiment Station,
Rice Division Dept. of Agriculture, Bangkhen,
Bangkok-9, Thailand

**Chairerg Maneephong**
Dept. of Agronomy
Kasetsart University, Bangkhen,
Bangkok-9, Thailand

**D. Chaudhary**
Central Rice Research Institute (CRRI),
Cuttack 6, Orissa. India

**R. C. Chaudhary**
Rajendra Agricultural University,
Agricultural Research Institute
Mithapur, Pantnagar 800001, India

**M. A. Choudhury**
West Africa Rice Development Association
(WARDA),
P. O. Box 1019, Monrovia, Liberia

**W. R. Coffman**
Dept. of Plant Breeding. Cornell University
Ithaca, Sew York 14853, USA

**I. Domingo**
La Granja Experiment Station,
La Carlota City, Philippines

**P. B. Escuro**
IRRI-Burma Cooperative Project,
P. O. Box 1369 Rangoon, Burma

**K. Fischer**
Centro Internacional de Mejoramiento de
Maiz y Trigo (CIMMYT),
Londres 40 Apdo, Postal 6-641, Mexico 6,
D. F. Mexico

**H. Fukui**
The Center lor Southeast Asian Studies,
Kyoto University
46 Shimoadachi, Yoshida Sakyo-ku,
Kyoto, Japan

**D. P. Garrity**
International Rice Research Institute,
P. O. Box 933, Manila, Philippines

**B. P. Ghildyal**
Dept. of Soil Science
G. B. Pant University of Agriculture and
Technology, Pantnagar Dist., Nainital, U. P.,
India

**A. R. Gomosta**
Bangladesh Rice Research Institute (BRRI),
G. P. O. Box M. Ramna, Dacca-2,
Bangladesh

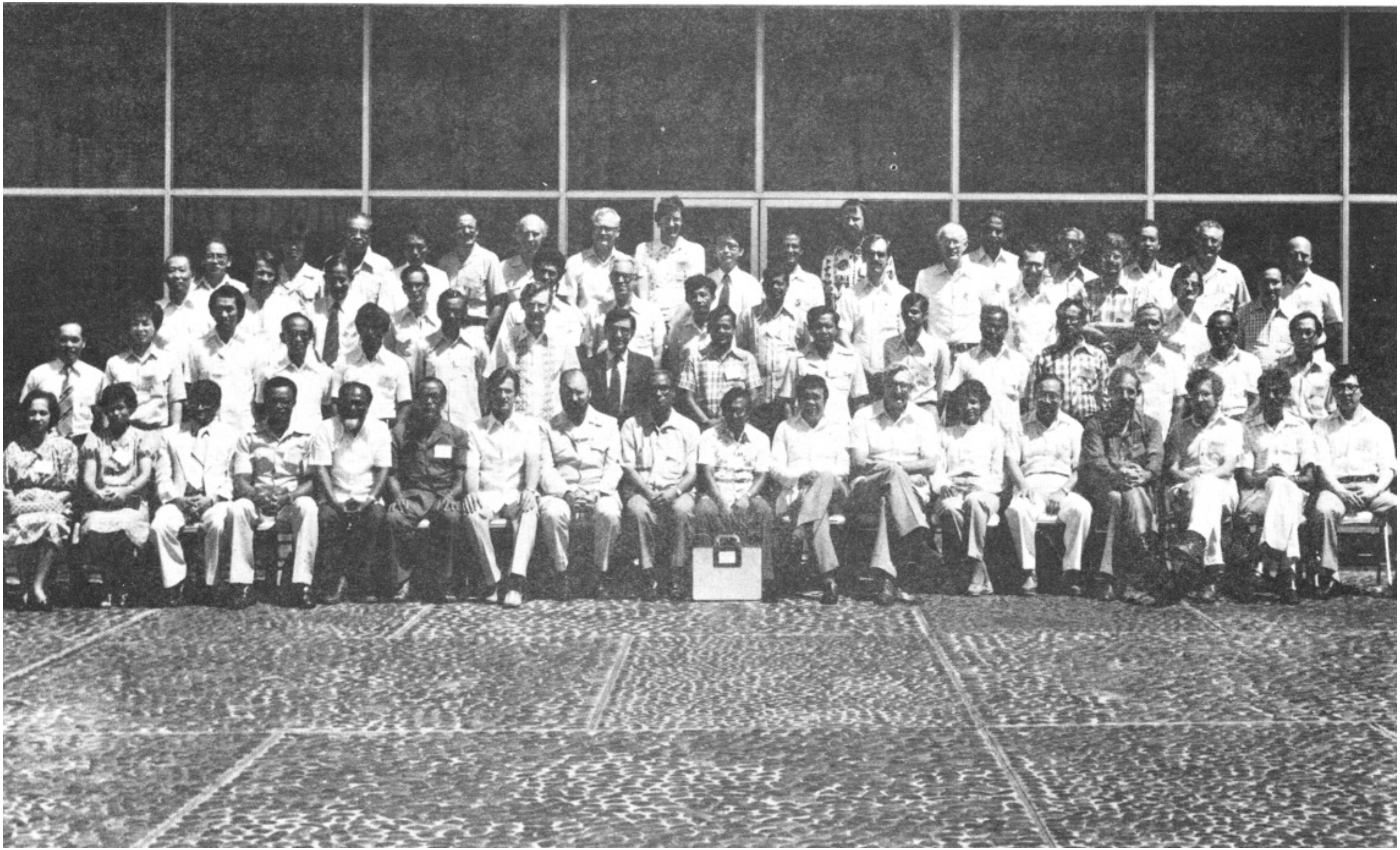
**P. J. Gregory**
Dept. of Soil Science. University of Reading,
London Road. Reading RG1 5AQ, U. K.

**I. Gunawardena**
Central Agricultural Res. Institute,
Gannoruwa, Peradeniya, Sri Lanka

**M. A. Hamid**
Breeding Division, BRRI
G. P. O. Box 911, Dacca, Bangladesh

**S. Hasegawa**
National Research Institute of
Agricultural Engineering
1-2 Kannondai 2-chome, Yatabe-machi,
Tsukuba-gun Ibaraki-ken, Japan

**N. I. Hashmi**
Pakistan Agricultural Research Council,
L-13. Almarkaz. F-7. P. B. 1031, Islamabad,
Pakistan



**T. C. Hsiao**
Dept. of Land, Air, and Water Resources,
University of California,
Davis, California 95616, USA

**M. Jacquot**
Institut de Recherches Agronomiques
Tropicales et des Cultures Vivrikres (IRAT),
110, Rue de I'Universite,
75340 Paris Cedex 07, France

**U Aung Khin**
Agrl. Research Inst.,
Gyogon, Insein, Rangoon, Burma

**G. Kuo**
The Asian Vegetable Research and
Development Center, P. O. Box 42, Shanhua,
Tainan 741, Taiwan. China

**U Ohn Kyaw**
Agricultural Research Institute, Rice Division,
Yezin, Pyinmana, Burma

**Rolando Lasso Guevarra**
Instituto de Investigacion
Agropecuaria de Panama (IDIAP), Apdo. 58,
Santiago de Veraguas, Panama

**Fernando Marquez**
Graduate School, Colegio Superior de
Agricultura. Apdo, Postal 24
Cardenas, Tabasco, Mexico

**T. M. Masajo**
Dept. of Agronomy, UPLB
Philippines

**D. M. Maurya**
Dept. of Genetics & Plant Breeding,
Narendra Dev University of Agriculture &
Technology, Faizabad-224001, Uttar Pradesh,
India

**P. R. Maurya**
Institute for Agricultural Research,
Ahmadu Bello University, Zaria, Nigeria

**H. K. Mohanty**
Orissa University of Agriculture &
Technology, Bhubaneswar,
Orissa, India

**K. S. Murty**
Central Rice Research Institute,
Cuttack4 Orissa, India

**B. S. Naidu**
Reg. Rice Res. Stn., VC Farm,
Mandya, Karnataka, India

**H. Nix**
CSIRO Div. of Plant Industry, P. O. Box
1600, Canberra City, A. C. T. 2601, Australia

**Nopporn Supapoj**
Rice Division, Dept. of Agriculture,
Bangkhen, Bangkok-9, Thailand

**S. Ono**
Chugoku National Agricultural Exp. Station,
Fukuyama-shi, Hiroshima-ken,
721 MZ, Japan

**E. Pacardo**
Dept. of Botany, UPLB
Philippines

**J. Passioura**
CSIRO Div. of Plant Industry,
P. O. Box 1600, Canberra City, A. C. T. 2601,
Australia

**S. C. Prasad**
Agricultural Res. Inst.,
Kanke, Ranchi 834006, Bihar, India

**E. T. Rasco, Jr.**
Institute of Plant Breeding
Los Baños, Philippines

**G. Ramakrishnayya**
Central Rice Research Institute,
Cuttack 6, Orissa, India

F. N. Reyniers
Institut de Recherches Agronomiques
Tropicales et des Cultures Vivrieres (IRAT).
B. P. 635, Bouake, Ivory Coast

**R. Richards**
CSIRO Div. of Plant Industry,
P. O. Box 1600, Canberra City,
A. C. T. 2601, Australia

**S. A. Risopoulos**
Consultative Group on
International Agricultural Research,
Technical Advisory Committee,
c/o FAO, Via delle Terme di Caracalla, 00100
Rome, Italy

**Dafrosa del Rosario**
institute of Plant Breeding
Los Baños, Philippines

**N. Seetharama**
International Crops Research
Institute for the Semi-Arid Tropics
(ICRISAT), 1–11-256 Begumpet,
Hyderabad-500016, A. P., India

**Soetjipto Partohardjono**
Central Research Institute for Agriculture
(CRIA), JL. Merdeka 99, Bogor, Indonesia

**D. De Souza**
Instituto Agronomico, Caixa Postal 28,
Campinas-Est So Paulo, Brazil

**P. L. Steponkus**
Dept. of Agronomy, New York
State College of Agriculture at
Cornell University, Bradfield and Emerson
Halls, Ithaca, New York 14853, USA

**Suvit Pushpvesa**
Rice Division, Dept. of Agriculture,
Bangkok, Thailand

**S. Takami**
Kyoto University, College of
Agriculture, Kitashirakawa,
Sakyo-ku, Kyoto, 606 Japan

**I. Tanabe**
The Asian Vegetable Research and
Development Center, P. O. Box 42,
Shanhua, Tainan 741, Taiwan, China

**Tay Chan Yong**
Malaysian Agricultural Research and
Development Institute
(MARDI), Bag Berkunci #202,
Pejabat Post Universiti
Pertanian, Serdang, Selangor,
Malaysia

**H. Taylor**
Iowa State University,
Department of Agronomy,
Ames, Iowa 50011, USA

**V. S. Tomar**
Dept. of Soil Science, G. B. Pant
University of Agriculture &
Technology. Pantnagar Dist.,
Nainital, U.P., India

**N. C. Turner**
CSIRO Div. of Plant Industry,
P. O. Box 1600, Canberra City,
A. C. T. 2601, Australia

**Kaung Zan**
International Institute of
Tropical Agriculture, Oyo Road, PMB 5320,
lbadan, Sigeria

***IRRI Staff***
N. C. Brady
T. T. Chang
S. K. De Datta
D. J. Greenland
J. C. O'Toole
D. V. Seshu
S. Yoshida