Physiology of Stress Tolerance in Rice

Proceedings of the International Conference on Stress Physiology of Rice
28 Feb - 5 March 1994, Lucknow, U.P., India

1996
NDUAT, IRRI

The International Rice Research Institute (IRRI) was established in 1960 by the Ford and Rockefeller Foundations with the help and approval of the Government of the Philippines. Today IRRI is one of the 16 nonprofit international research centres supported by the Consultative Group on International Agricultural Research (CGIAR). The CGIAR is sponsored by the Food and Agriculture Organization of the United Nations (FAO), the International Bank of Reconstruction and Development (World Bank), and the United Nations Development Programme (UNDP). Its membership comprises donor countries, international and regional organizations, and private foundations.

IRRI receives support, through the CGIAR, from a number of donors including FAO, UNDP, World Bank, European Union, Asian Development Bank, Rockefeller Foundation, Ford Foundation, Common Fund and Commodities, Sasakawa Foundation, and the international aid agencies of the following governments : Australia, Belgium, Canada, Colombia, Côte d' Ivoire, People's Republic of China, Denmark, Egypt, Finland, France, Germany, India, Indonesia, Islamic Republic of Iran, Italy, Japan, Republic of Korea, The Netherlands, Norway, Philippines, the Russian Federation, Spain, Sweden, Switzerland, United Kingdom and United States.

Los Banos, Philippines
Mailing address : P.O. Box 933, Manila 1099, Philippines
Phone : (63-2) 818-1926,812-7686
Fax : (63-2) 891-1292
Email : Postmaster @ IRRI.CGNET.COM
Telex : (ITT) 40890 Rice PM; (CWI) 14519 IRILB PS;
(RCA) 22456 IRI PH; (CWI) 14861 IRI PS

Suggested Citation :

Singh, V.P. et al. (eds) 1996. Physiology of Stress Tolerance in Rice : Proceedings of the International Conference on Stress Physiology of Rice, 28 Feb - 5 March 1994, Lucknow, U.P., India, 239 p.

ISBN No. 81-86789-00-6

CONTENTS

FOREWORD

The needs of the rainfed lowland rice ecosystem in Southeast Asia are enormous. The hundreds of millions of the worlds poorest people living in this region depend upon the almost 40 million hectares of rainfed lowland rice. The extent of the area combined with a difficult, heterogeneous, and variable environment demands that a new research approach be adopted. The Rainfed Lowland Rice Research Consortium was established in 1991 to provide a framework within which national and international institutes could bring their resources to bear on this important, though difficult environment. National programs from Bangladesh, India, Indonesia, the Philippines, and Thailand joined with IRRI, and supported by the Asian Development Bank, to develop a coordinated research strategy and program directed towards improving the sustainable productivity of this environment.

This conference on stress physiology represents several important steps in the growth of the Consortium. First, it is directed towards assessing the status of strategic understanding of two of the most critical constraints in the ecosystem: drought and submergence. Research investment has been increasing in these areas, yet there are few fora in which scientists can exchange views and findings while focussing on this ecosystem. A systematic compilation of the present status is essential to careful planning of future steps.

Second, scientists from Consortium member countries were able to interact with scientists from advanced research laboratories from Europe, North America and Australia and begin to plan joint "North-South" research and collaboration. Scientists from other countries with important rainfed lowland production areas were able to attend, even though their institutional strengths do not yet permit full Consortium research responsibilities. It is expected that the contacts made at this and other similar conferences will stimulate "South-South" collaboration.

Third, lively and vigorous discussions were carried on throughout the event; both in plenary sessions and in the corridors. The active participation of members from all the countries and institutions represented indicated that the spirit of scientific research has permeated the culture of the Consortium. This collegial spirit is essential if true partnership is to guide research in this complex ecosystem.

Finally, the event was hosted by one of the member institutes, Narendra Dev University of Agriculture and Technology, with support from the Indian Council of Agricultural Research, and the Uttar Pradesh Council of Agricultural Research.

This marks an important step in assuming the full range of responsibilities that come with Consortium membership. It is fitting that this event took place in the midst of such an important rainfed lowland rice growing area. That the opening was graced with the attendance of the Governor of the State of Uttar Pradesh is an indication of the importance that local governments place on improving their agricultural productivity. Indeed, if Uttar Pradesh were a separate country, it would be the 7th most populous nation in the world.

I congratulate the participants and the organizers for realizing this event. These proceedings will serve as a valuable reference for scientists working in this dynamic field. It is especially significant that, through the Consortium, this product will be readily available to scientists working in developing countries where access to the latest physiological literature is severely limited. The host country and the host institution have made this event a very memorable one. The scientific competence and a specially warm hospitality has impressed each and every participant. I am pleased that IRRI working with Consortium members has had the opportunity to contribute to this important event. I sincerely hope that there will be many more in this tradition in the future, and that IRRI's role will continue to evolve towards that of an equal participant among colleagues sharing a common goal.

Klaus J. Lampe
Director General, IRRI
12 September, 1994

ACKNOWLEDGEMENT

Several scientists and organisations made valuable contributions to this book, which without their help would not have been possible. Special acknowledgements go to the contributing scientists who embellished it with their precious time, experience and ability. The organisations which supported the scientists while they worked on this project merit myriad commendations and thanks. Valuable suggestions given by various reviewers are thankfully acknowkedged. In this context, the name of Dr. G.C. Srivastava, Principal Scientist, Division of Plant Physiology, Indian Agricultural Research Institute, New Delhi deserves special mention.

The editors are specially indebted to Dr. P.C. Ram, Dr. G.S. Chaturvedi, Dr. R.P.S. Chauhan and Dr. A.K. Singh of N.D. University of Agriculture and Technology (NDUAT) for their assistance in editing the papers. We are thankful to Dr. Maharaj Singh, Mr. H.P. Singh and Mr. S.P. Singh of the Department of Crop Physiology, NDUAT, for proof reading the manuscript.

Several people in the Computer cell of the NDUAT, have contributed much through their secretarial, technical and artistic talents. The editors fully appreciate their contributions which resulted in improving the book considerably.

Editors

INTRODUCTION

The rainfed lowland rice ecosystem covers half the rice growing area in the humid and subhumid tropics of Southeast Asia. Including the contiguous flood-prone areas, almost 50 million hectares are sown to rainfed lowland rice. The system is characterized by environmental heterogeneity and variability, with frequent droughts and floods damaging the rice crops. Modern rice technology has barely contributed to rice production and, consequently, yields remain low, in many areas less than 2 tons per hectare. None the less, this ecosystem provides the staple food for hundreds of millions of the worlds poorest urban and rural dwellers. But, as populations and economies continue to grow, increasing pressure is placed upon the rainfed lowlands to help meet the estimated 70% increase in rice demand projected over the next 30 years. This pressure is even more acute as investment in irrigation declines, and water and land are diverted from irrigated rice agriculture to urban and industrial uses.

Research is required to increase the productivity of this vast ecosystem, and this increase must be sustainable. That is, the sometimes conflicting demands of social and economic development must be reconciled with husbandry of our social and natural resources. Developing technologies that permit such productivity gains while preserving or enhancing the resource base will demand a fundamental understanding of the processes that detrermine plant adaptation to the environment, the dynamics of water and nutrient flow through the system, and the interaction of management practices designed to maximize efficiencies with the biotic, social, and economic environment.

The distribution and enormity of the rainfed lowland ecosystem combined with the complexity of the environment and the difficulties of the production constraint required that a new research approach be adopted. In 1991 the Rainfed Lowland Rice Research Consortium was formed. It is a formal linkage among institutions in five countries (Bangladesh, India, Indonesia, Philippines and Thailand) and the International Rice Research Institute. The member institutions agreed upon a research strategy specific to achieving sustainable productivity increases in the ecosystem, and apportioned responsibilities according to comparative advantages and available infrastructure and personnel. The Rainfed Lowland Rice Research Consortium certainly represents a paradigm shift from a target of uniformly favourable environments addressed from a centralized research effort, to a decentralized effort involving many institutions at all stages of research and targeting more difficult environments. In effect it provides a mechanism to move the needed strategic research from experimental centers located in irrigated environments to centres and farmers' fields situated within relevant environments. Although most of the resources dedicated to this research efforts are from IRRI and the participating national systems, supplemental research support has been provided by the Asian Development Bank in the form of a Technical Assistance grant.

The overall research strategy adopted for the rainfed lowlands is based on the development of adapted germplasm that can tolerate the prevalent stresses. With such tolerance it is then possible to develop responsive cultivars that, under higher nutrient status, can produce higher yields. This in turn opens a range of alternatives for farmers to diversify and intensify their production systems. While developing stress tolerant cultivars is not sufficient in itself to reach our goal of sustainable productivity increases in the rainfed lowlands, it is an essential component in the strategy.

Recognizing the importance of understanding the processes that determine adaptation and stress tolerance, the Consortium sponsored this conference to establish the "state of the art" in the physiology of stress tolerance in rice as it relates to drought and submergence. 75 scientists from 11 countries were invited to Eastern India, an area where both stresses are found and where a major research effort is underway within the Consortium. Participants were asked to present their best assessment of what is now known regarding drought and submergence tolerance, and plot a course for future research. We also asked that they assemble for informal brainstorming sessions to help the Consortium plot its future directions. By bringing scientists from advanced research centres in Europe, North America and Australia, it was hoped that collaborative projects meeting the needs of the Consortium and of the research laboratories could be developed. Finally, we included an assessment of the social environment in which farmers work and live. It is essential that process-oriented research be anchored within the social context for its output to be developed into relevant applications.

It is impossible to summarize here all the discussions and views that emerged. Since many points are very thoroughly covered in the papers, we will only touch on particularly strategic issues that were raised. Perhaps the most persistent theme that emerged from the discussions was the need to better understand the target environments in which we are working. Without suitable descriptions it is impossible to interpret experimental results and generalize or extrapolate from even the most strictly controlled studies. At the very least standard environmental descriptive data must be collected for every experiment to allow comparison of results among sites. The very nature of the stresses encountered and the environmental factors that contribute to severity and modify plant response are still poorly understood (e.g., interaction of water and nutrients in water- deficit conditions, and the interaction of turbidity, cloud cover and water temperature under submerged conditions). More complete descriptions and quantification of environmental variability are needed in oder to better understand how very different physiological processes may be confounded into similar phenotypic responses. The probabilities of stresses of given severity should be determined in order to develop extrapolation domains of tolerances at given levels. "Probe genotypes" should be selected that will aid in quantifying differences due to environment and genotype by environment interaction using replicated trials.

Research in a consortium mode, with a number of teams spread throughout a vast geographical region and working within diverse institutional environments can allow a proliferation of research activities that lose focus. Thus, experimentation should be restricted to a relatively small number of key experiments that are tightly linked to the principal themes being addressed by the Consortium. The development of multi-site experiments on key problems will be a major contribution both to environmental characterization and to understanding environment by physiology interactions. Concentrating on a set of such experiments will help us retain focus and will contribute to the development of a team approach to these difficult problems.

Standardization of methodologies will be a direct result of developing cross-site research . Current research output suffers greatly from the difficulty of directly comparing outputs from different sites. In order to establish a common working mode across the environments and across continents an effort will have to be made in training scientists in standard methodologies. Agreement should be reached on what particular measurements must be taken, and how. Clearly minimum data sets for particular kinds of experiments must be developed. These will include key weather/climate and soil/hydrology parameters. These agreed standards will contribute to our efficiency and, of course, will be more cost-effective. The development of this team approach is a direct consequence of the Consortium approach, and is an indication that the attempt to join forces can promote the integration of sound science at higher levels.

The rainfed lowlands still lack a clear articulation of "ideotypes" for target environments. This may simply reflect the previously stated need to clearly articulate our target environments. The ideotypes should incorporate adaptation to various timings and severity of stress, as well as major crop establishment alternatives. It is very likely that large rainfed lowland areas will convert to dry direct seeding, and that this will have a significant impact on tolerance to and management of early season drought. What plant types are most appropriate for this system, and where?

Finally, there was a very strong expression of need for greater links with social sciences and a need to incorporate a social science perspective in strategic stress tolerance research. It was felt that early in the research process our efficiency could be increased by understanding how social constraints contribute to technology adoption, or lack of adoption. Risk reduction is certainly a driving force for improving stress tolerance, but how is it perceived, measured, and managed by farmers today?. The central role of women in the management of rainfed lowland rice system is often ignored, with potentially serious consequences. The very low representation of social scientists in consortium teams and the relative lack of social issues within the research agenda were seen to be weaknesses of the present structure and approach.

There is little doubt that research into the physiology of stress tolerance can make a major contribution to improving sustainable productivity of rainfed lowland environments. However, with the finite resources available to us it is essential to sharply focus our efforts and take full advantage of the human resources available to us. Fragmentation of effort and a diffuse approach along more academic lines will simply delay our progress and frustrate our efforts. This conference has been an important step in developing the team approach and, if followed up by appropriate planning and training, should lead to rapid progress over the coming years.

Editors

IMPROVING CEREALS FOR THE VARIABLE RAINFED SYSTEM : FROM UNDERSTANDING TO MANIPULATION

☐ *K S. Fischer*[1]

SUMMARY

Inspite of the vast information on response to water deficits at the crop, and molecular level, there are few examples of designed change in crop performance through genetic improvement. This paper suggests that the lack of this knowledge is partly due to lack of research priority focus and organization of interdisciplinary teams. The case is made for a sequence of research activities broadly grouped under :

1) measurement of the resource and of the crop response in the components of resource capture (transpiration), resource use (water-use efficiency) and resource allocation (harvest index) to define targets for better focus; 2) study of mechanisms to identify putative traits and develop an "internal consistency" in the relationship between the traits and field performance; 3) design models at geographic, crop, genotype (ideotype), and gene level to both priority research opportunities and to enhance the efficiency of the improvement process; and 4) develop methods to incorporate selection for adaptation to moisture deficit in routine plant breeding programs.

This framework, to move from understanding to manipulation, is based on a case study for the improvement of tropical maize (*Zea mays* L.) to moisture deficits. In tropical maize, intermittent periods of moisture stress are estimated to cause yield losses of 15% in more than 32 million ha. Maize is particularly vulnerable around flowering, causing a loss in grain number and through harvest index, grain yield. Based on this understanding of the mechanism for adaptation of maize to drought, a "drought plant ideotype" was developed. Eight cycles of recurrent selections for the ideotype resulted in a gain of 500-800 kg/ha over a range of water-limited environments. Yield gains were associated with increased ear growth rate around flowering and harvest index at maturity (resource allocation).

INTRODUCTION

This paper does not review the wealth of information on rice adaptation to variable and moisture-limiting environments. Instead it provides a conceptual framework that will allow understanding of the physiology of adaptation to be used effectively to manipulate the crop and the environment for enhanced productivity.

---

[1] The International Rice Resarch Institute, P.O. Box 933, Manila, Philippines.

From the plant perspective, the crop in the field is a community of genetically, fairly uniform plants representing the "genotype". During a growing season the particular combination of soil, climate, and pests, plus the competition among crop plants and other species (weeds) forms a unique environment, which when interacting with the "genotype", leads to the expression of the phenotype, and ultimately yield.

Much of our success in improving rice productivity was the result of enhancing and stabilizing the environment, particularly for water (irrigation) and nutrients (fertilizer) and at the same time increasing the genotype's ability to respond to this change in the environment with increased yield. There was an additional benefit. Irrigation and nutrients reduced the number of unique environments determined mainly by temperature ranges" and the occurrence of pests. Fewer unique environments required fewer unique genotypes to maximize the phenotypic expression. We were able to develop rice cultivars adapted over a broad geographic range and responsive to a given and predictable environment.

In contrast, the rainfed lowlands have a range of environments whose diversity is driven by variability in, for example, the amount, intensity, and duration of water. Each of the key environmental variables, eg., moisture regime, fertility, flooding incidence, biota, daylength is complex in itself and interacts with the others and with the rice plant. The resultant phenotype-the expression of the genotype in these variable environments-is by way of the metabolic processes of the plant, i.e., its physiology. Given the environmental complexity, there are practically an infinite number of expressions of phenotype. Thus, to advance crop production in these environments through directed improvements in phenotype, those growth processes that are interacting, rather than the myriad of interaction themselves must be understood. That is, understanding leading to the rice phenotype is one means to reduce enormous complexity to a manageable level.

Wilson (1992) contends that formal treatment of physiology gave information as to how the crop grows, but little on how it might be manipulated genetically to achieve particular results. This paper examines some case studies in other cereals (but mainly maize) where such manipulations have occurred. Passioura (1981) contends that breeding — the changing of a genotype-is a practical affair with its successes and failures being judged by the farmer clients. In contrast, the success of physiology — understanding the growth processes of the plant-depends on how enlightening it is in providing ideas and tools for the breeding practitioners.

Our task is to develop realistic means to evaluate the contribution of physiology research. Thus a set of "signposts" that will generate realistic ideas and understanding, which then become appropriate tools for manipulation by the practical breeder is proposed. These are measurements, mechanisms, models, and methods.

SIGNPOSTS

Measurement

What to measure and why? When the new science of crop physiology began some 40 yr ago, there was an expectation that simply understanding and measuring such processes as photosynthesis and transpiration, would provide a direct benefit to yield. In retrospect, we began to look at very fine-albeit critical- processes at the very beginning without generating a broad conceptual framework of crop development. The first measurement needed considers the basic components of the limiting resource and how it is used, viz. resource capture, conversion and partitioning. Under water-limiting environments, grain yield is a function of the water transpired (T), the water-use efficiency (WUE) and the partitioning of dry matter to grain (HI). One or more of these components must be altered to increase grain yield:

Thus, before embarking on a breeding program for improvement under variable and water-scarce environments, one must first measure how the current system uses the scarce resource (water) and where the opportunities for genetic intervention lie. We need to measure how much of the total precipitation is actually transpired and how much is lost in runoff, soil evaporation and drainage, and how much is stored in the soil. We must also know if there is variation in WUE and HI (Fig. 1).

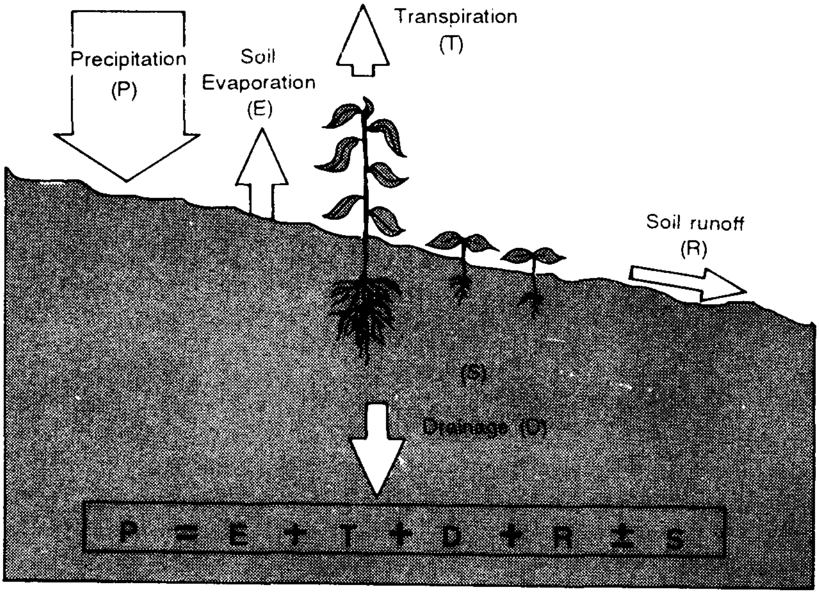


Fig. 1. A scheme of water balance showing stored soil water (S) as a target for improvement of sorghum under terminal drought.

Let us consider two case studies-maize and sorghum (*Sorghum bicolor* (L.).

In maize, Kassam *et al.* (1975), the pioneers of today’s modelers fitted the water requirements of maize to the bimodal rainfall patterns of the savannas in West Africa. Their model predicted two opportunities for improving the performance of maize in this environment (Fig. 2). In the first season, there was a high probability that demand for water for transpiration will exceed supply midway during growth-around flowering. Studies (Shaw, 1977; Westgate and Bassetti, 1990; Boyer, 1992) have shown flowering to be the most sensitive stage of growth in maize; moisture stress at flowering severely reduces grain number and harvest index (HI). Thus one target for the improvement of maize grown under variable and unpredictable moisture’ supply is to modify flowering behavior and grain number and thereby increase yield through higher HI. Edmeades *et al.* (1993) have estimated that more than 32 million ha of maize grown in the lowland tropics are exposed to intermittent drought around flowering causing 15% losses in yield.

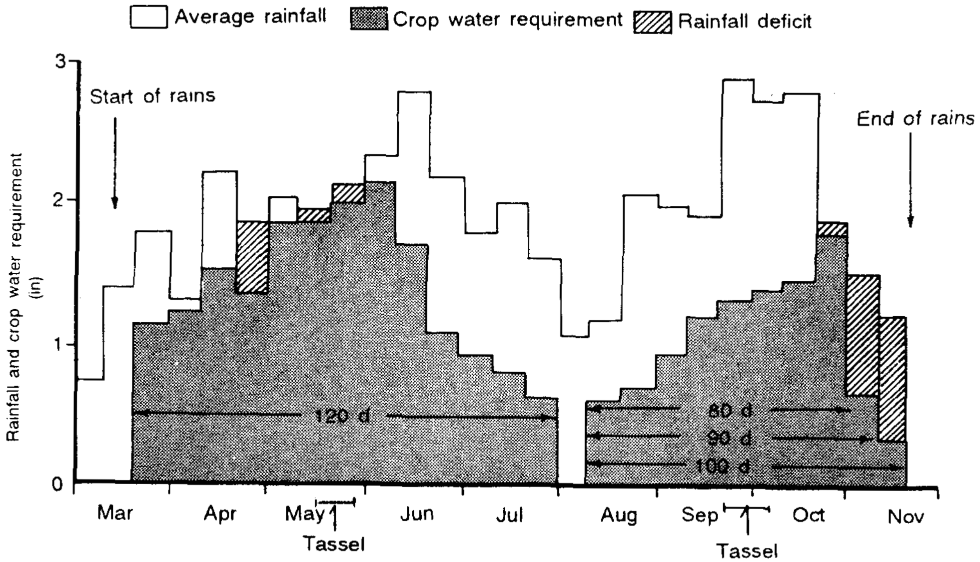


Fig. 2 Rainfall and crop water requirement for maize, Ibadan, Nigeria.

The second case study involves improvement of sorghum in Australia, where it is also grown in the savanna with variable and unpredictable rainfall. Maximum yields are obtained from full-season crops but these are often exposed to a terminal drought. In some soils, moisture remains stored at depth in the profile, even at maturity of the crop (Williams, 1990). The target is to increase the zone of resource capture for water in the profile and thereby the amount of water transpired (T) by the crop and thus yield.

In these two examples, measurement of the limiting resources and its effect on yield component set clear targets and focus for crop improvement. Setting such targets is critical in the rainfed ecosystem. Because of the variability (and large genotype × environment interaction), the selected targets will not be expressed in all locations at all times. Careful measurement allows for identifying the repeatable and useful positive genotype × environment interaction which will have greatest benefit over time at any one location.

Mechanisms

Thew is a need to understand the mechanisms and the processes that will increase either resoure capture, resource-use efficiency or allocation.

In the past, physiologists were content to show a correlation between a given plant character and yield-without differentiating causality from spurious, although statistically significant correlation. A good example of this misuse is the attempt to improve grain yield by selecting for either an increase in grain number or grain size. This is bound to be ineffective if grain yield is limited by the capacity to produce assimilates for grain storage and not by the storage system of the grain itself. Not only must the presence, strength and direction of a process be correlated with the targeted yield component there also must be physiological "internal consistency" in each of the intervening steps.

In sorghum, a target is to increase root exploration for soil moisture at depths during grain filling. One mechanism for that is osmotic adjustment (OA)- the change in osmotic potential due to the accumulation of solutes within the cell. Osmotic adjustment maintains turgor pressure under moisture stress and thus root activity. It also increases dehydration tolerance and in terminal stress, enhances the retranslocation of assimilates to the grain (Santa maria *et al.,* 1986). It is important to demonstrate that OA is not just related to grain yield, but also that there is an internal physiological consistency whereby

- OA influences turgor at a given potential and influences root growth;
- Increased root growth delays leaf area loss under moisture stress and increases dry matter; and
- Increased assimilate production increases yield.

Thus, the internal consistency links OA to an increase in grain yield under moisture deficits where there is water at depth in the soil profile.

Many studies have shown maize as being unusually susceptible to drought stress at flowering (Fig. 3) (Westgate and Bassetti, 1990; Boyer, 1992). This is partly because male and female flowers are separated by 30-100 cm, because silk must extend up to 30 cm to escape the husk, and because the pollination process demands that long and delicate stigmata tissue and pollen grains remain viable even while exposed to desiccating environments. Although a number of processes influence grain number before, during, and after anthesis under moisture stress, the greatest reduction occurs within the first 2 wk after pollination (Grant *et al.,* 1989).

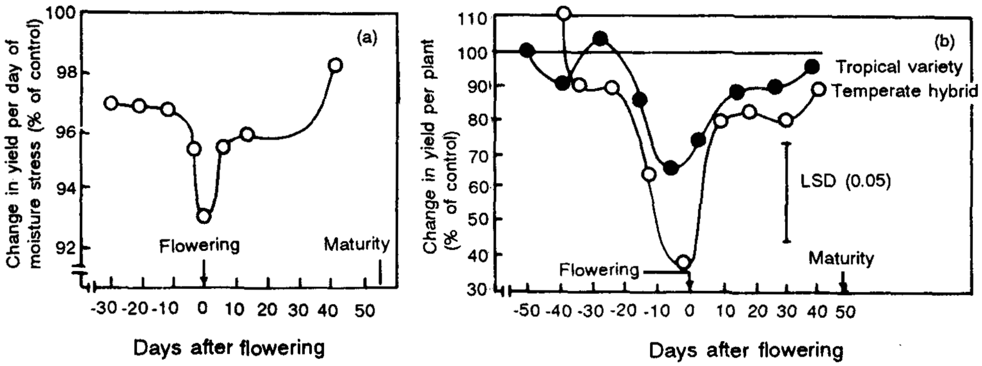


Fig. 3 Effect on maize grain yield from 1d of moisture stress (a) and 1d with 54% crop shading (b).

A characteristic of maize under environmental stress is increased anthesis-silking-interval. The reserves of carbohydrate in the maize plant at silking are comparatively small and the capacity of newly fertilized ovules to attract these reserves is limited. Boyle *et al.* (1991) infused the stems with a sucrose-rich solution to offset most of the effects of drought stress at flowering. Edmeades *et al.* (1993) concluded that the reduced grain number per plant under drought seems more of a chemical (CHO supply) than physical (separation of pollen and stigma) process, and that the anthesis-silking interval is a symptom of reduced assimilate flux rather than the direct cause of barrenness. Here the internal physiological consistency links the relationship between anthesis-silking interval and yield (Fig.4), with reduced assimilate supplies around flowering for ovule and silk growth (Fig.5) and to reduce grain number and HI.

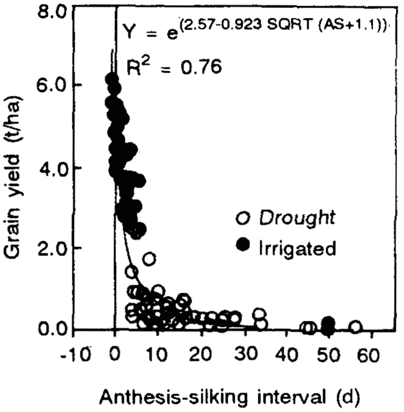


Fig. 4 Relationship between anthesis — silking interval and grain yield combined data from maize cultivars grown under drought (o) and well-watered conditions (•) at Tlaltizapan, Mexico. From Bolanos and Edmeades (1993).

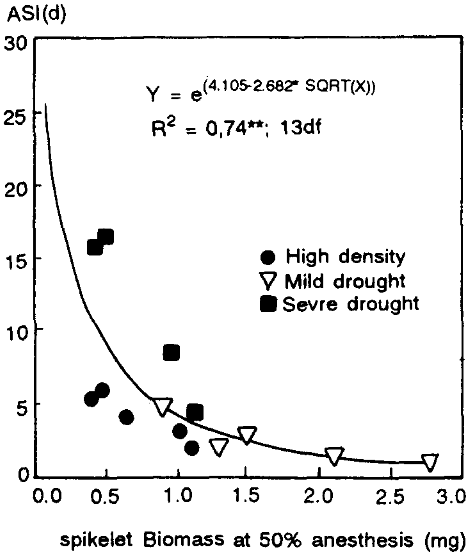


Fig. 5 Relationship between mean ear spikelet biomass at 50% anthesis and the anthesis-to-silking (ASI) interval for Tuxpeno Sequia cycles 0,2,4,6 and 8 grown under high plant density and mild severe drought stresses.

Models

Modelling processes and determining the likely effects of changes in plant characteristics aid in the development of "best bet" approaches. Processes that cannot be modelled are probably not understood. Without this understanding, our move from measurement to new technologies will be unpredictable (and quite often unsuccessful).

There are many levels of modelling-they do not have to be complex if that is not necessary for the job at hand, The conceptual model or the "ideotype" has served physiologists and breeders well. The most successful dates from 1960, with the IR8 story of IRRI. In 1974 Jennings, the IRRI breeder, involved in the green revolution said:

> "elegant work by the institute crop physiologists indicated in detail on paper an ideal plant type, i.e., an "ideotype", and pinpointed the vegetative characteristics of traditional varieties requiring drastic modification. In retrospect it was a relatively simple task for breeders to follow this blue print and produce a series of productive dwarfs beginning with IR8".

Fischer *et al.* (1983) and later refined by Edmeades *et al.* (1993) developed an ideotype for the selection of maize for better performance under limiting moisture around flowering. They used this information in a selection index for a field site recurrent selection program for the improvement of maize performance under moisture deficits.

The ideotype concept which creates scientific ideas, and a framework within which they can be tested should remain a strong tool for a breeding program. The latest application is in the development of a new plant type to raise the yield frontier in tropical rice. Originally, almost as an intuitive tool, our latest ideotypes have involved crop modelers and physiologists from the outset. We have advanced in our understanding of processes since the 1960s and now it is possible not only to develop the conceptual model (as for IR8), but also process-driven models with which sensitivity analysis-the "what if" questions- can be done in the computer before going into the field (Kropff *et al.,* 1994).

Models at the crop and molecular levels are now enhancing our efficiency in research. Recent applications of process-based rice crop models linked with GIS and to reliable data bases are allowing targeting ideotypes and assessing the performance of alternative crop ideotypes. At the molecular level, we are developing the genetic maps for the putative traits of root length, root penetration, osmotic adjustment and desiccation tolerance as "models"to aid the selection process. This work is reported in more detail elsewhere in these proceedings. And just as for past studies at the process level, we must ensure that our molecular maps are developed from appropriate populations to ensure that the genetic information is sufficiently robust for application for selection within the agronomically fit population growing in the breeder's field.

Method

This is the most critical of the signposts, requiring physiologists and breeders to work together to be productive. The synthesis of the previous steps must come here, or the effort invested will serve merely academic interests.

In the past, physiologists have tended to disregard genetic variation. Extrapolation and generalization were often derived from a few, or worse, one genotype. Correlations which depend on one extreme outrider entry were selected from unadapted material from a germplasm bank. Too often a relationship among yield-determining characters was established in controlled environments and never in the field. Indeed, physiologists have worked downstream from the breeding program spending time telling the breeders what they managed to accomplish, rather than assisting in the current selection process.

This has led to charges that physiology is a retrospective science. The guiding rules to applying our knowledge and skills should include (a) that physiologists work with many genotypes representative of the variation in breders fields; and (b) that the physiologists maintain a well-worn path to those breeders' fields.

The maize, ideotype was developed from the study of mechanisms in a broad range of maize germplasm and from an analysis of the variation that exist within one maize population (Tuxpeno), which is used as a breeding population for new varieties (Fischer *et al.,* 1983).

Using the ideotype characters for selection, divergent subpopulations were developed and their performance compared with that of subpopulations selected on yield alone. The study demonstrated that a) genetic variation for drought characteristics existed within agronomically fit populations being used in breeding programs; b) the ideotype selection enhanced performance under yield-limiting moisture around flowering; c) there was an internal consistency linking change in the population through selection to the processes that influence adaptation to moisture deficits; d) selection for the drought ideotype was more effective than selection for yield alone; and e) screening for the additional traits was practical (although costly) for a breeding program.

IMPACT

Recently Edmeades *et al.* (1993) have reported progress after six selection cycles for maize improvement to the target drought environment. The evaluation studies included entries from the same breeding population where selection was for yield (alone) done over a number of test locations (the more conventional approach for breeding). Selection for drought tolerance resulted in a significant increase in grain yield at levels ranging from 1 to 8 t/ha, with no significant interaction between rate of gain and yield level. At 2 t/ha (common under drought conditions) this genetic improvement represents a gain of 6.3% per cycle.

Gains in yield were the result of reduced barrenness under moisture dificit at flowering. Total biomass under drought was unaffected by selection, so the gains in grain yield arose from a systematic increase in harvest index-the target component of selection. This was accompanied by an increase in ear biomass at 50% anthesis and a decrease in the number of tassel branches (a change in the allocation of resources). Flowering behavior was markedly affected by selection, with a large decrease in the ASI, which was related to ear spikelet biomass at flowering (Edmeades *et al.,* 1993).

Based on this study, selection for adaptation to moisture stress around flowering is being practiced in a number of maize populations as a routine in the breeding program of CIMMYT.

REFERENCES

Bolanos J, Edmeades G O (1993) Eight cycles of selection for drought tolerance in lowland tropical maize. I. Responses in grain yield, biomass, and radiation utilization. Field Crops Res. 31:233-252.

Boyer J S (1992) Mechanism for obtaining water use efficiency and drought resistance. Pages 181-200 In: Plant breeding in the 1990's. H.T. Stalker and J.P. Murphy, eds. Commonwealth Agricultural Bureaux International, Wallingford, United Kingdom.

Boyle M G, Boyer J S, Morgan P W (1991) Stem infusion of liquid culture medium prevents reproductive failure of maize at low water potential. *Crop Sci.* 31:1246-1252.

Edmeades G O, Bolanos J, Hernandez M, Bello S (1993) Causes for silk delay in a lowland tropical maize population. Crop Sci. 33:1029-1035.

Fischer K S, Johnson E C, Edmeades G O (1983) Breeding and selection for drought resistance in tropical maize. El Batan Mexico.

Grant R F, Jackson B S, Kiniry J R, Arkin G F (1989) Water deficit timing effects on yield components in maize. *Agron.* 1. 81:61-65.

Kassam A H, Kowal J, Dagg M, Harrison M N (1975) Maize in West Africa and its potential in Savanna areas. *World Crops* 27:73-78.

Kropff M J, Cassman K G, van Laar H H (1994) Improving yield potential: the role of ecophysiological crop models. In : Proceedings of the International Rice Research Conference, 1992 IRRI, Los Banos, Philippines.

Passioura J R (1981) The interaction between the physiology and the breeding of wheat. Pages 191-200. In : Wheat science-today and tomorrow. LT Evans & WJ Peacock, eds. Univ. Press, Cambridge, London.

Santamaria F J, Ludlow M M, Fukai S (1986) Drought resistance traits in hybrids and lines of *Sorghum bicolor* L Moench. Pages 127-143. In: Proceedings of the first Australian Sorghum Conference, M.A. Foale and R.G. Henzell, eds .

Shaw R H (1977) Climatic requirement: Corn and Corn Improvement. G.F. Sprague, ed. *Am. Soc Agron.* 18:591-623.

Westgate M E, Bassetti P (1990) Heat and drought stress in corn: what really happens to the corn at pollination? Pages 12-28. In: Proceedings of the 45th Annual Corn and Sorghum Research Conference, 5-6 Dec 1990. D. Wilkinson, ed. American Seed Trade Association Washington, DC, USA.

Williams R L (1990) Genotypic variation in delayed leaf senescence in sorghum. MS Thesis Univerisity of Queensland Australia.

Williams T V, Snell RS, Ellis JF (1976). Methods of measuring drought tolerance in corn. *Crop Sci.* 7:179-181.

Wilson G L(1992). Crop physiology: Some recollections and current perceptions. Pages 2-10 In: Proceedings of the 6th Australian Society of Agronomy Conference, Armidale, Australia.

IS THERE ANAEROBIC METABOLISM IN SUBMERGED RICE PLANTS ? A VIEW POINT

☐ *H.Greenway*[1] *and T.L. Setter*[2]

SUMMARY

Submergence of rice is a complex phenomenon acting mainly via the 10^4-fold slower diffusion of gases in solution than in the gas phase. This will lead to both increases and decreases of supply of oxygen and CO_2 and increases in the concentration of the phytohormone ethylene. This paper focuses on possible O_2 deficiencies; without claiming that O_2 deficiency is more important than other possible adverse effects of submergence. The occurrence of O_2 deficiency in submerged rice is reasonably certain. However, we do not know whether such O_2 deficiency will affect survival, or at least long-term growth and yield of the crop.

Low O_2 concentration occurs in the water of flooded rice fields, particularly at greater water depths and also during the night. Available evidence suggests that O_2 deficiency occurs, in partially or wholly submerged rice plants, at least at certain hours of the day and in certain regions. During the night, O_2 concentration at the epidermis of the root tips is zero and the roots synthesize ethanol, the end product of anaerobic catabolism. All this ethanol is consumed during the first hours of the light period. This suggests the possibility that ethanol may be used as a source of carbon, both in submerged rice and in nonsubmerged plants of paddy fields. Armstrong's model indicates that O_2 deficiency in roots of vascular plants is particularly likely in the stele of the root tips; O_2 supply from the environment to this core being limited by diffusion and O_2 uptake along the pathway. We review metabolic evidence for roots which is consistent with these models, no information being available on submerged leaves.

In reviewing mechanisms of anoxia tolerance, we assume universal requirements for retention of membrane integrity despite a greatly reduced energy supply and reductions in requirements of energy for maintenance. Using these requirements as a prerequisite, we present evidence that there are two different modes of adaptation to anoxia, based on (i) rapid and (ii) slow rates of catabolism, respectively. We also suggest anoxia tolerant plants with the mode of slow rates of catabolism may be particularly useful during transient O_2 deficiency as often occurs in floodprone rainfed environments.

---

[1] The University of Western Australia, Nedlands. West. Australia

[2] The International Rice Research Institute, P.O. Box 933, Manila, Philippines

Injury due to exposure to anoxia can also be aggravated upon return from anoxia to aerated conditions, for example production of free radicals of oxygen would aggravate membrane damage and injury in several species. Whether this occurs in rice is unknown.

The response to anoxia, which involves a large-reduction in energy production is also relevant to other situations, for example to carbohydrate starvation, which can in principle occur due to other factors of a submerged environment such as low CO_2 supply and low light.

INTRODUCTION

The complex environment in flooded rice fields is shown in Fig. 1. The 10^4-fold slower diffusion of gases in solution than in the gas phase (Armstrong, 1979) means the solution immediately outside the shoot epidermis can contain high O_2 concentrations during the day and low concentrations during the night. Theopposite holds for CO_2 concentrations. This conclusion receives support for O_2 from data by Setter *et al.* (1988a) for gas concentrations in floodwater in rice fields in Thailand. These studies also showed that floodwater contained high concentrations of the phytohormone ethylene (Setter *et al.,* 1988b).

The rest of this review will be confined to the posssible occurrence of O_2 deficiency in submerged rice and if so what mechanisms of adaptation may be required. However, it should be pointed out that one requirement for tolerance to anoxia, ability to survive at a low level of energy production, is also relevant to cases

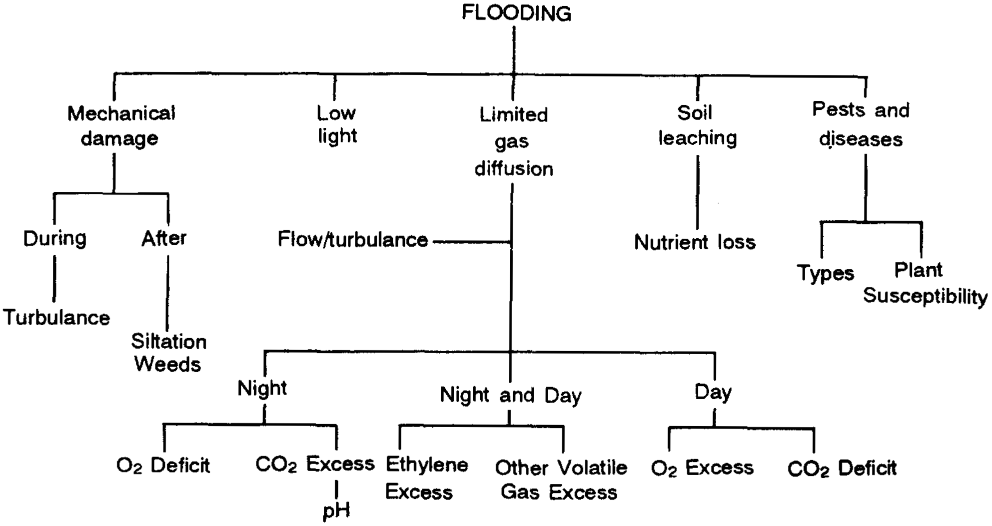


Fig. 1. Diagram showing the large range of adverse factors which may occur during submergence of rice (Setter *et al.,* 1993).

of carbohydrate starvation, whether these are due to low CO_2 low light, or chlorosis caused by high ethylene concentrations, which develops in a submergence intolerant cultivar (Jackson *et al.,* 1987).

Occurrence of O_2 deficiency depends on :

1) Plant factors, reviewed by Armstrong and Beckett (1987) for mots in waterlogged soils depending on O_2 supply from the shoots. These include: i) distance from the O_2 supply, longitudinally via the aerenchyma, as well as radially from the aerenchyma through the cortex into the stele, ii) porosity of the tissues, iii) rate of O_2 consumption in respiration and iv) radial O_2 loss to the environment. The integration of these four factors will favour the earliest development of anoxia in the stele of the root tip.

2) Environmental factors as discussed by Setter *et al. (1988a), being:*

i) The degree of turbulence in the water, which will determine the O_2 movement to the tissues, and

ii) The temperature, which will affect O_2 consumption by both plants and micro-organisms.

iii) O_2 production during photosynthesis. Hence O_2 supply to submerged rice will vary with the diurnal cycle and also depend on light intensity, as affected by shading and turbidity, and on CO_2 concentration, which will be a function of total inorganic carbon and the pH of the floodwater.

The transient nature of any O_2 deficiency in submerged rice means that we can not deduce from the literature whether O_2 deficiency contributes to the adverse effects of partial or complete submergence.

In physiological terms we can only speculate on the best mode of adaptation. Adaptation by plant cells to O_2 deficiency is complex and includes the capacity to sustain and regulate alcoholic fermentation ability to reduce maintenance requirements for energy and maintenance of membrane integrity. We present evidence for different rates of metabolic activity in various tissues.

1) Low metabolic activity coupled with survival, i.e. by the tissue going into suspended animation, thus conserving carbohydrates for recovery after the floodwaters recede.

2) High metabolic activity, sometimes coupled with partial maintenance of growth and nutrient uptake.

Possible "post anoxic injury" due to return to aerated conditions has also to be considered. Transfer of tissues from anoxia to air, i.e. restoring the oxygen supply. Introduction of O_2 may lead to formation of free radicals of oxygen and further membrane damage, particularly when there has been deterioration of membrane components during the O_2 deficiency itself.

Finally, the relevance of the present paper is for the rice ecosystem rather than for rice *per se* : the rice weed, barnyard grass, is probably even more efficient than rice growing under anoxic conditions. Understanding the mechanisms of the adaptation of barnyard grass could lead to more efficient methods of its control (Kennedy, et al., 1993).

Definition of Terms

anaerobic catabolism : breakdown of sugars to supply energy in the absence of air.

anaerobic proteins: proteins induced by O_2 deficiency.

anoxia: absence of oxygen.

anoxic core: centre of a tissue which does not receive oxygen.

ATP: adenosine trios-phosphate.

daltons: a measure of molecular size similar in magnitude to molecular weight.

glycolysis: breakdown of sugars to the three carbon compound pyruvate.

hypoxia: low but not zero oxygen.

Km: substrate concentration at which half the maximum velocity of a reaction is attained.

maintenance requirement: energy required without any increase in cell substances.

NAD: nicotinamide adenine dinucleotide.

O_2 deficiency: Plant tissues can not obtain sufficient oxygen for maximum respiration

post anoxia: after return from anoxia to air.

PPi : pyrophosphate.

RNA: ribonucleic acid.

DETAILED REVIEW

Occurrence of O_2 deficiency in the field

Low O_2 concentrations have been shown at greater depth and during the night in floodwaters of fields of floating rice in Thailand (Setter *et al.,* 1987, 1988a) and India (Setter *et al.,* this proceedings). O_2 concentrations in the floodwaters decreased with water depth, while in the surface layers of water O_2 concentrations increased during the day and decreased during the night. O_2 concentrations inside floating rice plants are only available for the lacunae, and these show the expected decrease in O_2 concentrations with increasing distance from the O_2 supply, i.e. with increasing water depth (Setter *et al.,* 1987). Similar patterns of O_2 distribution in roots of paddy rice were established in the pioneering studies by van Raalte (1940) in the Botanical gardens of Bogor. Such patterns are predicted by the elegant models on O_2 distribution within mots of vascular plants, depending on O_2 supply via the aerenchyma (Armstrong and Beckctt, 1987).

No such models for O_2 supply exist yet for submerged plants, nevertheless we can use the model of Armstrong and Beckett to predict that : (i) during the night,

O_2 supply to roots of submerged rice plants will be substantially lower for submerged than for non-submerged plants: with O_2 close to the shoot root junction at 7% for the submerged plants (Setter *et al.,* 1987) and an expected 20% O_2 in the gas spaces of non-submerged plants(Armstrong and Beckett, 1983, (ii) O_2 supply is likely to be less for tissue away from the principal O_2 supply, i.e. the lacunae or aerenchyma. As one example, in deep water rice O_2 deficiency may become acute in aquatic roots in deep water unless their epidermis has a low permeability to O_2.

Different modes of response by vascular plants to O_2 deficiency

We distinguish four different modes of response of plants to low O_2 concentrations in at least part of their environment.

Mode 1 : intolerant to waterlogging or submergence. These plants have both low porosity and low cellular tolerance to anoxia and comprise the bulk of plant species.

Mode 2: tolerant to waterlogging and submergence based on high porosity of tissues to facilitate O_2 flow from the air or from water containing O_2 (Armstrong, 1979, Armstrong and Beckett, 1987). Some plants with this mode are not necessarily tolerant to anoxia (cf.ap Rees et al., 1987) and this has been claimed for rice roots (Webb and Armstrong, 1983). We do not agree and include rice into Mode 4, as discussed below.

Mode 3: tolerance based on cellular tolerance to anoxia. This mode can be further divided into two types: 3A) where a tissue can grow under anoxia, for example, rice coleoptiles (Jackson and Drew, 1984; see also Fig.2) and some species of Echinochloa (Kennedy et al., 1992), 3B) tissue survives, but does not grow until aeration is restored. The best examples are germinating seeds of several species (to be discussed in section 3).

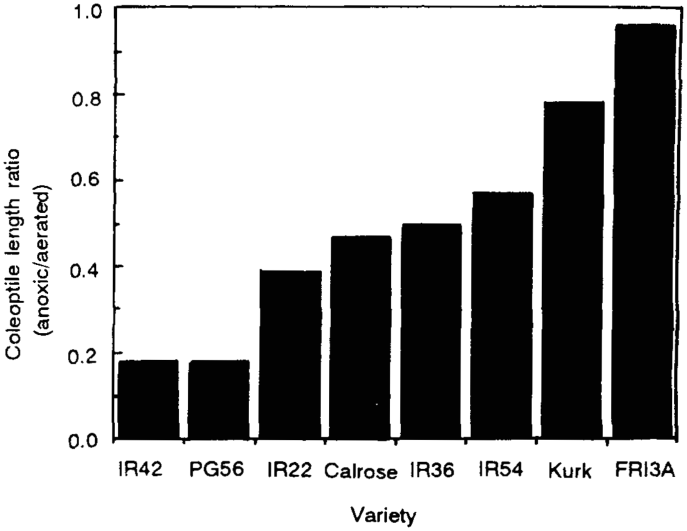


Fig. 2. Genotypic differences in anoxia tolerance of rice during germination (Setter *et al.,* 1994). Conditions : seeds imbibed 1 day air, followed by 3d anoxia or air treatment.

Mode 4: a tolerant mode based on a combination of Modes 2 and 3. This mode can cope with temporal decreases in O_2 regime for example during diuranal cycles of O_2 supply. This combined mode also allows for "symbiosis" between anoxic and aerobic regions in the same tissue. Well known examples are aerenchymous root tissues with anoxic steles and aerobic cortices (Armstrong and Beckett, 1987). Submerged established rice plants presumably belong in this group (to be discussed in more detail in Section 5).

Anoxia tolerance and the production and flow of energy under anoxia

We postulate that universal requirements for anoxia tolerance are the reduction of maintenance requirements for energy and the maintenance of membrane integrity, Evidence for the second proposition was obtained for beet root in which the endogenous dye betacyanin is an excellent marker for cell death (Zhang *et al.,* 1992). Rapid leakage of K^+, $C1^-$ and Na^+ started up to 9h before leakage of betacyanin indicating increases in membrane permeability caused death, rather than vice versa (Zhang et al., 1992, Zhang and Greenway, 1993).

Production and flow of energy to processes essential to survival. Generation of energy during anoxia will occur mainly via glycolysis {equation 1) with ethanol as the principal end product of anaerobic catabolism in nearly all plants (equation 2 : Davies, 1980; ap Rees *et al.,* 1987). The overall reactions are:

$$\text{hexose}+2\text{ADP}+2\text{Pi}+2\text{NAD}^+ \rightarrow\rightarrow\rightarrow 2\ \text{pyruvate}+2\text{ATP}+2\text{NADH}+2\text{H}^+ \qquad (1)$$

$$2\text{pyruvate}+2\text{NADH}+2\text{H}^+ \rightarrow\rightarrow 2\ \text{ethanol}+2\text{NAD}^+ \qquad (2)$$

The purpose of ethanol synthesis (equation 2) is to enable energy production to continue from glycolysis(equation 1) by recycling the essential cofactor NAD; these combined pathways are referred to as alcoholic fermentation. The production of energy from alcoholic fermentation per mol hexose is only 2 mol of ATP, compared with 24-36 mol ATP produced in aerated tissues mainly by oxidative phosphorylation. The energy yield under anoxia may be increased to 2.5 mol ATP per mol hexose units when these units are produced from sucrose via the enzyme sucrose synthase(based on Stitt , 1990). In some tissues the large reduction in energy production under anoxia can be alleviated by increases in rate of sugar consumption, traditionally referred to as the Pasteur Effect (Drew, 1990). This effect is expressed as the ratio of carbohydrate flux through glycolysis under anoxia over the rate of glycolysis in air (Table 1, the ratio is called from now on Canoxia/Cair). The determination of this ratio allows distinction of two mechanisms of adaptation to anoxia such as 1) rapid catabolism and 2) slow catabolism.

1) *Rapid catabolism.* indicated by high ratios of C_{anoxia} / C_{air} found in rice coleoptiles and aged storage beetroot and carrot roots during the first 24 h of anoxia (Table 1). None of these increases in rates of sugar consumption come close to compensating entirely for the inefficiency of energy production during glycolysis i.e. 14 to 18-fold increases in carbohydrate flux would be required for equivalent energy production (calculated from above).

2) *Slow catabolism:* indicated by low ratio of C_{anoxia}/C_{air} is found for storage tissue after prolonged exposure to anoxia. More spectacularly, germinating lettuce seeds exposed to anoxia went into suspended animation (Table 1). Energy production in these seeds must have been negligible, yet these seeds germinated when they were returned after 14 days anoxia to air(Pradet and Bomsel, 1978). Similar pattern have been found for an *Echinochloa crus pavonis* (Zhang *et al.,* 1994).

Table 1. Different rates of catabolism in anoxia tolerant species. The change in rate of glycolysis is expressed as the ratio for carbon flow through glycolysis: $\text{Carbon}_{anoxia}/\textbf{Carbon}_{air}$.

Plant	$\textbf{Carbon}_{anoxia}$ / $\textbf{Carbon}_{air}$	Reference
A) *High rates of catabolism*		
Rice seedlings	1.8	Calculated by us from Alpi and Beevers (1983)
Carrot storage tissue (first h of anoxia)	3.0-3.7	Faiz-ur Rahman *et al.* (1974)
Beetroot storage tissue (first *2A* h anoxia)	1.9	Zhang and Creenway (1994)
B) *Low rate of catabolism*		
Seeds of several spp.	<1.0	Pradet and Bomsel(1978) Raymond and Pradet(1980)
Aged beetroot tissues *(>2A* h anoxia)	0.7	Zhang and Greenway(1994)

The energy produced during glycolysis in anoxic tissues is used for different processes:

1) *Maintainance.* This would include turnover of proteins and membrane components and essential solute transport, e.g.sugar and proton transport. This reqirement presumably exists in most tissues excepting the seeds which go into suspended animation as described above.

2) *Synthesis of anaerobic proteins which,* mainly function in sugar catabolism (for maize, Bailey Serres *et al.,* 1988) and perhaps synthesis of specific membrane component of adaptive value under anoxia. The synthesis of anaerobic proteins is particularly pronounced during the first 24 h of anoxia; and may explain the higher rates of catabolism during the first 24 h of anoxia than after 24 h in the beetroot tissues (cf. Table 1).

3) *Growth.* Elongating rice coleoptiles require net cell wall and protein synthesis (Alpi and Beevers, 1983), as well as uptake of solutes to generate osmotic pressure (Atwell *et al.,* 1982). The high energy requirements, particularly for protein synthesis, may account for the high rate of catabolism found in rice coleoptiles (Table 1).

The above requirements for energy have to be considered in relation to the large reduction in rates of ATP synthesis discussed earlier; even the high rate of catabolism in the carrot tissue (Table 1) indicates ATP yields under anoxia are 3-6 fold lower than that in air. So in all anoxia tolerant species there must be a sophisticated regulation of energy flow. One type of regulation is a reduction in maintenance requirements for energy. Such requirements can be best assessed for storage tissue which does not grow even under aerated conditions. For aged tissues of storage root of red beet we have estimated that the maintenance requirement for energy is 10-25 times lower under anoxia than under air (Zhang and Greenway 1994). This reduction is so large that we assume there is reduced turnover of protein and to a lesser extent membrane components since these processes use the bulk of the energy for maintenance in aerobic cells (Penning de Vries, 1975).

Examples of regulation. Examples of regulation of various processes under anoxia can be found at different levels of organisation.

1) *Echinochloa crus pavonis* investigated by Zhang *et al.* (1984) can: a) either survive for at least 30 days in suspended animation (anoxia from start of imbibition), or b) develop a coleoptile and hypocotyl after aerobic treatment for the first 1-18 h followed by transfer to anoxia.

2) Regulation is demonstrated both by the switching on of synthesis of anaerobic proteins and the cessation of synthesis of many other proteins, even though their messenger RNA still persists (Drew, 1990). For example in rice cultured cell there are substantial increases in activities of several enzymes (Table 2) including PPi dependent phosphofructokinase. In contrast, ATP dependent phosphofructokinase changed little in activity, presumably because activity was already high under aerated conditions.

3) There are much larger reductions in transport of Cl than of sugar even in anoxia tolerant rice coleoptiles (I. Zhang and II. Greenway, 1994. person. commun.). A reasonable teleological speculation is that the cells direct limited amounts of energy to the essential transport of sugars required for anaerobic catabolism, rather than to Cl. However, we do not know by what molecular mechanism this regulation is achieved.

4) Rice shoots achieve a remarkable regulation of the pH of the cytoplasm. After sudden transfer from 20% to zero O_2 the $pH_{(cyt)}$ decreased first to 7.0 but recovered to 7.15 after 10 h at 1%, O_2 compared with a $pH_{(cyt)}$ of 7.4 to 7.5 in aerated shoots (Menegus *et al.,* 1991). In this case there is a plausible mechanism of regulation of energy flow since the tonoplast of plant cells contains a PPi dependent-H^+ translocase in addition to

the more ubiquitous ATP dependent-H^+ translocase (Rea and Poole, 1993). Hence conversion of ATP to PPi might be one way to direct a limited amount of energy to the crucial process of preventing acidosis of the cytoplasm.

Table 2. Increases in activity of several enzymes under anoxia indicated restricted synthesis of a set of proteins, the anaerobic proteins, most of which are involved in sugar mobilisation and catabolism. Data for cultured rice cells by Mohanty *et al.* (1993).

Enzyme	increase over activity found in air
Alcohol dehydrogenase	7 fold
Lactate dehydrogenase	4 fold
Sucrose synthase	3 fold
PPI dependent-phosphofructokinase	7 fold

Importance of hypoxic pretreatment (acclimatizing) to anoxia

Anoxic shock often leads to rapid injury which can be prevented in some tissues by acclimatizing them by exposure to low but not zero O_2 concentrations before exposure to anoxia (reviewed by Drew, 1990). As one example, survival of root tips of intact maize plants is extended from less than 24 h anoxia to 96 h anoxia by acclimatizing (Drew, 1990). In many soils it is likely that O_2 concentrations decrease gradually when soil become waterlogged (Drew, 1990), emphasising the relevance of data obtained using hypoxic pretreatment. Furthermore when data are obtained using anoxic shock it remains uncertain whether the changes in metabolism measured are merely a consequence of injury and approaching death or a more subtle metabolic response to anoxia.

One reason for the protective value of hypoxic pretreatment is the observed synthesis of ADH and therefore presumably also other anaerobic proteins (Johnson *et al.,* 1989), while the tissue as a whole has still substantial oxidative phosphorylation (Johnson *et al.,* 1989). Thus once the tissues are transferred to anoxia they would face smaller demands on the restricted energy production than tissues exposed to anoxic shock (Zhang and Greenway, 1994) . Alternatively ADH may not be synthesised at all following anoxic shock (Johnson *et al.,* 1989).

Evidence for coexistence of anoxic and aerobic tissues in the same organ

This section deals with the central issue of this paper since it is unlikely that submerged established rice plants are ever completely anoxic. This contrasts with the early developmental phase during direct seeding when the whole seedling may become anoxic. Once O_2 supply to a tissue becomes restricted rather than cut off altogether anoxic and aerobic tissues will coexist in the same organ. The hypothesis that this combination occurs is based on the very high affinity of cytochrome oxidase for O_2 indicated by a K_m of 24 m molm^{-3} (Yocum and Hackett, 1957). So electron flow and oxidative phosphorylation will continue till very low O_2 concentrations are reached. As shown schematically in Fig. 3, O_2 will diffuse into the tissue, while O_2 consumption will decrease the O_2 concentration along the pathway. In environments of low external O_2 concentration the concentration gradient will be insufficient to deliver O_2 to the core of the root i.e. this core will become anoxic. Analogous arguments hold for other tissues, such as submerged leaves and when the O_2 supply is the aerenchyma rather than the external environment.

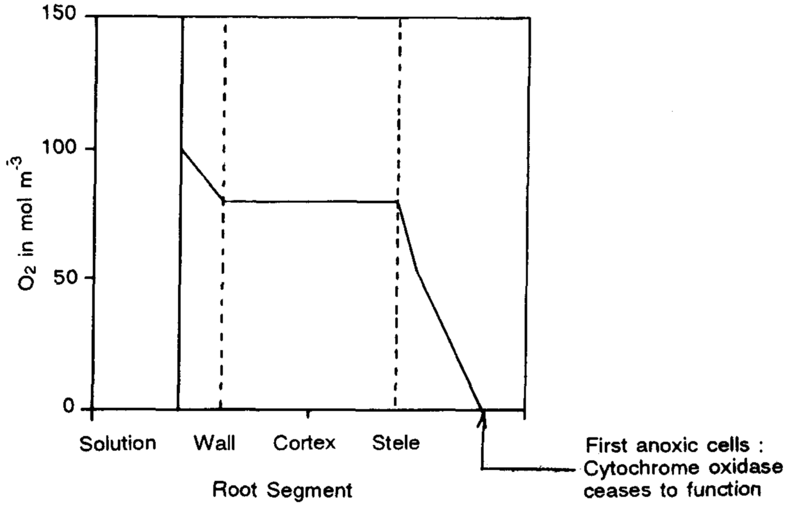


Fig. 3. Diagram showing the O_2 profile expected in a root when the O_2 supply is from the nutrient solution surrounding the roots (adapted from Armstrong and Beckett, 1987).

Evidence for anoxic steles and aerobic cortices in maize mots.

Anoxic cores in aerenchymous rice mots have been demonstrated using an O_2 micro electrode (Fig. 4). The radial pattern of O_2 concentrations is consistent with earlier formulated sophisticated models (Armstrong and Beckett, 1987) based on : 1) porosity of the tissues; 2) O_2 uptake by respiration; 3) radial O_2 loss to the environment and 4) length of longitudinal pathway. No such models exist for submerged leaf tissue but these could be developed in cooperation between biologists and mathematicians.

The data on O_2 concentrations are complimented with metabolic evidence for an anoxic stele and aerobic cortex in maize roots (Thomson and Greenway, 1991), exposed to low but not zero O_2 concentrations or depending on O_2 supply from the shoots via the aerenchyma. Evidences are as follows:

1) Higher concentrations of ethanol in the stele than in the cortex (Table 3).
2) An increase in ratios of alanine to free amino acids in the stele but not in the cortex of hypoxic roots (alanine is an end product of anaerobic catabolism: ap Rees *et al.,* 1987).
3) "Active" states of the key enzyme pyruvate decarboxylase (PDC) in the stele of hypoxic roots while the same roots have "inactive" states of this enzyme in the cortex (Table 4). This is key evidence since PDC is the entry port for carbon flow to ethanol and hence will determine whether carbon of glycolysis flows to ethanol or into the aerobic catabolic pathway of the Krebs cycle.

Table 3. Ethanol (mol m^{-3}) in cortex and stele of excised maize mots exposed to different O_2 concentrations at 25°C. (Thomson and Greenway, 1991).

O_2 external (mol m^{-3})	Ethanol (mol m^{-3})		
	stele	cortex	external solution
0.06*	0.39	0.12	0.11
0.00	0.34	0.43	0.42

* Air saturated water at 25°C contains 0.26 mol m^{-3} O_2.

In Table 4, the inactive and active state of PDC in the cortex and stele, respectively, is shown by: (i) a lag after addition of pyruvate i.e. the enzyme is gradually activated in the presence of its substrate. In hypoxic roots such lags are pronounced in the cortex but slight in the stele, ii) differences in activation of the isolated enzyme when incubated at pH 6.0; these were large for the cortex but small for the stele of hypoxic roots (Table 4) suggesting most of the PDC is already activated.

Evidence for occurrence of anoxic regions in submerged, established rice plants :

The following evidence is available :

1) O_2 concentrations measured with a cylindrical O_2 micro electrode surrounding the tip of nodal roots of submerged rice plants demonstrated that O_2 becomes very low during dark periods, and increases substantially during light periods (Fig.5); this increase was associated with O_2 evolution in the shoots during photosynthesis (Waters *et al.,* 1989). Concurrently root elongation commenced a few h after the start of the light period and ceased at the start of the dark period (Fig. 4).

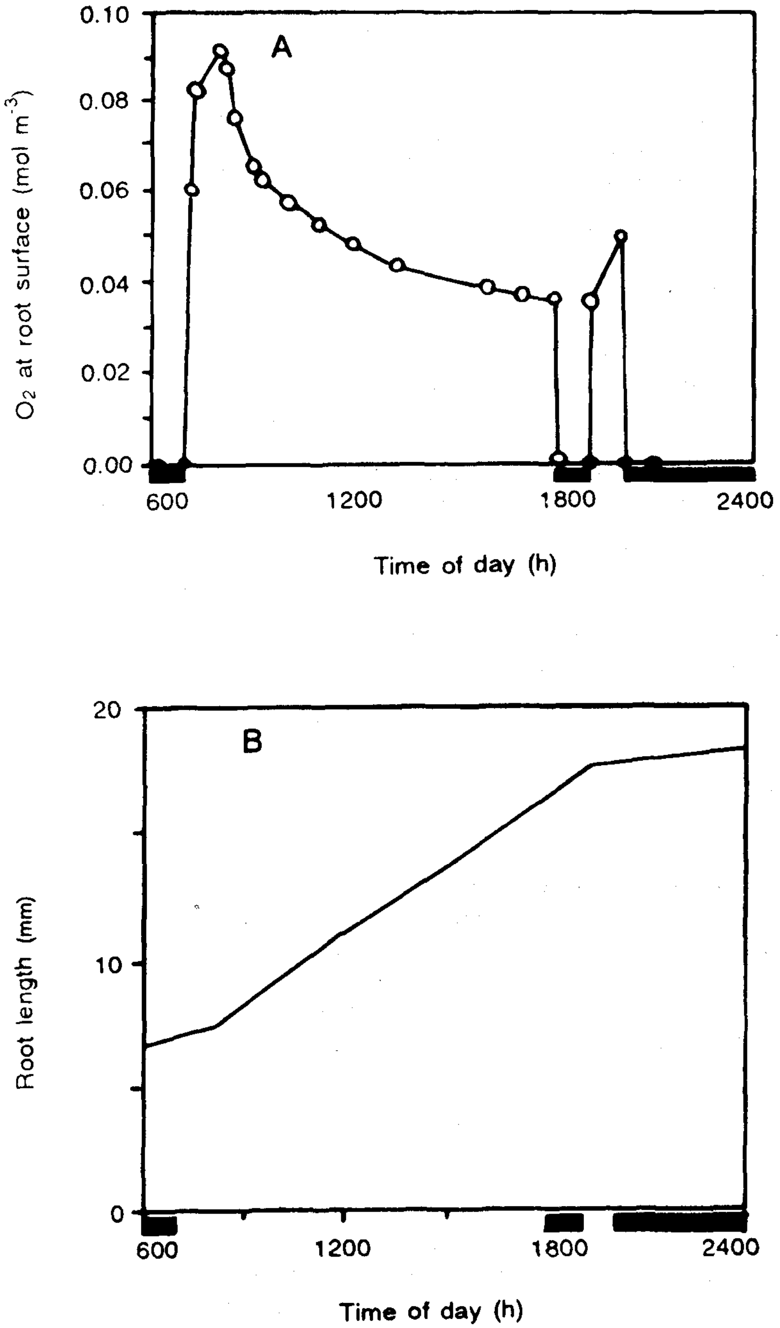


Fig. 4. O_2 concentrations (A) and growth of root tips (B) during submergence of rice. O_2 was measured with a micro O_2 electrode at the epidermis of the 2-7 mm zone behind the root apex of submerged rice plants (Waters *et al.,* 1989). Solid bars on the x-axis represent dark periods.

Table 4. Active and inactive states of pyruvate decarboxylase to diagnose blockage of oxidative phosphorylations in cortex and stele of maize roots at different O_2 regimes (from Thomson and Greenway, 1991). The lag indicates how fast the maximum rate is established upon addition of substrate (pyruvate); when the enzyme is fully active the lag will be only a few seconds. The % increase in activity shows the increase in activity after incubating extracts for 1-2 h at pH 6.0 at 22-25°C.

	Lag (min)		*% increase in activity*	
O_2 Treatment	Stele	Cortex	Stele	Cortex
0.26 mol/ m^{-3} *roots, shoots in air	1.1	1.9	63	68
0.0 mol/ m^{-3} roots, shoots in air	0.2	1.4	25	50
0.0 mol/ m^{-3} shoots and roots	0.3	0.7	20	23

* Air saturated

2) Roots of intact submerged rice plants produced ethanol during the night and consumed ethanol at the start of the light period (Fig. 5). Mirror image diurnal cycles were found for O_2 with loss from the roots during the day and O_2 uptake during the night (Fig. 5)

The demonstration that anaerobic metabolism occurs at least in roots of submerged intact rice plants emphasises the importance of observed genotypic differences in anoxia tolerance in germinating rice (Fig. 2). No information is available for established plants. However, the two most anoxia tolerant genotypes, Kurkaruppan and FR13A, were selected during submergence of established seedlings. So, there is strong inference that anoxia tolerance contributes to the ability of established rice seedlings to survive submergence.

Available information on ethanol consumption by plant tissues

The evidence for coexistence of aerobic and anoxic metabolism in different regions of the same organ opens the possibility of metabolic exchange between these regions. This exchange is in principle possible since transport through the plasmodesmata has been suggested for solutes with molecular weights between 465 and 1830 Daltons (Robads and Lucas, 1990).ATP has a molecular size of 507 Daltons and can pass through gap junctions between animal cells (Darnell *et al.,* 1990); plasmodesmata are analogous to the gap junctions in animal cells. We can therefore envisage flow of end products of anaerobic catabolism from anoxic to aerobic regions

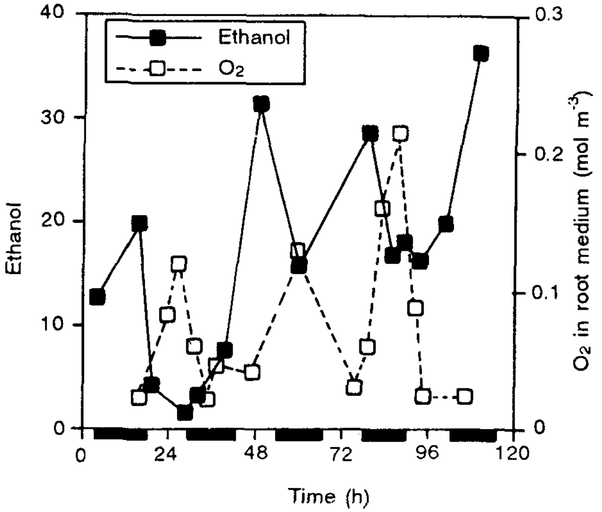


Fig. 5. Ethanol synthesis during night and ethanol consumption during the day by roots of intact submerged rice plants (Waters *et al.*, 1989). The roots were in a sealed container so that O_2 and ethanol in the nutrient solution surrounding the roots could be measured. Solid bars on the x-axis represent dark periods.

where they can contribute to the carbon balance. Similarly, compounds able to contribute to energy supply such as ATP and PPi may be transported from aerobic to anoxic regions. Presumably such an input would allow much more synthetic activity than when the entire tissue was anoxic. Most of this argument is mere speculation and the only evidence available is for ethanol shown in Fig 5 and by transport of ethanol from waterlogged roots of tomato plants to their shoots (Fulton and Erickson, 1964).

In this paper we further consider possible ethanol metabolism in the aerobic regions of an hypoxic tissue without claiming this is the only or most important exchange of metabolites occurring in tissues with aembic and anoxic regions. Rates of ethanol consumption are of the same order of magnitude as those of ethanol formation (Table 5). The observed rate of ethanol consumption by rice mots is 4-fold lower than the maximum observed rate in peas (Table 5), however, this could be due to the difference in exogenous ethanol concentration rather than due to species difference.

During ethanol consumption, acetate is formed together with 2 mols of NADH/mol of ethanol as observed for pea and mungbean tissues (Cossins, 1978). The carbon is subsequently incorporated in a large range of metabolites, similar to carbon derived fmm glycolysis (see Cossins, 1978 for review). The pathway from ethanol to acetate can continue as long as the tissues are aerated because NAD can then be regenerated from NADH in several reactions and by conversion to ATP in oxidative phosphorylation.

Table 5. Comparisons between rates of ethanol consumption and ethanol formation. All data are in m mol g^{-1} fresh $weight^{-1}$ min^{-1}.

Ethanol consumption in rice roots (0.33 mol/mm^{-3} external ethanol: calculated from Fig 5)	0.033
Ethanol consumption for peas (maximum observed; 150 mol m^{-3} external ethanol, Cossins and Beevers, 1963)	0.12
Ethanol formation in rice roots(John and Greenway, 1976)	0.042

We have also substantial information on the characteristics of alcohol dehydrogenase. The K_m for ethanol conversion to acetaldehyde is 10 mol m^{-3} for rice roots (John and Greenway, 1976) i.e. the enzyme had a low affinity for ethanol. However, a substantial range in K_m for ethanol between 35 and 34 mol m^{-3} was found for isoenzymes of barley (Mayne and Lea, 1985) indicating the potential for enzymes with a lower K_m i.e. with a high affinity for ethanol and therefore more suitable to ethanol consumption at low endogenous or exogenous levels. The *in vitro* activity of ADH for ethanol consumption indicated that there is 12 times more activity than the observed *in vivo* rates of net ethanol synthesis (Table 5). This assessment of in vitro activity allows for pH of the cytoplasm, the known pH spectrum of the reaction, a cytoplasmic pH of 7.5 and assumes an exogenous substrate concentration of 0.33 (calculated from Waters *et al.,* 1989). The present data indicate the potential for ethanol as a carbon source and this also applies for any ethanol produced in the soil. That is ethanol and other organic solutes occurring in waterlogged soils may supplement carbon gain derived from photosynthesis. These alternate carbon sources may be particularly important during periods of low potential photosynthesis i.e. at low light intensities. There is at present no evidence available to support or reject this hypothesis which in our view merits ecological and physiological research. Further elucidation of the possible importance of ethanol consumption in aerobic regions of hypoxic tissues of rice requires the following information:

1) Concentrations of ethanol in soil and in plant tissues.
2) Rates of ethanol consumption as related to external ethanol concentration.
3) Consumption of internal ethanol with time sequences so as to evaluate the relation between endogenous substrate and rate of reaction *in vivo.*
4) Comparison between genotypes.
5) Comparisons between different types of tissues.
6) Comparison of *in vivo* data with activities of ADH at the same substrate concentration and pH as found in tho cell.

7) Fate of ethanol using "realistic" external concentrations rather than the very high concentrations used in previous studies.

Possible post anoxic injury

Some of the adverse effects of exposure to anoxia may occur following return from anoxia to air rather than during exposure to anoxia. Specifically partial break down of fatty acids of membranes during anoxia may lead to formation of free radicals of oxygen when this becomes available leading to further damage to membranes. Strong evidence for this possibility has been presented by Monk *et al.* (1987), Crawford (1993), Crawford and Wollenweber-Ratzer (1992). Data for rhizomes of marsh species are summarised in Table 6. The anoxia tolerant species had less lipid degradation products and generated less free oxygen than the anoxia intolerant species (Table 6).

Table 6. Evidence for formation of free radicals of O_2 in rhizomes of an anoxia tolerant species, *Iris pseudacorus,* and anoxia intolerant species, I. *germanica* and *Glyceria maxima.* No evidence for free radical formation was found in the anoxia tolerant species *I. pseudacorus* (Crawford, 1993. Monk *et al.,* 1987, 1989).

Species	Lipid degradation products (1)	Free radical formation (2)	Superoxide dismutase(3)
Iris pseudacorus (tolerant)	Few	None observed	Yes (13x increase)
Iris germanica *Glyceria maxima* (intolerant)	Large number	Rapid generation	Either decreased or small increase

Furthermore, the anoxia tolerant species increased 13 fold in superoxide dismutase, an enzyme, which contributes to removal of free radicals:

$$2O_2+2\,H^+ \rightarrow H_2O_2+O_2 \qquad (3)$$

The synthesis of the enzyme superoxide dismutase in the anoxia tolerant species occurs under anoxia, i.e. it is one of the anaerobic proteins, yet it becomes only functional after return to air. That some of the limited amount of energy produced under anoxia is directed to the synthesis of an enzyme required only after relief of anoxia is an example of the remarkable subtlety of adaptation of plants to adverse environments. Further evidence for the existence of free radicals of O_2 consists of the improved health of chickpeas when treated with ascorbic acid, a free radical scavenger, before returning seedlings from anoxia to air (Fig.6). One key

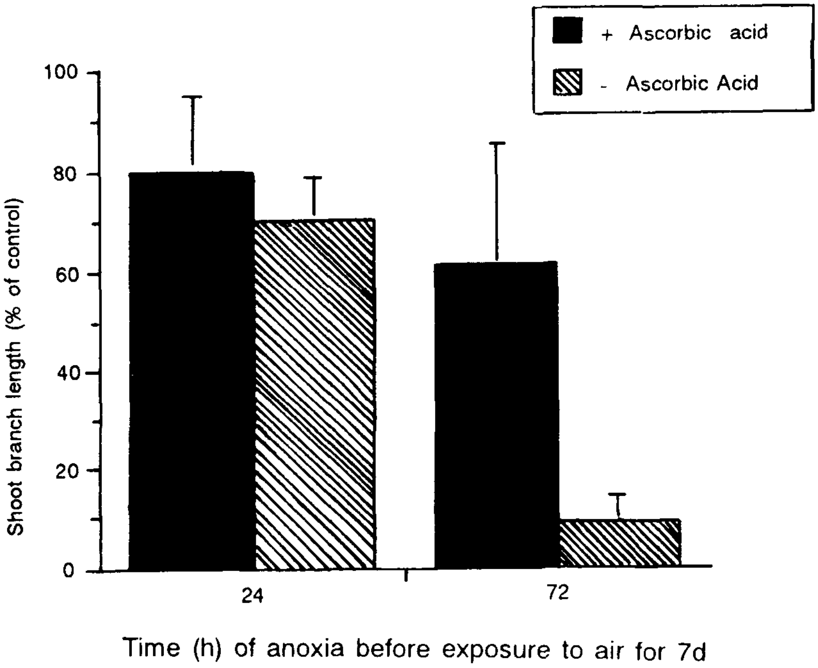


Fig. 6. Ameliorating effect of addition of a scavenger of oxygen radicals, ascorbic acid at 10 mol m^{-3} in the root medium (pH 5.6) on post anoxic recovery as evaluated by shoot length of chickpeas after exposure to anoxia for 24 or 72 h followed by exposure to air for 7 days : shoot branch length was measured after 7d aeration. Ascorbate was in distilled water. Control plants were aerated continuously (from Crawford and Wollenweber Ratzer, 1992).

question is whether the failure of anoxia intolerant species to synthesise superoxide dismutase during anoxia is a primary factor or a consequence of injury. The latter possibility is indicated by the much more pronounced post anoxic injury after 1 h than after 5 h anoxia, concurrently, free radical generation was higher and levels of superoxide dismutase were lower after 1 h than after 5 h anoxia (Van Toai and Bolles, 1991).

CONCLUSION

Anoxia tolerance

We postulate two modes of anoxia tolerance. Both modes require maintenance of membrane integrity and sophisticated regulation to direct the limited amounts of energy to processes essential to survival, however, they differ in the rate of catabolism :

i) high rates of anaerobic catabolism
ii) low rates of anaerobic catabolism despite a high sugar supply

Occurrence of anoxia in submerged rice plants

i) Long term anoxia of all plant tissues probably only occurs under flooded conditions during the early period after direct seeding.
ii) Anoxic regions coexisting with other regions receiving sufficient O_2 for oxidative phosphorylation may be the norm for submerged rice and may even occur in the roots of paddy rice. At least in submerged rice the anoxic regions will be more voluminous during the night than during the day.
iii) The best mode of anoxia tolerance for the association of aerobic and anoxic tissue is unknown.
iv) It is also unknown whether O_2 deficiency adversely affects submerged rice plants.

General comment on research approach

Clearly, adaptation to submergence is a complex phenomenon and there are no easy solutions. Scientists dedicated to increasing plant productivity may well question whether research on elucidating the mechanisms of adaptation to submergence is worthwhile. This question is common to many studies on adverse environments; one has to choose between pragmatic research, elucidation of mechanisms of adaptation, or a combination of both. The proportion of the different approaches depends on the scale of the problem.

REFERENCES

Alpi A, Beevers H (1983) Effects of O_2 concentration on rice seedlings. *Plant Physiology* 71:30-34.

ap Rees T, Jenkin L E T, Smith AM, Wilson PM (1987) The metabolism of flood tolerant plants. Pages 227-238. In : Plant life in aquatic and amphibious habitats. R.M.M. Crawford.ed. Blackwell Scientific Publication, Oxford.

Armstrong W (1979) Aeration in higher plants. Pages 226-332 In: *Advances in Botanical Research.* H.W.W. Woolhouse, ed. Academic press, London.

Armstrong W, Beckett PM (1987) Internal aeration and the development of stelar anoxia in submerged roots. *New phytologist* 105:221-245.

Armstrong W, Cringle S, Brown M, Greenway H (1993) In: Interacting stresses on plants in a changing climate, NATO advanced workshop AS1 Series 1 Vol 16. M.B. Jackson and C.R. Black, eds. Wye College.

Atwell BJ, Waters I, Greenway H (1982) The effect of oxygen and turbulence on elongation of coleoptiles of submergence tolerant and submergence intolerant rice cultivars. J.Expt. Rot 33: 1030-1044.

Bailey-Serres J, Kloeckener Gruissem B, Freeling M (1988) Genetic and molecular approaches to the study of the anaerobic response and tissue specific gene expression in maize. *Plant Cell and Environment* 11: 352-357.

Cossins E A (1978) Ethanol metabolism. Pages 169-202 In: Plant life in anaerobic environments. D.D. Hook and R.M.M. Crawford, eds. Ann Arbor Science Publisher Inc, Michigan.

Cossins E A, Beevers H (1963) Ethanol metabolism in plant tissues. Plant Physiology 38: 375-380.

Crawfod R M M (1993) Plant survival without Oxygen. *Biologist* 40: 110-114.

Crawford R M M, Wollenweber-Ratzer B (1992) Influence of L- Ascorbic Acid on Post-anoxic growth and survival of chickpea seedlings *(Cicer arietinum* L.) *J.Exy. Bot.* 43: 703-708.

Darnell J, Lodish H, Baltimore D (1990) Molecular Cell Biology 2nd Edition Scientific American Books W.H. Freeman and Co. New York.

Davies D D (1980) Anaerobic metabolism and the production of organic acids. Pages 581-611. In: The Biochemistry of Plants. Vol.2 D.D. Davies. ed. Academic Press, London.

Drew M C (1990) Sensing soil oxygen. *Plant Cell and Environment* 13: 681-693.

Faiz-ur-Rahman A T M, Trewavas A J, Davies DD (1974) The Pasteur effect in carrot root tissues. *Planta* 118 : 195-210.

Fulton J M, Erickson A E (1964) Relation between soil aeration and ethyl alcohol accumulation in xylem exudate of tomatoes. *Proc. Soil Sci. Soc of America* 28 : 610-614.

Jackson M B, Drew MC (1984) Effects of flooding on growth and metabolism of herbaceous plants. Pages 47-128 In:Flooding and plant growth. T.T. Kozlowski, ed. Academic Press, London.

Jackson M B, Waters I, Setter TL, Greenway H (1987) Injury to rice plants caused by complete submergence: a contribution by ethylene(Ethene). *J.Exp. Bot.* 38:1826-1838.

John C D, Greenway H (1976) Alcoholic fermentation and activity of Some enzymes in rice roots under anaerobiosis. *Aust J. Plant Physiol.* 3:325-336.

Johnson J, Cobb BG, Drew M C (1989) Hypoxic induction of anoxia tolerance in root tips of Zea maize. *Plant physiology* 91:837-841.

Kennedy R A, Rumpho M E, Fox TC (1992) Anaerobic metabolism in plank. *Plant Physiology.* 100:1-6.

Mayne R G, Lea P J (1985) Properties of three sets of isoenzyme of alcoholdehydrogenase isolated from barley *(Hordeum vulgare). Phytochemistry* 24: 1433-1438.

Menegus F, Cattaruzza L, Mattana M, Beffagna N, Ragg E(1991) Response to anoxia in rice and wheat seedlings. *Plant Physiology* 95: 760-767.

Mocquot B, Prat C, Mouches C, Pradet A (1981) Effect of anoxia on energy charge and protein synthesis in rice embryo. *Plant Physiology* 68:636-640.

Mohanty B, Wilson P M, ap Rees T (1993) Effects of anoxia on growth and carbohydrate metabolism in suspension cultures of soybean and rice. *Phytochemistry* 34: 75-82.

Monk L S, Fagerstedt K V, Crawford R M M (1987). Superoxide dismutase as an anaerobic polypeptide. *Plant Physiology* 85: 1016-1020.

Monk L S, Fagerstedt K V, Crawford R M M (1989) Oxygen toxicity and superoxide dismutase as an antioxidant in physiological stress. *Physiologia Plantarun* 76:456-459.

Penning de Vries F W T (1975) The cost of maintenance processes in plant cells. Annals Rot. 39: 77-92.

Pradet A, Bomsel J L (1978) Energy metabolism in plants under hypoxia and anoxia. Pages 89-118. In: Plant life in anaerobic environments. D.D.Hook and R.M.M. Crawford, eds. Ann Arbor Science Publisher Inc, Michigan.

Rea P A, Poole R J (1993) Vacuolar H^+ translocating pyrophosphatase. *Annu Rev Plant Physiol. Plant Mol.Biol.* 44: 157-180.

Raymond P, Pradet A (1980) Stabilization of adenine nucleotide ratios at various values by an oxygen limitation of respiration in germinating lettuce *(Lactuca sativa)* seeds. *Biochem. J.* 190:39-44.

Robards A W, Lucas W J (1990) Plasmodesmata. *Annu. Rev. of Plant Physiol. Plant Mol. Biol.* 41: 369-419.

Setter T L, Kupkanchanakul T, Kupkanchanakul K, Bhekasut P, Wiengweera A, Greenway H (1987) Concentration of CO_2 and O_2 in floodwater and in internodal lacunae of floating rice growing at 1-2metre water depths. *Plant* Cell *Environ.* 10:767-776.

Setter T L, Kupkanchanakul T, Waters I, Greenway H (1988a) Evaluation of factors contributing to diurnal changes in floodwater in deep water rice fields. *New Phytologist* 110:151-162

Setter T L, Kupkanchanakul T, Kupkanchanakul K, Rhekasut P, Wiengweera A.Greenway H (1988b). Environmental factors in deepwater rice areas in Thailand: O_2, CO_2 and ethylene. Pages 55-66. In: Symposium of the 1987 International Deepwater Rice Workshop. IRRI, Los Banos., Philippines.

Setter T L, Waters I, Wallace I, Bhekasut P, Greenway H(1989) Submergence of rice I. Growth and photosynthetic response to CO_2 enrichment. *Aust.J.Plant Physiol.* 16:251-263.

Setter T L, Ingram K T, Tuong T P (1995) Environmental characterisation requirements for strategic research in rice grown under adverse conditions of drought, flooding or salinity. Pages 3-18. In : Rainfed lowland rice-agricultural research for high risk environments. KT Ingram, ed. International Rice Research Institute, Los Banos, Philippines.

Setter T L, Ella E S, Valdez A P (1994) Relationship between coleoptile elongation and alcoholic fermentation in rice exposed to anoxia. II.Cultivar differences. *Ann.Rot.* 74:273-279.

Setter T L, Ramkrishnaya G, Maurya Ram P C, Singh B R (1994) Environmental characteristics of floodwater in flood-prone areas of northern and eastern India: Relevance to flooding tolerance of rice. *Indian J.Plant* Physiol. 38: 34-40.

Stitt M (1990) Fructose-2-6-bisphosphate as a regulatory molecule in plants.*Annu* Rev. *Plant Physiol.Plant* Mol.Biol. 41:153-185.

Thomson C J, Greenway H (1991) Metabolic evidence for stelar anoxia in maize roots exposed to low O_2 concentrations. *Plant Physiology* 96:1294-1301.

Van Raalte M H (1940) On the oxygen supply of rice roots. *Ann. Bot. Gardens Buitettzotg* 50:99-113.

Van Toai T T, Bolles C S (1991) Postanoxic injury in soybean (*Glycine max*)seedlings.Plant Physiology 97:588-592

Waters I, Armstrong W, Thomson C J, Setter T L, Adkins S, Gibbs I, Greenway H (1989) Diurnal changes in radial oxygen loss and ethanol metabolism in roots of submerged and non-submerged rice seedlings. *New Phytologist* 113:439-451.

Webb T, Armstrong W (1983) The effects of anoxia and carbohydrates on the growth and viability of rice, pea and pumpkin. *J.Exp.Bot.* 34:579-603.

Yocum, C.S., Hacket D.P., (1957) Participation of cytochromes in the respiration of the aroid spadex. *Plant Physiology* 32:186-191.

Zhang F, Lin J J, Fox T C, Mujer C V, Rumpho M E, Kennedy R A (1994) Effect of aerobic priming on the response of *Echinochloa crus-pavonis* to anaerobic stress: Protein synthesis and phosphorylation. (Submitted to Plant Physiology).

Zhang Q, Greenway H (1993) Energy dependent transport in anoxic plant tissues. Pages 189-191. In: Proceedings of the Plant Nutritions Colloqium. N.J. Harrow ed. Kluwer Academic Publishers, Perth, Australia.

Zhang O, Lauchli A, Greenway H (1992) Effects of anoxia on solute leakage from beetroot storage tissue. *J.E.xp.Bot* 43: 897- 905.

Zhang Q, Greenway H (1994) Anaerobic catabolism of aged beetroot storage tissue. *J. Exp. Bot.* (in press).

TOLERANCE TO SUBMERGENCE AND ANAEROBIOSIS : RICE SEEDLINGS HAVE SOMETHING STILL TO LEARN

☐ *Michael B. Jackson*[1], *Deborah M.E. Pearce*[2] *and*
Jacky E. Summers[1]

SUMMARY

Rice seeds germinate without oxygen, and the emerging coleoptile may elongate to a greater lengths without oxygen than in its presence. In presence of oxygen the coleoptile responds positively in enhancing carbon dioxide and ethylene production which is expected under these conditions. However, germinating rice fails to produce a root anaerobically, the coleoptile is limited in length to a few millimeters and the first true leaves show low tolerance to oxygen shortage. When totally submerged in clear water, small seedlings fail to gain dry mass through photosynthesis and are dependent on seed reservers for survival. Other aquatic or amphibious species, including *Trapa natans* (Water chestnut), *Echinochloa oryzoides* (barnyard grass), and *Potamogeton pectinatus* (pond weed) appear to have overcome these shortcomings.

INTRODUCTION

Higher plants must be well aerated in order to survive, compete and complete their life cycle successfully. All plant parts require oxygen for respiration and other biochemical oxidations/ oxygenations. Besides, green shoots require an external input of carbon dioxide for photosynthesis that benefits the whole plant. Plants also need to dispose the potentially active or damaging volatile metabolites such as photosynthetic oxygen, acetaldehyde, ethylene or methyl jasmonate produced by various metabolic pathways. The principal environmental factor affecting aeration is water. Little available water adversly affects the growth whereas, too much water can asphyxiate and may kill growing seedlings in majority of cases. Slow diffusion of gas in water compared to air (D_{water} / D_{air}) is approximately 1.13×10^{-4} which is responsible for this traumatic effect of an otherwise harmless substance.

Despite these caveats, a sizable number of species tolerate flooded and submerged conditions well to a large extent and constitute a vigorous and ecologically significant aquatic or amphibious flora in many parts of the World (Maltby, 1991). Rice (*Oryza sativa* L.) is the only crop plant that can easily be placed in this group and hence its dietary preeminence in the humid tropics.

---

[1] Department of Agricultural Sciences, University of Bristol, Long Ashton Research Station, Bristol BS18 9AF, Great Britain

[2] School of Biological Sciences, Queen Mary and Westfield College, University of London, London E14NS, Great Britain.

The physiological and metabolic characteristics of flood-tolerant plants are varied and differ depending upon the stage of development and the species. Tolerance often is achieved through a combination of short-term resistance to absence of oxygen, physiological responses such as fast elongation under water that minimise the duration of submergence or anoxia, and the ability to fix carbon dioxide photosynthetically or bicarbonate dissolved in flood water. Tolerant plants must also be able to survive the potentially damaging effects of the entry of oxygen into previously anaerobic conditions (i.e., post anoxic injury - Andreev *et al.,* 1991.) The extent to which rice possesses these characteristics is reviewed in the present paper.

ANAEROBIC GERMINATION

Rice is well-known for its ability to germinate without oxygen. In this regard it has few rivals only since the number of other species known to germinate anaerobically is small. These include *Erithrina caffra, Nuphar luteum and Scripus mucronatus* (Menegus *et al.,* 1992a), and various species of *Echinochloa* some of which are weeds in rice field (Barrett and Seaman, 1980). In each case only the shoot emerges from the anoxic seeds. Thus, anaerobically germinating seedling is without an anchoring rootlet. This can be a problem in fields to direct-sown rice where anaerobic conditions make it difficult for the crop to become firmly established. The reason for the failure of the emerging embryonic root under anaerobic condition is not clear, however it survives, and quickly elongates when oxygen is made available (Kordan, 1977). However, one species, *Trapa natans* (the water chestnut), is able to germinate by radicle emergence (Menegus *et al.,* 1992a). This is the only species known where root growth is not inhibited by anoxia. On the contray in seedling, root extension is actually promoted by the absence of oxygen in this plant. The metabolic and physiological basis of this unique characteristic are not yet fully understood. Metabolic studies (Menegus *et al.,* 1992a) of *T. natans* have shown a high rate of alcoholic fermentation (20 u mol ethanol g^{-1} FW h^{-1}), the availability of respirable starch reserves, and an ability to avoid cytoplasmic acidification achieved through. (i) minimal production of potentially fatal lactic acid, (ii) proton consumption in conversion of malate to succinate, (iii) arginine to putrescine, (iv) glutamate to Y-aminobutyric acid (GABA). These metabolic features are strongly reminiscent of the rice coleoptile (Menegus *et al.,* 1992b; Fan *et al.,* 1993; Perata *et al.,* 1992; Ricard *et al.,* 1991). They are considered to help in avoiding acidification of the cytoplasm, maintain sufficiently high levels of ATP and dissolved solutes to support cell expansion and membrane integrity, while other energy consuming processes such as the overall levels of protein synthesis (Mocquot *et al.,* 1977) and fatty acid production (Vartapetian *et al.,* 1978) are suppressed. However, a large number of proteins can be synthesised anaerobically in the coleoptile (Chirkova and Hoang 1981; Atwell and ApRees, 1986), and two dimensional gels of radio- labelled proteins synthesised in aerobic and anaerobic conditions show remarkably similar patterns (Ricard and Pradet, 1989).

One way of improving the performance of germinating rice seeds would be to induce the embryonic root axis to elongate as a coleoptile, while retaining the positive gravitropism typical to aerobic rice roots. This may be possible because anoxia and root growth are not mutually incompatible in *Trapa natans.* A large screening programme might be useful to have this capability in rice. Genetic engineering is an alternative if differences in gene expression can be shown to understand the contrasting behaviour of root and shoot. The number of proteins synthesised by anaerobic roots is small compared to the coleoptile (Ricard and Pradet, 1989) but the nature of anaerobic energy metabolism in roots and shoots of rice seedlings appears remarkably similar (Mayne and Kende, 1986), at least in the short term when switched from aerobic to anaerobic conditions (Fig. 1). This suggests that deficiencies in fermentative sugar metabolism do not explain why roots fail to emerge from the seed anaerobically, and that some other phenomenon in blocking growth is involved. The absence of cell division in anoxic roots (Amoore 1961; Kordan, 1976) may be one although it is notable that anoxia does not entirely stop cells from dividing in the emerging rice coleoptile (Kordan 1976; Opik, 1973) or in stems of *P. pectinatus* (Summers and Jackson, 1993). However, studies of the so-called 'gamma plantlets', in which cell divisions in the mature embryo of wheat *Triticum vulgare*) or maize (*Zea mays*) are prevented by prior irradiation, show that, on imbibition, the primary rootlet can still extend 9- 15 times its original length without the need for cell divisions (Foard and Haber, 1961). But, anoxic rice seeds fail to achieve even this limited amount of root extension, indicating that some other process inhibits the radicle emrgence. Identifying the physiological and genetic basis of this blockage would be an important step in achieving the goal of producing rice seeds in which anaerobic germination incorporates root emergence.

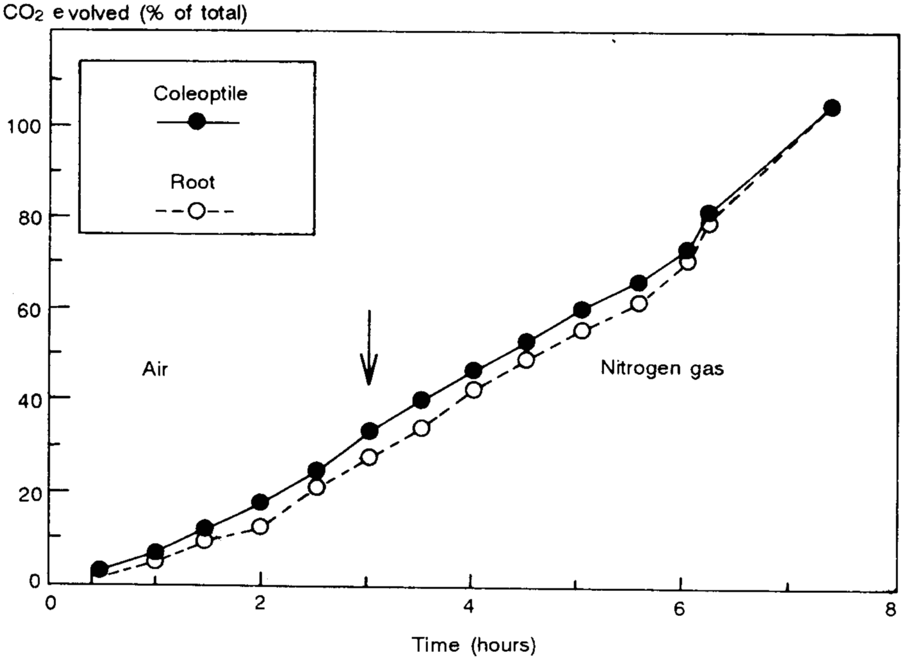


Fig. 1. Comparison of the production of radioactive carbon dioxide by root or coleoptile of rice supplied with [U-^{14}C] glucose at time zero. After 3 h (arrow) the atmosphere was changed from aerobic to anaerobic. (After Mayne and Kende, 1986).

GROWTH OF COLEOPTILE WITHOUT OXYGEN

Anaerobic germination can lead to successful development of the seedling if some source of oxygen is made available before reserves in endosperm run out. This is usually the surface water which is well aerated or the atmosphere where the coleoptile allows oxygen to penetrate and move the entire seedling (the ’Schnorkel’ effect - Kordan, 1974) through the hollow coleoptile (Kutschera et al., 1990) and highly permeable aerenchymatous leaf and root interiors (Fig. 2). Aerenchyma is created constitutively by the collapse of cells and in roots, it can be initiated within a day of their leaving meristem and involves cell wall degradation (Webb and Jackson, 1986). Additional aerenchyma may be induced by the action of ethylene in some cultivars (Justin and Armstrong, 1991), not in all (Jackson *et al.,* 1985).

Fast elongating coleoptile has greater chances to reach the oxygenated zones closer to the surface. Thus the rice coleoptile not only survives and even grows in length without oxygen for serveral days, but the rate of extension can also be stimulated in the absence of oxygen. In Fig.3 it has been shown that in

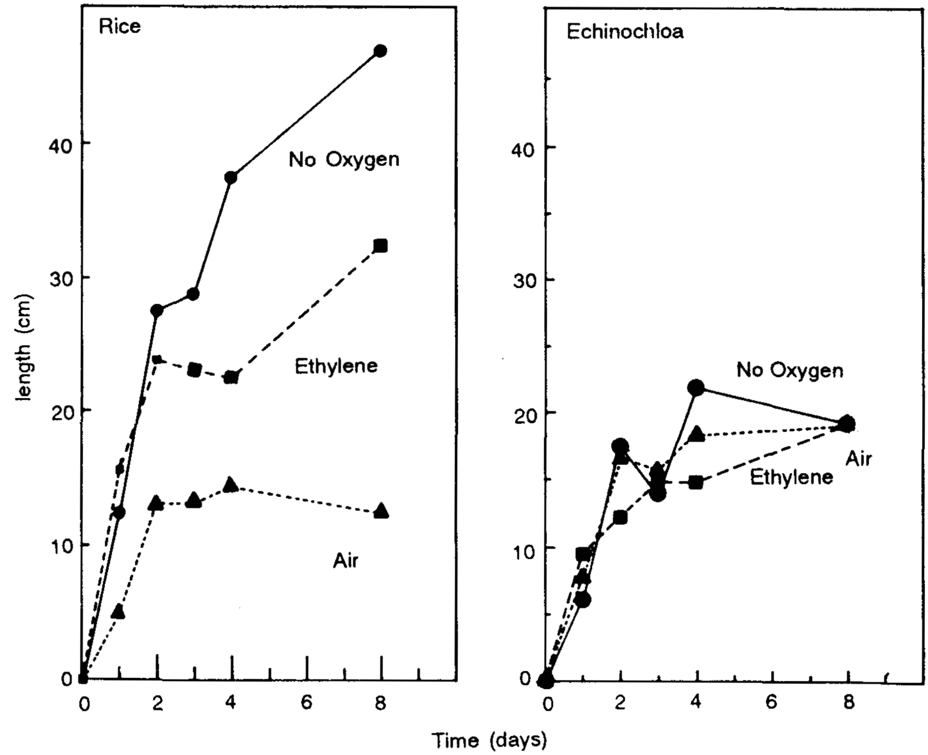


Fig. 2. Extension growth by the coleoptile of rice and *Echinochloa oryzoides* seedlings grown in air (’Air’), air containing 1.0 Pa ethylene (‘Ethylene’), or in nitrogen gas (‘No oxygen’) for up to 8 d (taken from Pearce and Jackson, 1991).

the submergence tolerant rice cultivar 'Calrose' the length of coleoptile was 3.4 cm longer in nitrogen environment than air after 8 day. This growth is unlikely due to endogenous hormones such as auxin, ethylene or gibberellins since they are inactive when supplied to anoxic coleoptiles (Jackson and Pearce 1991; Horton, 1991). However, the diamine putrescine appears to play a positive role in anaerobic coleoptile elongation (Reggiani *et al.,* 1989) while abscisic acid could be inhibitory (Horton, 1991). Futhermore, interference in the already weak gravitropism in anoxic rice coleoptile by auxin transport inhibitor such as N-1 naphthylphthalamic acid (recently reported by Horton, 1994) implies that endogenous auxin has some role under oxygen-free conditions. However, it is contrary to competing weed *E. oryzoides,* where coleoptile elongation is neither stimulated nor inhibited in absence of oxygen (Fig. 3) In these species, a 20- mm long coleptile can easily be obtained regardless of the availability of oxygen or the presence of elevated levels of ethylene (Fig. 3) or carbon dioxide (Pearce and

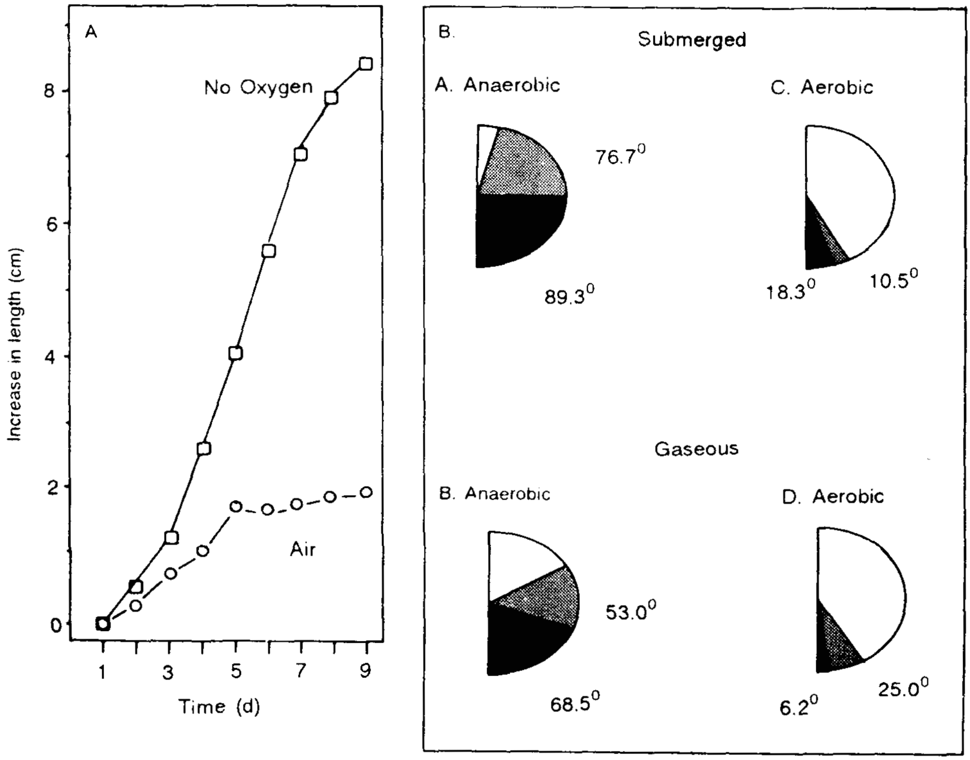


Fig. 3. Anaerobic growth by shoots of *Potamogeton pectinatus* tubers. A. Stem extension of shoots submerged in water sparged with air ('Air') or with an anaerobic gas mixture of hydrogen and oxygen ('No oxygen'). B. Negative (i.e, upward) gravitropic curvature by shoots in submerged or in a gas phase with ('Aerobic') or without (Anaerobic') oxygen. (Summers and Jackson, 1993).

Jackson, 1991). Thus, such indifference to extremes in the gaseous environment is unprecedented.

The positive effect of the absence of oxygen on elongation in rice coleoptiles is small compared to those reported for the stem of the overwintering tubers of a temperate aquatic weed *Potamogeton pectinatus.* This species is the only known example where shoot elongation is stimulated by the complete lack of oxygen (Summers and Jackson, 1993). In this case it is the stem tissue that reponds, but with a vigour which far exceeds the rice coleoptile (Fig. 4). Further, growth may proceed for 14 d and is highly responsive to gravity (Fig. 4), suggesting that elongation is oriented upwards and towards the better aerated surface zones. In contrast, the anaerobic rice coleoptile has an impaired ability to respond to gravity (Kutchera *et al.,* 1990; Horton, 1994) resulting in disorientated extension that may affect the adaptive value of the stimulation caused by anoxia to extension growth (Kordan, 1975).

COLEOPTILE EXTENSION IN PRESENCE OF DISSOLVED OXYGEN

When sumerged, coleptiles of rice move towards water that contains some dissolved oxygen, several additional mechanisms are involved for the continuous and unabated coleoptile elongation. The presence of some oxygen permits ethylene biosynthesis which would have rather been blocked during the preceeding anaerobic condition because the oxidation of ethylene precursor 1- aminocyclopropane-I-carboxylic acid (ACC) requires free oxygen. When oxygen is admitted, initially ethylene production is unusually fast because the accumulated ACC is converted to ethylene (Table 1).

Table 1. Effect of transferring seedling of rice *(Oryza sativa)* from anaerobic to aerobic conditions on coleoptile length, ethylene production and concentrations of 1-aminocyclopane-1- carboxylic acid .(ACC). From Pearce *et al.,* (1992).

Condition	Coleoptile length (mm)	Ethylene production (nl g^{-1} h^{-1})	ACC (nmol g^{-1} fresh wt.)
No oxygen for 4 d	29.7	00	23.1
Air for 4 d	18.7	2.1	02.5
No oxygen " air on day 3	32.0	3.7	11.7

The surrounding water then entraps the newly synthesised ethylene (Ishizawa and Esashi, 1984), and the presence of some oxygen also allows cells to respond physiologically to the ethylene. In case of coleoptile cells, elongation is enhanced (Table 1 and Pearce and Jackson, 1991) by ethylene in association with the action of auxin (Ishizawa and Esashi, 1983). The rice coleoptile was the first organ, of any specices, found to elongate faster in respone to ethylene gas (Ku *et al.,* 1970). This positive response of gas (optimum 0.1 Pa) can be related to the presence of ethylene binding sites (Sander *et al.,* 1990) and to enhanced translocation of sucrose into the coleoptile (Ishizawa and Esashi, 1988). Ethylene action is augmented by other features of the submerging environment also. These include elongation promoting influences of carbon dioxide (optimum 10-15 kPa), partial oxygen shortage (optimum 3 kPa) and the stretching influence of buoyant tension (Pearce and Jackson, 1991). Ethylene, carbon dioxide and low oxygen act either separately (Raskin and Kende, 1983), or interactively (Ku *et al.,* 1970). However, neither low oxygen nor high carbon dioxide act by stimulating ethylene biosynthesis (Raskin and Kende, 1983; Pearce and Jackson, 1991) and presumably possess intrinsic growth promoting activity in their own right. In addition to promoting elongation, the extra 'post-anoxic' ethylene conceivably could help in reducing injury (Ushimaru *et al.,* 1992) arising from hydrogen peroxide generation (Mehlhorn 1990) by promoting the activity of ascorbate peroxidase.

Emergence of leaves and stems

When the elongation of coleoptile stops, the first true leaves, enclosed by the coleoptile, emerge in presence of some amount of oxygen. Leaf elongation is strongly inhibited in abscence of oxygen in rice (Turner *et al.,* 1981). Thus, further growth underwater is not possible unless a source of oxygen is met. This is probably true for majority of other species. However there can be exceptions. For example, leaves on shoots of *P. pectinatus* tubers extend vigorously in absence of oxygen, although the rate is slower than in well-aerated water (Table 2).

Table 2. Effect of anaerobic conditions on elongation by the first leaf of overwintering tubers of *Potamogeton pectinatus,* over 5 d. From Summers and Jackson, unpublished.

Condition	Water	Gas phase
Aerobic	6.2*	4.5
Anaerobic	3.3	3.9

* Significantly different from 'anaerobic' (p= 0.05)

If oxygen is present alongwith light, extension in one of the young rice leaves is promoted by total submergence (Fig.5), while senescence in the first leaf of the seedings is promoted. Both effects are probably mediated by ethylene since submerged shoots become enriched with endogenous ethylene (Jackson *et al.,* 1987) whereas application of ethylene to non-submerged plants stimulate extension in the youngest visible leaf (Fig. 5; Ku *et al.,* 1970; Jackyon *et al.,* 1987, but see Raskin and Kende, 1984) and promote loss of chlorophyll in the oldest leaf (Jackson *et al.,* 1987). Unexpectedly, the effect of ethylene is linked with increased dry weight (Jackson *et al.,* 1987 and Fig. 5). This probably indicates the ability of ethylene to increase the assimilate import from the seed (Ishizawa and Esashi, 1988). The promoting effects of submergence, and ethylene on leaf extension are not shared by the competitive weed i.e. *E. oryzoides* (Pearce, 1990) but can be found in some other species e.g., *P. pectinatus* (Summers and Jackson, 1993). Elongation in the roots of rice is also favoured by modest increases in ethylene (Fig.5, Smith and Robertson, 1971; Konings and Jackson, 1979). As noted in coleoptile, carbon dioxide entrapped in submerged condition also enhances the leaf extension in rice (Raskin and Kende, 1984). In the dark this may suggest growth regulating activity of carbon dioxide, but in light it is due to increased photosynthetic carbon fixation rate (Setter *et al.,* 1989).

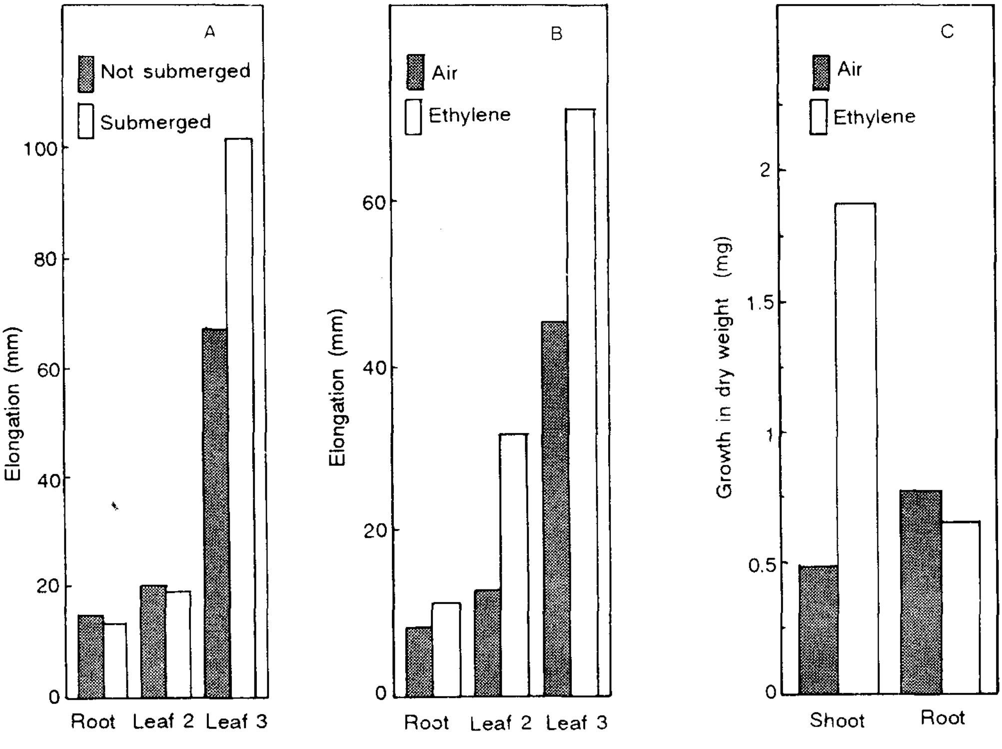


Fig. 4. Effect of complete submergence or of ethylene treatment given for 3 d to 7-d-old light-grown seedlings of rice. Effect of submergence (A) or 10 Pa ethylene (B) on elongation by the longest root and the second and third oldest leaves. Effect of ethylene on growth in dry weight (C). From Pearce, 1990.

Increase in dry mass

A close examination of the dry mass gain in 7-d old rice plants submerged in the light (850 u mol m^{-2} s^{-1}) shows that the shoot and root can gain only a small amount of dry mass over 3d. This is achieved at the expense of the seed reserve (Table 3), indicating just survival with little or no net gain from external carbon. The decrease in photosynthetic rate is not due to damage of the photosynthetic machinery since submerged leaves release oxygen-rich gas bubbles in light and the surrounding water becomes enriched with dissolved oxygen. Others have shown that submerged rice plants, if supplied with carbon dioxide, fix it photosynthetically showing high growth rates (Setter *et al.,* 1989). Thus, it is clear that submerged rice seedlings can and do fix carbon photosynthetically, but mostly utilize the respiratory released carbon dioxide. However, *E. oryzoides* is a contrasting type as its seeds are very small and have small amount of reserves (Table 3).

Table 3. Effect* of 3 days complete submergence and 3 days recovery (de-submergence) on shoot, root and seed dry weights of rice (cv. Calrose) and *Echinochloa oryzoides* seedlings.

Day	Rice			Echinochloa		
	Shoot wt(mg)	Root wt(mg)	Seed wt(mg)	Shoot wt(mg)	Root wt(mg)	Seed wt(mg)
Day 0	7.4	3.2	11.8	5.0	3.7	2.4
Day 3						
Not Submerged	14.4	5.3	6.6	22.0	9.6	2.1
Submerged	8.9	2.6	5.6	6.9	3.0	2.3
Day 6						
Not submerged	20.1(5.7)	13.4(8.1)	2.9(-3.7)	33.0(11)	24.7(15.1)	2.1(0)
De-submerged	13.4(4.5)	6.5(3.9)	6.2(0.6)	30.5(23.6)	21.9(18.9)	1.6(-0.7)

* Plants were 7-d old at the start; Figures in parentheses are changes over the last 3 days of the experiment.

Besides, seedlings submerged in light survive and gain a small increase in dry weight. *E. oryzoides* has a superior ability to fix carbon dioxide (Smith and Walker, 1980). This may be expected from a C_4 species compared to a C_3 plant rice because a C_4 plant has low compensation point (Madsen, 1993). The difference between the two species in their dependence on external carbon dioxide is shown in Fig 5. If seedlings of both the species are grown with their shoots in moist air from which carbon dioxide has been removed completely, growth in dry mass by the root and

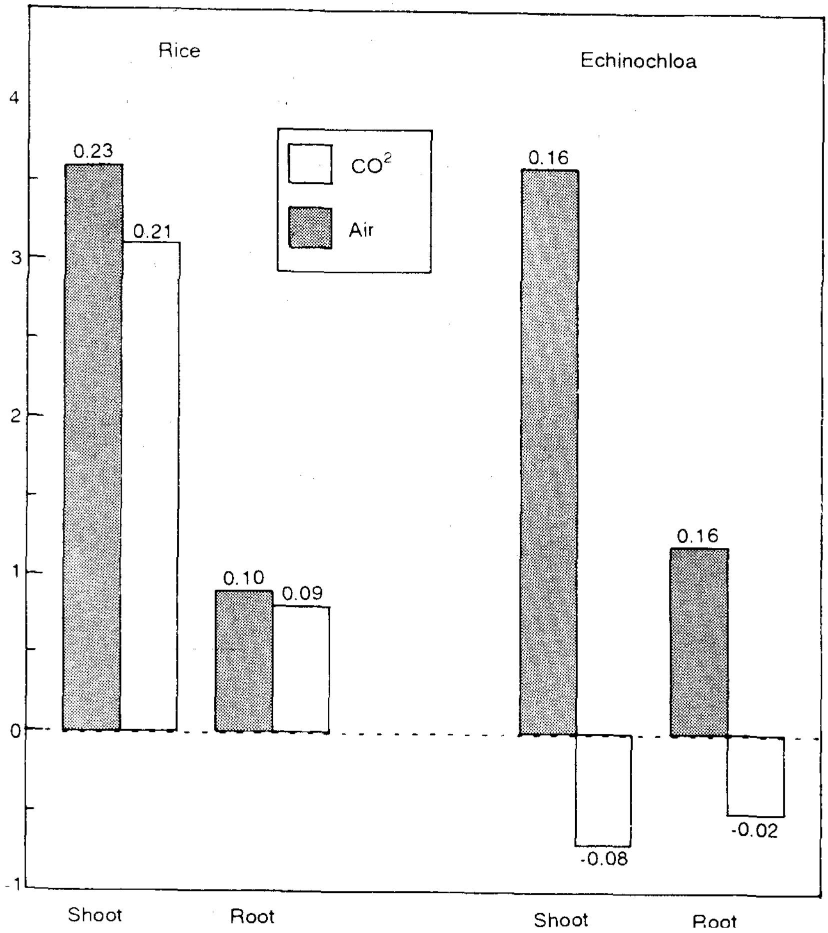


Fig. 5. Effect of absorbing carbon dioxide from air on growth in dry mass by initially 7-d old light-grown seedling with the roots in nutrient solution and the shoots in a gas phase flowing at approximately 2L min^{-1} at 850 u mol m^{-2} s^{-1} PAR. Figures above the bars are relative growth rates (mg mg^{-1} d^{-1}). From Pearce, 1990.

shoot stops in *E. oryzoides.* But in rice, root and shoot growth continues but at the expense of seed reserves. Thus, submerged *E. oryzoides* achieves its small increase in mass by fixing carbon dioxide from the water and not by using seed reserve. In contrast, rice while being unable to fix carbon dioxide from the dissolved water, compensates it by drawing from the seed reserves. This way both the species survive three days total submergence in well-illuminated water at the 7-leaf stage and are able to grow strongly if shoots are exposed to air (Table 3).

CONCLUSION

Rice can germinate without oxygen, and its seedlings can grow in submerged conditions that are partially depleted of oxygen. The coleoptile elongates to a greater length than in normal in response to anaerobiosis, partial oxygen shortage, and enriched ethylene or carbon dioxide. These factors are inhibitory for most of the species. However, roots fail to emerge from rice seeds unless some oxygen is present, while anaerobic stimulation of coleoptile elongation is limited to only a few millimetres. Forthermore, extension of the first true leaves is dependent on oxygen, although its effect is increased by ethylene and carbon dioxiode . If the shoots of small seedlings are submerged, photosynthetic fixation of carbon dioxide from the flood water is minimal and the shoot and roots depend on seed reserves for survival over at least for 3 days.

Certain other species are shown to perform better than rice in several aspects. *Trapa natans* can produce a root when germinating anaerobically and stems of anaerobic *Potamogeton pectinatus* tubers elongate much more vigorously for longer period than rice coleoptiles and have stronger negative gravitropism. The coleoptile of *Echinochloa oryzoides* can extend its full length irrespective of presence or absence of oxygen whereas the leaves of *P. pectinatus* can elongate strongly with oxygen. The shoots of *E. oryzoides* are able to survive independently of the seed reserves when submerged for 3 days and grow more vigorously than rice after exposed to re-submergence. Studies show how these species out-perform rice under conditions of poor aeration, and ultimately, may help select or create strains of rice with superior performance in flooded conditions. These studies show the capabilities of the species other than rice to perform better under the poor condition of aeration and thus open the scope for developing better strains of rice with such characteristics to perform well under flooded conditions.

REFERENCES

Amoore JE (1961) Arrest of Mitosis in roots by oxygen lack or cyanide. *Proc. Roy. Soc. B.* 154 :95-108.

Andreev VY, Generozova I P, Vartapetian B B (1991) Energy status and mitochondrial ultrastructure of excised pea root at anoxia and post anoxia. *Plant Physiol. Biochem.* 29:171-176.

Atwell B J, ApRees T (1986) Distribution of protein synthesised by seedlings of *Oryza sativa* grown in anoxia. *J. Plant Physiol.* 123: 401-408.

Barrett S C H, Seaman D E (1980) The weed flora of California rice fields. *Aquatic Bot.* 9: 351-376.

Chirkova T V, Hoang K L (1981) Electrophoretic pattern of cytoplasmic and mitochondrial proteins in wheat and rice roots under anaerobiosis. *Fiziol. Rast.* 28:136-143,

Fan T W M, Lane AN, Higashi R M (1993) Energy and fermentation metabolism in hypoxic rice coleoptile - a multinuclear NMR approach, Pages 333-352 In: Interacting stresses on plant in a changing climate. M B Jackson and C R Black, eds. Springer- Verlag, Berlin, Germany.

Foard D E, Haber A H (1961) Anatomic studies of gamma-irradiated wheat growing without cell division. *Amre. J. Bot.* 48:438- 446.

Horton R F (1991) The effect of ethylene and other regulators on coleoptile growth of rice under anoxia, *Plant Sci* . 79:57- 62.

Horton R F (1994) Gravitropism in rice seedlings: the effects of anoxia and N-1 naphthylphthalamic acid. *Plant Sci.* 95:41- 47.

Ishizawa K, Esashi Y (1983) Co-operation of ethylene and auxin in the growth regulation of rice coleoptile segments. *J.Exp.Bot.* 34: 74-82.

Ishizawa K, Esashi Y (1984) Gaseous factors involved in the enhanced elongation of rice coleoptiles under water. *Plant Cell Environ.* 7 : 239-25.

Ishizawa K, Esashi Y (1988) Action mechanism of ethylene in the control of sugar translocation in relation to rice coleoptile growth I. Sucrose metabolism. *Plant Cell Physiol.* 29 : 131-141.

Jackson M B, Pearce D M E (1991) Hormones and morphological adaptation to aeration stress in rice. Pages 47-67. In: Plant life under oxygen deprivation. Ecology, physiology and biochemistry. M.B. Jackson, D.D. Davies and H. Lambers, eds. SPB Academic Publishing, The Hague, The Netherlands.

Jackson M B, Fenning T M, Jenkins W (1985) Aerenchyma (gas space) formation in adventitious roots of rice (*Oryza sativa* L.) is not controlled by ethylene or small partial pressures of oxygen. *J. Exp. Bot.* 36: 1566-1572.

Jackson M B, Waters I, Setter T, Greenway H (1987). Injury to rice plants caused by complete submergence; a contribution of ethylene *J. Exp. Bot.* 37 : 1826-1838.

Justin S H F, Armstrong W (1991) Evidence for the involvement of ethylene in aerenchyma formation in adventitious roots of rice (*Oryza sativa* L.). *New Phytol.* 118: 49-62.

Konings H, Jackson M B (1979) A relationship between rates of ethylene production by roots and the promoting or inhibiting effects of ethylene on root elongation. *Z Pflanzenphysiol.* 92: 385-397.

Kordan H A (1974) Patterns of shoot and root growth in rice seedlings germinating in oxygen. *J.Plant Ecol.* 11: 685- 690.

Kordan HA (1975) Relationship between oxygen availability and transverse and vertical shoot geotropism during germination of submerged rice seedlings. *Ann. Bot.* 39: 249-256.

Kordan H A (1976) Mitotic activity in rice seedling under oxygen deficiency. *J. Cell Sci.* 20 57-59.

Kordan H A (1977) Latent effect of anaerobiosis on root growth in germinating rice seedlings. *Plant Sci. Lett.* 9 53-56.

Kordan H A, Ashraf M (1990) Environmental anoxia is unnecessary for inhibiting chloroplast photomorphogenesis in rice coleoptiles (*Oryza sativa* L.). *J. Exp. Bot.* 41 : 435-440.

Ku H S, Suge H, Rappaport L, Pratt H K (1970) Stimulation of rice coleoptile growth by ethylene. *Planta* 90 : 333-339.

Kutschera U, Siebert C, MasudaY, Sievers A (1990) Effects of submergence on development and gravitropism in the coleoptile of *Oryza sativa* L. *Planta* 183: 112-119.

Madsen T V (1993) Inorganic carbon assimilation and growth of aquatic macrophytes. Pages 267-285. In: Interacting stresses on plants in a changing climate. M.D. Jackson and C.R. Black, eds. Springer-Verlag, Berlin, Germany

Maltby E (1991) Wetlands-their status and role in the biosphere. Pages 3-21 In: Plant life under oxygen deprivation. Ecology, physiology and biochemistry M.R. Jackson, D.D. Davies and H. Lambers, eds. SPB Academic Publishing, The Hague, The Netherlands.

Mapelli S, Bertani A (1993) Endogenous phytohormones and germination of rice under anoxia: indoleacetic acid and abscisic acid. Pages 353-363. In: Interacting stresses on plants in a changing climate. M.B. Jackson, C.R. Black, eds. Springer-Verlag, Berlin, Germany

Mayne G R, Kende H (1986) Glucose metabolism in anaerobic rice seedlings. *Plant Sci.* 45:31-36.

Mehlhorn H (1990) Ethylene-promoted ascorbate peroxidase activity protects plants against hydrogen peroxide, ozone and paraquat. *Plant Cell Environ.* 13:971-976.

Menegus F, Cattaruzza L, Scaglioni, Ragg E (1992a) Effects of oxygen level on metabolism and development of seedlings of *Trapa natans* and two ecologically related species. *Physiol. Plant.* 86 : 168-172.

Menegus F, Cattaruzu L, Molinari H, Ragg E (1992b) Rice and wheat seedlings as plant models of high and low tolerance to anoxia. Pages 53-66. In: Surviving hypoxia: Mechanisms of control and adaptation. P.W. Hochachka, ed. CRC Press, Boca Raton, USA.

Mocquot B, Pradet A, Litvak S (1977) DNA synthesis and anoxia in rice coleoptiles. *Plant Sci. Lett.* 9 : 365-371.

Opik H (1973) Effect of anaerobiosis on respiratory rate, cytochrome oxidase activity and mitochondrial structures in coleoptiles of rice (*Oryza sativa.* L.). J.Cell Sci. 12 : 725-739.

Pearce D M E (1990) A comparison of the responses of seedlings of rice and *Echinochloa oryzoides* to submergence. PhD dissertation, University of Bristol, Great Britain.

Pearce D M E, Jackson M B (1991) Comparison of growth responses of barnyard grass (*Echinochloa oryzoides)* and rice (*Oryza sativa*) to submergence, carbon dioxide and oxygen shortage. *Ann. Bot.* 68:201-209.

Pearce D ME, Hall KC, Jackson M B (1992) The effect of oxygen, carbon dioxide and ethylene on ethylene biosynthesis in relation to shoot extension in seedlings of rice (*Oryza sativa*) and barnyard grass (*Echinochloa oryzoides*). *Ann. Bot.* 69: 441- 447.

Perata P, Pozueta J, Akazawa T, Yamaguchi J (1992) Effect of anoxia on starch breakdown in rice and wheat seeds. *Planta* 188: 611-618.

Perata P, Alpi A (1993) Plant responses to anaerobiosis. *Plant* Sci. 93:1-17.

Raskin I, Kende H (1983) Regulation of growth in rice seedlings. *Pl. Growth Regul* 2: 192-203.

Raskin I and Kende H (1984) Regulation of growth in stem sections of deepwater rice. Planta 160 :66-72.

Reggiani R, Hochkoeppler A, Bertani A (1989) Polyamines and anaerobic elongation of rice coleoptile. *Plant Cell Physiol.* 30:893-898.

Ricard B, Pradet, A (1989) Anaerobic protein synthesis in different organs of germinating rice seedlings. *Plant Physiol, Biochem.* 27: 761-768.

Ricard B, Rivoal J, Spiteri A (1991) Anaerobic stress induces transcription and translation of sucrose synthase in rice. *Plant Physiology.* 95: 669-672.

Sanders I O, Ishizawa K, Smith A R, Hall M A (1990) Ethylene binding and action in rice seedlings. *Plant Cell Physiol.* 31 :1091-1099.

Setter T L, Waters I, Wallace I, Bhekasut P D, Greenway H (1989) Submergence of rice I. Growth and photosynthetic response to CO_2 enrichment of floodwater. *Aust, J. Plant Physiol.* 16: 251-263.

Smith K A, Walker N A (1980) Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO^-_3 and to carbon isotope discrimination. *New Phytol.* 86: 245-259.

Smith K A, Robertson P D (1971) Effect of ethylene on root extension of cereals. *Nature* 234: 148-149.

Summers J, Jackson M B (1993) Promotion of stem extension in an aquatic monocot (*Potamogeton pectinatus* L.) by the complete absence of oxygen, and by partial oxygen shortage. Page 315-326. In: M B Jackson and C R Black, eds. Springer-Verlag, Berlin, Germany.

Turner F T, Chen C-C, McCauley G N (1981) Morphological development of rice seedling in water at controlled oxygen levels. *Agron. J.* 73 : 566-570.

Ushimaru T, Shibaska M, Tsuji H (1992) Development of the O_2 detoxification system during adaptation to air of submerged rice seedlings. *Plant Cell Physiol.* 33 :1065-1071.

Vartapetian B B, Mazliak P, Lance C (1978) Lipid biosynthesis in rice coleoptiles grown in the presence or in the absence of oxygen. *Plant Sci. Letts.* 13 : 321-3213.

Webb JD, Jackson M B (1986) Transmission and cryo-scanning electron microsocopy study of the formation of aerenchyma (cortical gas-filled space)in adventitious roots of rice) *Oryza sativa*) *J Exp. Bot.* 34: 579-603.

ENVIRONMENTAL AND PLANT MEASUREMENT REQUIREMENTS FOR THE ASSESSMENT OF DROUGHT, FLOOD AND SALINITY TOLERANCE IN RICE

□ *P.C. Ram*[1], *B.B. Singh*[1], *A.K. Singh*[1], *V.K. Singh*[1]
O.N. Singh[1], *T.L. Setter*[2], *R.K. Singh*[1] and *V.P. Singh*[2]

SUMMARY

For the assessment of stress tolerance of rice, a set of environmental and plant measurements are presented which need to be monitored prior to and during the different growth and developmental phases of plants. These measurements on soil, plant, atmosphere and flood water systems are essential for integration and characterization of rice ecosystems which may facilitate interpretation of stress tolerance mechanism of plants.

The findings of experiments done at the Faizabad consortium site alongwith a brief review are presented in order to prioritize and establish relationships between environmental measurements and rice productivity under adverse ecosystems of rainfed lowland rice culture.

INTRODUCTION

Diversity and variability of environment in different rice growing countries and regions (Herdt and Barker, 1977) would make the development of an appropriate technology difficult. Herdt and Barker (1977) have listed a set of environmental factors that vary across sites, seasons and years. With the available literature on soils and climate, information is still lacking on many rice-growing environments.

The average rice yields in different countries range from less than 1 t/ha to more than 6 t/ha. There are a number of biological, environmental and socio-economic reasons for the large differences in rice yields associated with rainfed lowland, deepwater and upland rice in tropical and temperate regions. Of these, temperature, solar radiation and rainfall influence rice yield most by directly affecting the physiological processes involved in grain production. Yield is also indirectly affected through diseases and insects. These factors are often difficult to separate from one another in the field and influence crop period, productivity and stability which are the important aspects of rice cultivation. The complete information on environmental measurements are seldom collected along with plant measurements, hence the interpretation of data becomes difficult; and at times, inaccurate and misleading conclusions are drawn. Further, such experimental data can not be extrapolated to other sites or times unless essential environmental and

---

[1] N.D. University of Agriculture and Technology, Kumarganj, Faizabad,U.P., India
[2] International Rice Research Institute, P.O. Box 933, Manila, Philippines

plant measurements are generated and quantified accurately. Screening of rice genotypes for flood and salinity tolerance should be done under well defined and characterized sites. For example, saline areas may also have the alkalinity problems along with high levels of soluble salts in the medium. Similarly for flooding, the depth and duration of submergence, the growth stage of plant at the time of submergence, turbulence and turbidity etc. may be important factors which affect biomass and yield production. These environmental and plant measurements can well be used for development of basic models to quantify growth and development of rice under drought, flooding and salinity situations.

MATERIALS AND METHODS

The findings reported are from a number of experiments conducted under drought, submergence or salinity conditions.

Drought

Three rice genotypes were tested during 1992 wet season for their relative performance under drought imposed at vegetative and boot stages of plant growth. The details of methodology are described below :

* Culture : Pot experiment - Soil culture, 30 cm pot size
* Genotypes - IR 28 (intolerant) IRAT -142 (medium tolerant) and Kachani (tolerant)
* Stages of water stress : Tillering (T) and Booting (B)
* Method of stress : With-holding of irrigation until the appearance of permanent wilting point (PWP).
* Revival : After 48 hours at PWP the plants were revived by application of water into the pots.

Observations

* Soil water content : Gravimetrically at field capacity and PWP (Jackson, 1973).
* Leaf water potential: Liquid equilibration method (Shardakov 1948).
* Growth and Yield : Tillers, biological and grain yields, grain sterility etc.

Flooding/submergence

* The performance of some of the elite rice lines was assessed under prolonged partial submergence during 1992 and 1993 wet seasons under field conditions.
* No. of Genotypes - 201
* Age of seedling at planting - 30 days
* Water depth - Variable (monitored during the crop season)

Observations

- Climatic parameters : Rainfall, sunshine hours, temperature, relative humidity.
- Plant parameters : Survival, growth and yield parameters.
- Water characterization of rainfed lowland rice fields: The measurement of dissolved oxygen, temperature, CO_2 and total inorganic carbon (TIC) was done during 1993 wet season at crop research stations, Pagalabhari and Ghagharaghat. Dissolved oxygen was measured using a submersible polarographic O_2 electrode (Syland model 610, Heppenheim, West Germany) attached to a measuring rod. The electrode was calibrated in the field using aerated water prepared by vigorously shaking distilled water in air for 1-2 min. The data on temperature and dissolved O_2 concentrations have been presented here while dissolved CO_2 and total inorganic carbon alongwith other parameters have been presented in another paper (Setter *et al.,* 1995).

Salinity/sodicity

The experiments were conducted in two situations: the normal soil which was moderately alkaline (pH 8.5) and partially reclaimed sodic soil which had a pH 9.7. Rainfed lowland rice genotypes were planted in field during 1992 (64 lines) and 1993 (55 lines). The details of experiments are given below :

- No. of Genotypes : - 64 (1992), 55 (1993)
- Seedling age at planting : 30-35 days
- Number of seedlings planted : 3-4 seedlings/hill
- Fertilizer applied : 120 , 60, 60 N P and K (Kg/ha)

Observations

- Climatic parameters -Rainfall, sunshine, temperature (Max. Min.) relative humidity during crop season.
- Soil characteristics- Physical and chemical parameters (pH, ECe, organic carbon, texture, ESP, $CaCO_3$, N, P, K and Zinc) were monitored before planting.
- Plant parameters - A number of plant parameters were measured at different growth stages in order to assess the performance of varieties and possible mechanism of salt tolerance.

RESULTS AND DISCUSSION

Drought

Drought is a recurrent feature of rainfed rice cultivation limiting its growth and productivity. Ironically, the timing, intensity, duration and distribution of rain in many parts of rainfed rice growing areas arc uncertain, which cause mild to severe water deficit during different phases of plant growth. About half of the 38 million ha of the rainfed lowland rice ecosystem in the world has been classified either as drought prone or drought and submergence prone (Garrity *et al.,* 1986).

A number of soil parameters which affect plant establishment and growth under drought prone rainfed lowland areas need to be measured. These include soil matric potential, hydraulic conductivity, bulk density, field capacity, wilting point etc.

Water availability and uptake by rice plants decrease as soil matric potential drops below zero i.e. the matric potential of saturated soil. A careful monitoring of soil matric potential and leaf water potential is required because ample reduction in leaf expansion, tillering and leaf photosynthesis occurs long before leaf rolling and wilting, the two common symptoms of drought stress. CO_2 assimilation is Educed by soil water potential of only -0.5 bar (O'Toole and Baldia, 7982). Generally, impact of water deficit was not observed until the soil matric potential dropped below -1 bar and leaf water potential below -1.5 bar when leaf rolling generally begins (Setter *et al.,* 1993).

Table 1. Essential and desirable data for environmental and plant characteristics during drought, flash flooding and salinity.

(Abbreviations : S-single measurement; 2W-twice weekly; W– weekly; 2d- every 2 days. d- daily; E-essential assuming equipments are available, D- desirable).

Measurements	**Frequency**					**Stress**		
	S	2W	W	2d	d	Drought	Flooding	Salinity
1- SITE DESCRIPTION								
a. Altitude, Latitude and Longitude	X					E	E	E
b. Topographical location including slope	X					D	D	D
2- SOILS								
a. Soil profile description, bulkdensity, F.C., wilting point, saturation point and soil texture	X					E	E	E
b. Soil chemical properties including nutrients	X					E	E	E
c. Water table (Piezometer, ground water tube)					X	E	E	E
d. Soil moisture or matric potential within one day of rainfall event, otherwise weekly.			X			E	D	E

Continued ....

Measurements	Frequency					Stress		
	S	2W	W	2d	d	Drought	Flooding	Salinity
e. EC of soil (state depth measured) and ground water.	X					D	D	E
f. pH of soil (state depth measured)	X					D		E
g. Hydraulic conductivity/ percolation rate	X							E
h. Depth and thickness of $CaCO_3$ layer	X							E
3- FLOOD WATER								
a. Flood water depth-rate of increase or decrease					X		E	
b. Turbidity of flood water (monitor during event)				X			E	
c. Temperature of flood water (monitor at mid afternoon during an event)				X			E	
d. Lateral movement of flood water (monitor during event).			X				E	
e. pH (monitor during event)		X					D	E
f. EC (including source of flooding)			X				D	E
g. O_2 concentration (monitor at water and soil surface and half way within canopy; before dawn and at mid afternoon)			X				E	
h. CO_2 concentration(monitor as per O_2)			X				E	
i. Ethylene concentration (monitor as per O_2)		X					E	
4- CLIMATE (AT 0800H)								
a. Rainfall by experiment					X	E	E	E
b. Air temperature (max. & min.)				X		E	E	E
c. Radiation					X	E	E	E
d. Wind speed (at 2m height)					X	E	E	E
e. Air humidity or vapour pressure					X	E	E	D
f. Evaporation by site					X	E	D	D

Continued................

Measurements	Frequency					Stress		
	S	2W	W	2d	d	Drought	Flooding	Salinity
5- PLANT CHARACTERISTICS AND PESTS								
a. Percent survival			X			E	E	E
b. Height, density and tiller number			X			E	E	E
c. Biomass and grain yield at maturity	X					E	E	E
d. Yield components	X					D	D	D
e. Plant processes and metabolic events (phasic otherwise weekly)			X			E	E	E
f. Leaf tip drying or rolling or burning			X			E		E
g. Date of 50% panicle emergence	X					E	E	E
h. Plant water balance - water potential, osmotic potential RWC, T P (weekly or phasic)			X			E		E
i. Percent unfilled spikelets	X					E	E	E
j. Root parameters (depth, volume, and density) up to flowering	X					E	D	E
k. Dry matter partitioning (phasic otherwise single)	X					D	D	D
1. Disease, weeds and insects damage (occurrence and severity)			X			D	D	D
m. Siltation on the leaves	X						E	
n. Leaf characters (Waxy, hairy, glaborous etc.)	X					D	D	D

Exposure of plants to mild drought induced hardening of plants (Table 2, Figures 1 and 2). Leaf roiling and tip drying were inversely related to leaf water potential (r = -0.85 and -0.80 respectively; O' Toole and Moya, 1978). Hence, these factors are considered as essential plant measurements (Table 1). Soil types and their physical conditions heavily influence growth and tillering of rice plants. Heavy puddled soils exert strength and thus reduce tillering. If soil dries, cracks develop even though soil water potential below 10-15 cm depth remains as high as -0.1 bar (Castillo *et al.,* 1992).

Plants can overcome drought effects either through avoidance or tolerance (Levitt, 1980). Drought avoidance is the ability of plants to maintain high water potential under reduced soil water availability and, infact, avoid dehydration. Dehydration tolerance is the ability of plants to withstand internal water deficits with minimal injury. In other words it is true protoplasmic resistance.

Another way to cope up with drought is escape. This is where the plant completes its life cycle well ahead of the onset of drought. Crop duration is adjusted so that critical stages like panicle emergence do not coincide with probable drought periods. Early or late maturing, photoperiod-sensitive varieties may be able to escape and recover quickly from drought. The exposure of rice genotypes to severe water deficits at vegetative and boot stages depicted a contrasting response in the three genotypes studied (Table 2). Leaf water potential, however, was initially similar in all the lines at tillering, the appearance of PWP was at significantly lower water potential in the tolerant genotype, Kachani (-21.2 bar) than in the susceptible genotype, IR 28(-19.0 bar). On the removal of stress, Kachani revived quickly. Water deficit imposed at boot stage either alone or in Combination with tillering, depicted the same pattern for PWP and revival. Biological and grain yields and total grains per panicle also reflected the adverse effects of water deficit (Figs. 1 and 2).

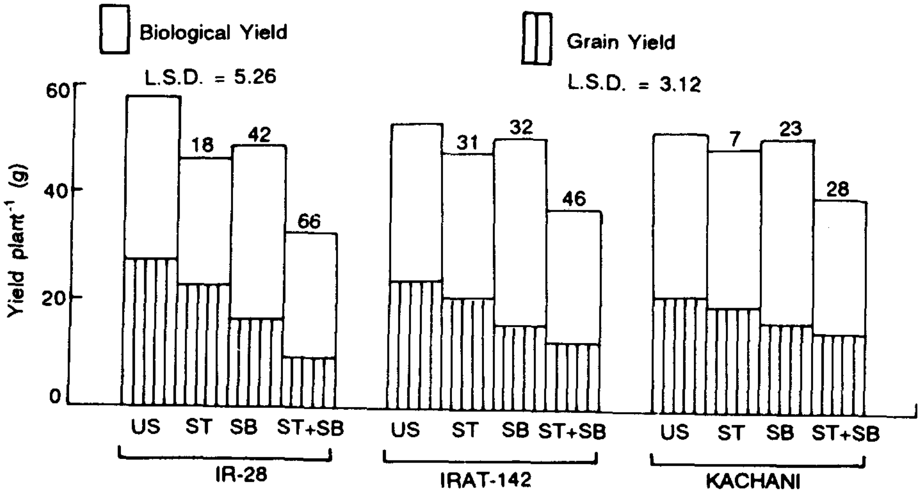


Fig. 1. Effect of water deficits on yield in rice genotypes (per cent reduction over unstressed at top of the bars.)

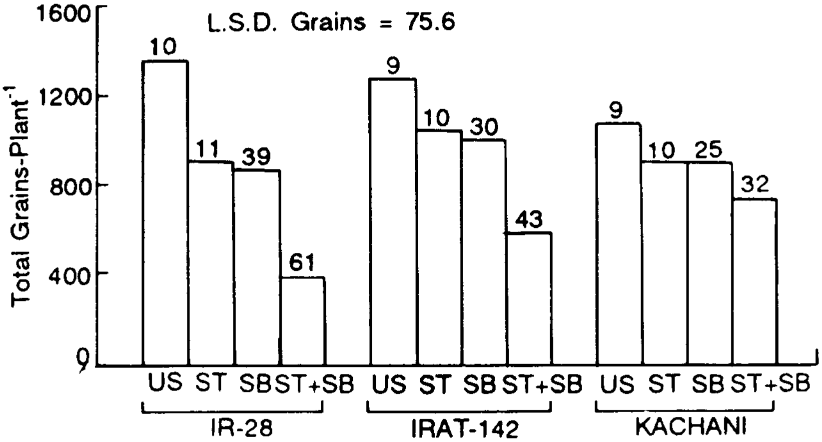


Fig. 2. Total grains and per cent sterility (at the top of bars) in rice genotypes under water deficits.

Stress at tillering induced irrepairable loss in total biomass of all the genotypes, but the grain yield was reduced more due to water deficit at booting stage. A combined stress was more detrimental, but the effect was less severe in the tolerant genotype, Kachani (Figures 1 and 2) and it was possibly due to appearance of PWP at still lower water potential. Grain sterility was the main component responsible for yield reduction which was 61% in IR 28 against only 32% in Kachani with stress at tillering + boot stages. In order to quantify the stress response and explore the mechanisms of tolerance/susceptibility to drought, the environmental parameters listed in Table 1 need to be measured.

Effect of drought varies with the genotype, the phasic development at which plants experience stress, the severity and the duration of drought. Rice yields are most susceptible to water deficits at flowering than at vegetative phase (Ram *et al.,* 1988; Hsiao, 1982; Reyniers *et al.,* 1982). Drought at vegetative stage causes irrepairable loss of canopy whereas at flowering stage, water deficit hampers anthesis and seed setting leading to higher spikelet sterility and lower yields (Ram *et al.,* 1988). Drought at flowering also reduced effective leaf area and photosynthesis, thus plants have to depend on pre anthesis reserves which may impart tolerance against internal water deficits (Chaturvedi and Ingram, 1988; Austin *et al.,* 1980). Furthermore, if stress coincides with anthesis, the panicle excertion may be inhibited, spikelet sterility occurs (Ekanayake *et al.,* 1989; Ram *et al.,* 1988) and yields decrease without any scope for recovery. Data on panicle emergence, and spikelet sterility, thus provide an indication of timing and intensity of drought (Setter *et al.,* 1993).

Drought is often associated with high temperature and intense solar radiation alongwith low relative humidity during the dry spells in the rainy season. Soil cracks develop and strength and bulk density increase, restricting the availability and uptake of water and nutrients by the plants. Sizeable reductions in soil water potential due to drought may increase salt concentrations in the soil solution which may induce dehydration of tissues leading to cell collapse and death of plants.

Table 2. Soil moisture content (% of dry weight) and leaf water potential (-bar) in rice genotypes under water deficit condition (Pot expt.)

Stages of stress:	Genotypes IR-28 (Susceptible)	 IRAT-142 (Moderate)	 KACHANI (Tolerant)	LSD (P 0.05)
1. **Stress at Tillering** (30-DAS)				
Before stress	6.8	6.4	6.6	N.S.
AtP.W.P.	19.0	20.9	21.2	0.60
After revival (48 h.)	8.9	8.3	8.1	N.S.
2 **Stress at Booting** (60-65 DAS)				
Before stress	7.9	7.4	7.9	N.S.
At P.W.P	20.0	21.0	21.5	0.58
After revival (48 h.)	9.9	9.4	9.3	N.S.
3. **Stress at Tillering + Booting**				
Before stress	7.9	7.4	7.8	N.S.
At P.W.P	21.5	22.8	23.0	0.60
After revival (48 h.)	9.9	9.0	9.0	N.S.
4. **Soil moisture**				
At field capacity	28.3±1.3	28.3±1.3	28.1±1.0	
At PWP	11.2±0.9	10.1±0.95	9.8±0.72	
After revival	28.35±1.1	28.0±1.2	27.5±0.95	

Weed populations under drought invariably exert a threat to crop stand and render plant easily accessible to insects and diseases. Hence, data on temperature, relative humidity and light intensity above and inside the plant canopy, weed, insect and disease profiles may also be included in the environmental measurement data set (Table 1). All these environmental variables can effectively be integrated through simulation models for understanding the response of drought on crop growth and productivity. Such simulation models have been suggested by a number of workers which include measurements on soil, climate and plant factors (Penning de Vries *et al.,* 1989; Woopereis *et al.,* 1993; Singh, 1993).

With the above set of environmental and plant measurements, one can easily predict the timing, duration and intensity of water deficits. This knowledge may enable breeders to synthesize a new rice genotype suitable for drought prone rainfed lowlands.

Flooding

Flooding is a serious constraint to rice yields in rainfed lowland and deepwater areas due to partial or complete submergence of plants. Partial submergence is defined as when 40 to 99 per cent shoot is submerged in water. Flooding in rice fields is of two types : i) Flash or intermittent (ii) Stagnant or prolonged. Approximately 22 m ha of rice is affected by flooding which includes 15 m ha of flash flood areas of rainfed lowland rice and 5 m ha of deepwater rice (Khush, 1984). In India, approximately 60% of *Kharif* rice area is subjected to waterlogging due to flash and stagnant floods (Balkrishna Rao and Biswas, 1979).

Flash flooding refers to a situation where the rice crop gets submerged due to sudden increase in floodwater for varying periods, normally not exceeding 10-12 days (Dwivedi and Hille Ris Lambers, 1991; Senadhira, 1992). The period of flooding is often prolonged in Eastern India. Flash flooding normally occurs near river, riverlets and streams. The rice area near Ghaghara, Ganges, Rapti, Gandak, Kosi, Baiterni, Mahanadi, Rishikulya, Brahmaputra, Krishna and Cauvery rivers and in the tidal wetlands coastal area of India, are more vulnerable to flash flooding (Singh, 1982). The flash flooding occurs mainly during vegetative stage of rice and its severity depends on the intensity and duration of rainfall, nature of water source and topography.

Rice, by nature, is tolerant to waterlogging, flash flood and associated anoxia which makes its cultivation possible under flood prone lowland ecosystem. A number of morphological, physiological and biochemical features are responsible for tolerance to submergence which are influenced by genotype, submergence depth and duration and other environmental conditions. Features, like coleoptile, that tolerate anoxia (Taylor, 1942) and the ability of the coleoptile (Ohwaki, 1967) and stem (Vergara *et al.,* 1976) to elongate vigorously when submerged, provide chance to escape complete inundation or minimize the duration. Other attributes include a root system that can elongate more rapidly in the presence of ethylene (Konings and Jackson, 1979), a highly porous morphology that facilitates internal diffusion of oxygen down the plant (Armstrong, 1971) and a hydrophobic outer surface that traps a coating of air when leaves are submerged. This forms a gaseous film that may facilitate basipetal diffusion and mass flow of oxygen from the aerial environment when some leaf tissues remain above the water surface (Raskin and Kende, 1984).

Despite these adaptive features, most rice cultivars can not survive complete submergence for a long time, more so, during early stage of development. The experiments conducted at NDUAT and elsewhere indicate that 45-day old seedlings showed better tolerance to submergence (7, 11 and 15 days submergence) than 30 or 15-day old seedlings with good genetic variability (Mazaredo and Vergara, 1982; Chaturvedi *et al.,* 1993).

Experiments conducted at the consortium site at Masodha indicated that with similar experimental conditions and crop management, rice yields among genotypes during 1992 and 1993 wet seasons showed a variation of 0.2 to 2.9 t/ha (Table 3). It is clear from the data that environmental factors like water depth and duration of submergence, temperature, light, rainfall and humidity have an important role in changing the phenology, for example, flowering delayed during 1993. (Figures 3, and 4). Environmental characterization (Table 1) thus, is of utmost importance for interpreting the performance and determining the stability of the genotypes across locations and at the same location over different years.

Table 3. Performance of elite lines of rainfed lowland rice under partially submerged condition.

Genotypes	**50% flowering-DAS***		**ERT*/hill**		**Yield t/ha**		**Yield Difference**
	1992	1993	1992	1993	1992	1993	
NDR-30030	113	122	7.8	7.5	5.3	7.2	+1.9
NDR-30076	118	121	8.2	7.4	5.2	7.0	+1.8
NDR-30039	115	118	8.4	8.1	4.5	6.0	+1.5
NDR-30023	112	118	9.3	7.8	4.3	6.2	+1.9
NDR-40013	120	127	6.7	6.7	4.8	6.4	+1.6
NDR-40032	114	123	8.4	7.4	4.5	7.4	+2.9
Madhukar (Check)	115	126	5.2	7.0	2.0	1.8	-0.2
SEm±	0.66	0.71	0.24	0.14	0.23	0.15	-
LSD (P0.05)	207	223	0.75	0.43	0.72	0.47	-

* Days after sowing; ** Earbearing tillers

There were large differences in water depth (Figures 3 and 4), showing lower water levels (mean depth 5.9-11.0 cm) during July and August in 1992 (active tillering phase) and deeper water level in 1993 (mean depth 19.8 to 23.9 cm). In contrast, during 1992 higher water depths (11.0-34.5 cm) were observed at flowering to milk stages than in 1993 (4.0-26.5 cm). The physiological implication of such variations needs to be looked into as a key to the effect of environmental factors affecting growth and yield. Water temperature variations and sunshine hours should also be taken into consideration.

A number of physiological and biochemical explanations for death and survival under submergence has been reported which include a possible interaction between CO_2 low O_2 and high ethylene concentrations (Setter *et al.,* 1988, 1989). Low photosynthesis due to low CO_2 diffusion leads to lower carbohydrate assimilation and energy deficiency which restrict nutrient uptake and growth. Submergence may also result in solute leakage due to low O_2 concentration and affect membrane permeability (Smith and ap Rees, 1979).

The rice plants respond and adapt to various types, timing and duration of flooding in different ways which include elongation for deepwater rice varieties and submergence tolerance for lowland varieties exposed to transient flash floods (Hille RisLambers and Seshu, 1982).

A number of environmental and plant factors are associated with damage due to flooding namely low light, siltation on the leaves, mechanical damage, solute leakage, limitation to gas diffusion, accumulation of toxic metabolites inside the plant, insect-pests and diseases (Creenway and Setter, 1994). Additional adverse

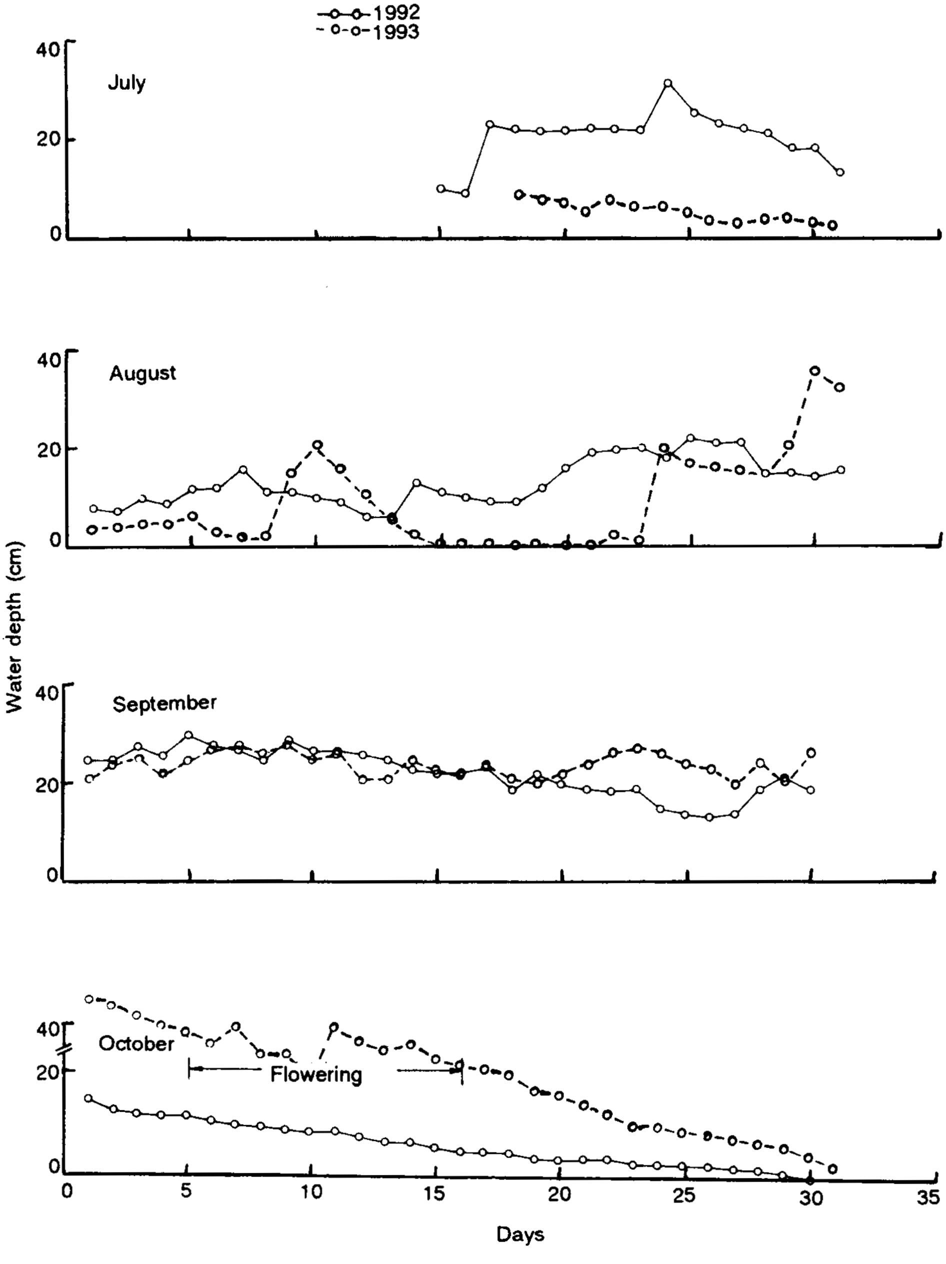


Fig. 3. Variation in daily water depth during 1992-93 wet season crop at C.R.S. Masodha, India.

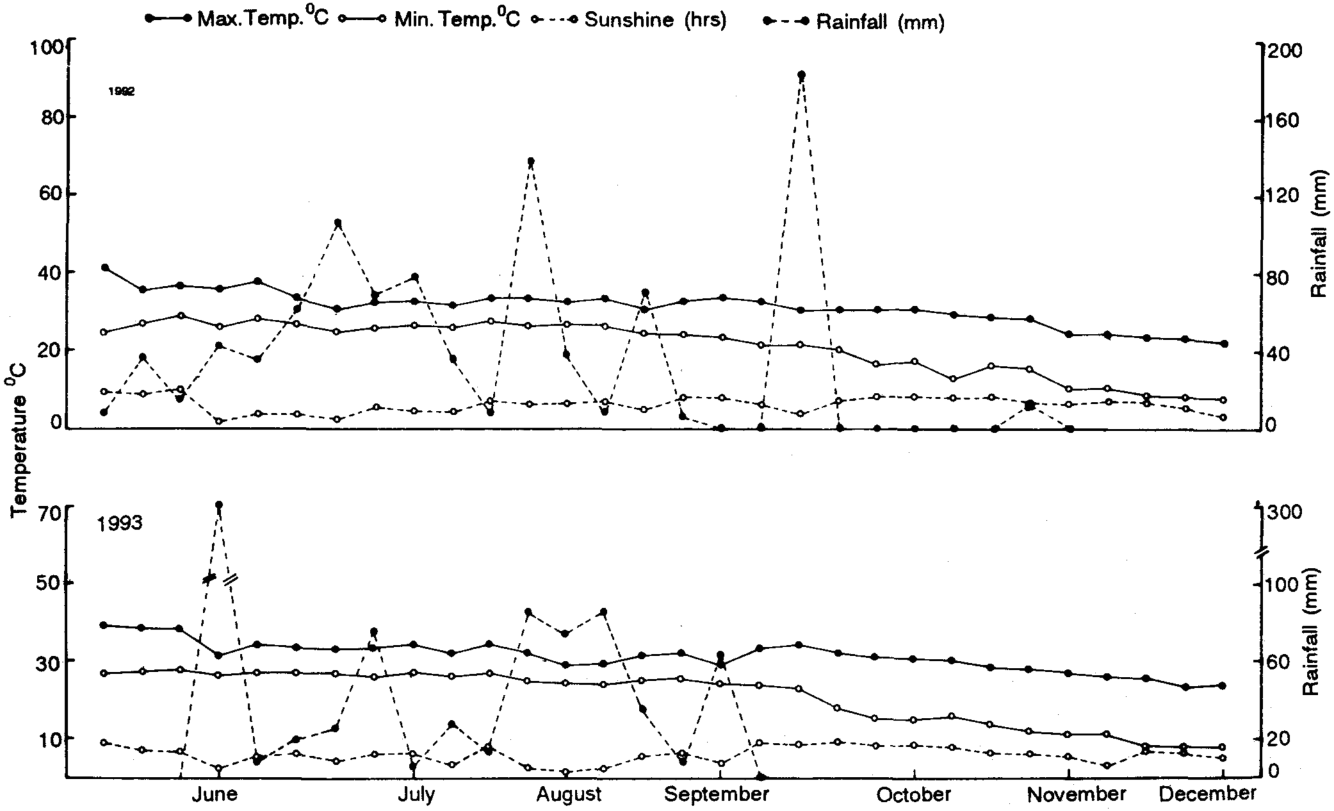


Fig. 4. : Weekly meteorological information during wet crop season (1992 & 1993) at C.R.S. Masodha, India.

effects may be associated with desubmergence and post hypoxic injury (see Crawford, 1992, for review). These factors seldom act alone since alteration in one component may lead to a number of other adverse effects which ultimately affects survival and growth of plants under submerged conditions.

Submergence at seedling stage is most harmful (reducing plant population), followed by submergence at tillering stage which cuts down the tiller production. Submergence at boot and flowering stages prevents panicle emergence and increases spikelet sterility (Pandey *et al.,* 1979). High nitrogen level in the soil accentuates adverse effects of submergence (Palada and Vergara, 1972). Gas diffusion during submergence is quite low in water, hence any gas (CO_2 ethylene and methane) which is produced under water increases in concentration, while that O_2 consumed decreases in concentration. Any of these changes may reduce growth, and survival of rice during flooding.

The composition of floodwater may vary with locations, hence proper measurement and characterization of flood water is essential in order to assess its effect on plant growth and yield. During 1993 wet season, a brief environmental characterization of stagnant water in submerged rice fields was done at crop research stations, Pagalabhari, (Faizabad) and Ghagahraghat, (Bahraich) (Figures 5, 6 and 7). A diurnal variation in O_2 concentration of water at different depths was noted showing a decrease in O_2 with increase in water depth (0.01 - 0.4 m). Maximum O_2 in water was observed during mid day possibly due to photosynthesis of algae and submerged rice plant tissues which gradually declined to the lowest before dawn. Plant respiration during night might have consumed at least some of the dissolved oxygen (Figure 5). In deepwater, a gradual decline in dissolved O_2 was noted upto 1.4 m depth, beyond which, a sharp decrease occurred leading to zero oxygen at 2 m depth well above the soil surface (Figure 6). The temperature profile through water depth at 10.00 h during day decreased with depth but it ranged only between 27.5 to 28.0 °C in the deepwater at Ghagharaghat.

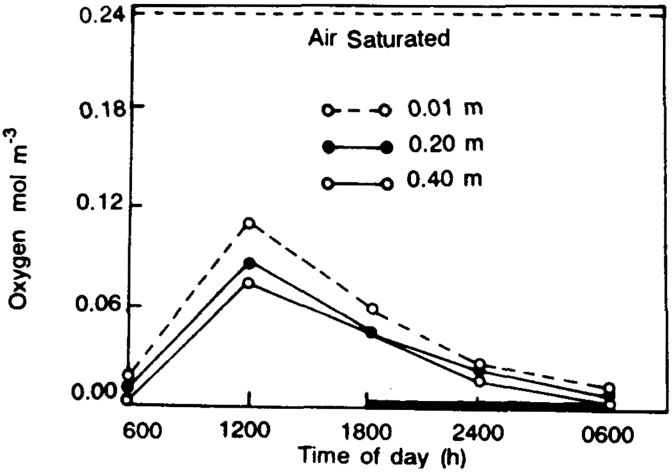


Fig. 5. Diurnal variation in O_2 concentration of water in partially submerged rice field at C.R.S. Pagalabhari, Faizabad, India Blackbar on X-axis indicates dark period.

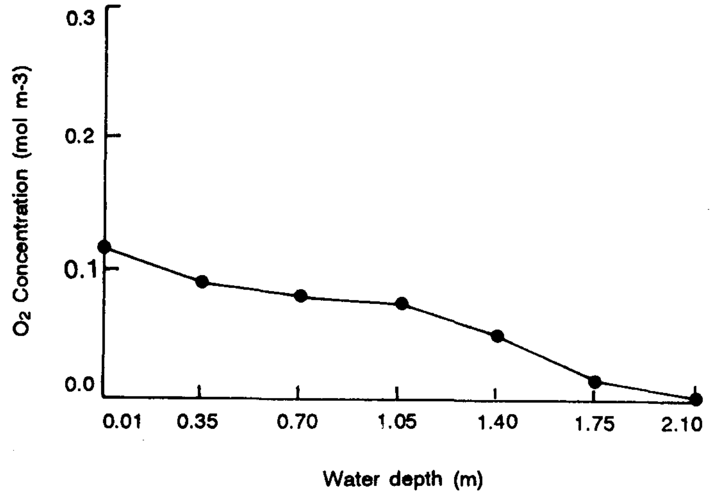


Fig. 6. Oxygen concentration of flood water in deep-water rice field at Ghagharaghat, Bahraich, India. Maximum water depth was 2.4 m.

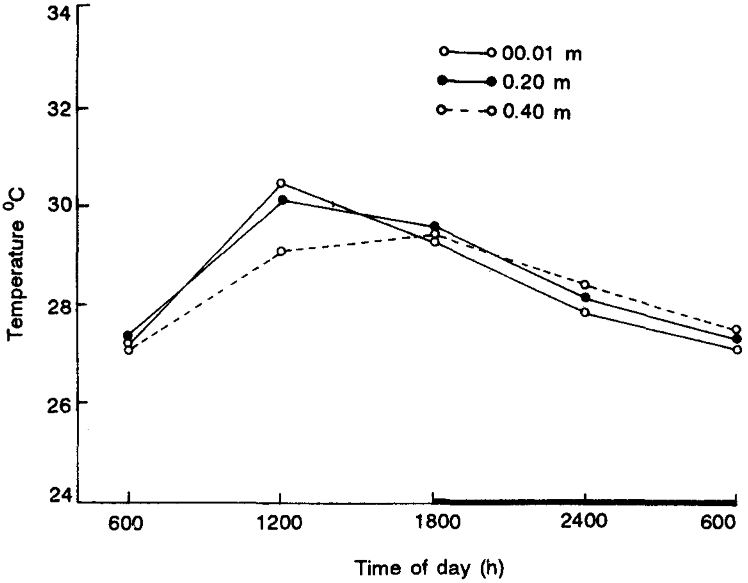


Fig. 7. Temperature of water in a field of partially submerged rice at C.R.S. Pagalabhari, Faizabad, India. (Black bar on X-axis indicates dark period).

Diurnal variation in temperature of shallow water at Pagalabhari showed that the maximum temperature occurred at midday (1200 h) being higher at the surface layer, decreasing downwards upto 0.4m depth (soil surface). However, during night, the temperature of the water in deeper layers was higher than surface layers (Figure 7). The lower temperature of the surface water layers during night have been due to evaporative cooling. These variations in O2/CO2 concentrations and temperature in rice fields may induce a number of changes in plant metabolism leading to altered growth and yield. Genotypes with well equipped systems to combat anoxia may survive and yield better. The data presented here on O2/CO2 and temperature are only from one wet season and hence need confirmation at other times and locations to direct the research strategies for alleviating adverse effects of submergence on rice.

Genotypes with higher total carbohydrate and starch content prior to submergence along with lower rate of depletion during submergence showed better tolerance to submergance (Chaturvedi *et al.,* 1993). Since the flood water conditions in stagnant and turbulent situations vary, the duration of complete submergence and water current alongwith its turbidity should be measured in all experiments to quantify the degree of severity of damage to plants.

In summary, the environmental and plant factors need to be carefully measured during submergence to allow extrapolation and interpretation of results. These factors include, flood water turbulence, pH, turbidity, O_2 and CO_2 concentration, water depth relative to plant height, levels of non-structural carbohydrate and toxic metabolites inside the plant (Table 1). Future research must focus on means of manipulating floodwater O_2 during submergence as well as on quantitative determination of the importance of different O_2 concentrations to growth and survival of rice during submergence . At present there is no published information on the latter though it is well known that O_2 is one of the major factors limiting growth during waterlogging (Jackson and Drew, 1984) and Submergence of rice plants (Setter *et al.,* 1989).

Salinity

An estimated 150 m ha of current and potential rice lands in the tropics and subtropics are affected by salinity (Massoud, 1974). in South and South East Asia alone about 90 m ha of lands suited to rice production, lie idle largely because of soil toxicities of which nearly 49 m ha are saline and 12 m ha are alkali (sodic) in nature (Ponnamperuma and Bandyopadhya, 1980). In general, soil salinity is caused by presence or by intrusion of sea water or by surface evaporation of brackish soil water. Salt accumulation increases in the drier climates and diminishes strongly in equatorial climates without a pronounced dry season.

Rice is generally reported to be a moderately salt tolerant crop but no rice variety can withstand high salinity or sodicity throughout its growth cycle. High content of sodium chloride in soil solution with specific conductance values of more than 8-10 dS/m are harmful to rice plants and cause as much as 50% yield reduction. In tidal areas, the specific conductance values change from day to day depending on tidal regimes (De Datta, 1981).

Inland saline sodic soils generally have pH more than 7 alongwith high amounts of soluble salts. The underground water invariably is brackish. Saline-sodic soils have high amounts of soluble salts along with high concentrations of carbonate and bicarbonates of sodium. High sodium replaces calcium from the clay complex with concurrent precipitation of calcium carbonate which forms an impermeable (upto 1 m thick) *kankar* layer. The soil becomes strongly dispersed and hence highly impermeable to water. This necessitates the careful characterization of coastal and inland saline and sodic soils in terms of topography, bulk density, hydraulic conductivity, variations in pH, electrical conductivity (ECe) and chemical properties at essential and desirable levels. Salt affected soils show a number of problems which hamper normal growth and development of plants (Ponnamperuma and Bandyopadhya, 1980).

It is evident from the data presented in Tables 4 and 5 that a large variability exists in the physico-chemical properties of soil including nutritional status which should be accurately characterized if the results obtained at one location are likely to be extrapolated to other locations. Underground water is often brackish at certain locations and this too needs careful monitoring.

Table 4. Soil characteristics of experimental site of Main Experiment Station, Kumarganj, Faizabad, India. Data are mean of four replicates; SEMs were less than 12% of individual values.

Soil parameter		**Soil Depth (cm)**	
	Soil	0-15	15-30
Soil pH (1: 2.5)	Sodic	9.5	9.8
	Normal*	8.5	8.7
ECe (dS/m)	Sodic	1.4	1.8
	Normal*	0.6	1.0
Exchangeable sodium percentage	Sodic	35	55
	Normal*	15	17
Hydraulic conductivity (mm/hr)	Sodic	0.8	0.3
	Normal*	2.5	2.0
Cation exchange capacity	Sodic	14-16	13-15
(me/100g)	Normal*	16-19	14-17
Texture	Sodic	silty loam	–
	Normal*	silty loam	–
Topography	undulating	–	–

* Normal designates a soil where 10 t/ha pyrite was applied to sodic soil two years earlier, followed by continuous cropping.

In glycophytes including rice, the effect of salinity on plant growth and development depends on temperature, humidity and radiation (Levitt, 1980). Vegetative growth of rice, for instance in NaCl affected soils, is better during wet season, when plants survive 0.4% (W/V) NaCl as opposed to 0.3% in dry season (Mercado *et al.,* 1974).

Table 5. Nutritional status of the soil at Main Experiment Station Kumarganj, Faizabad (As per Table 4). Data are mean of four replicates; SEMs were less than 14% of the individual values.

Soil parameters		**Soil depth (cm)**	
		0–15	15–30
Organic carbon (%)	Sodic	0.1–0.2	0.05–0.2
	Normal	0.3–0.4	0.2–0.3
Available nitrogen (ppm)	Sodic	20	–
	Normal	25	–
AvailableP_2O_5 (ppm)	Sodic	28	–
	Normal	25	–
Available K_2O (ppm)	Sodic	300	–
	Normal	320	–
Micronutrient Status (ppm) (DTPA Extractable)			
Iron	Sodic	3.8	3.7
	Normal	9.5	7.2
Manganese	Sodic	2.9	2.3
	Normal	3.0	2.7
Zinc	Sodic	2.2	1.2
	Normal	5.6	4.5
$CaCO_3$ (%)	Sodic	6.0	5.5
	Normal	1.5	2.0
Thickness of $CaCO_3$ (Kankar) layer	Sodic	present (25–40 cm thick)	present
	Normal	rarely present	–
Underground water quality	–	good	–

The response of genotypes to adverse soil conditions vary greatly depending upon a number of environmental factors. The data pertaining to survival and productivity clearly indicate that tolerant rice genotypes show less Eduction in grain and biological yields than susceptible genotypes (Tables 6 and 7). A large variability was also noted in dry matter partitioning into grains indicating a reduced CO_2 fixation or reduced translocation of carbohydrates under high salt concentrations. Tolerant genotypes had lower salt injury index (0.11 - 0.29) against 0.48 - 0.71 in susceptible genotypes (Table 7). A comparison of yield versus trait combinations (Table 8) and harvest index versus trait combinations (Table 9) indicates that interaction between biological yield, harvest index and grain fertility plays an important role in determining yield of the genotype. Genotypes with higher total biomass and better partitioning may be looked into as the future cultivars for salt affected rice areas.

Table 6. Total biomass production in salt tolerant and susceptible ricegenotypes.

Genotype	**Biological yield g/hill**		**% reduction over normal**
	Normal Soil (PH 8.5)	Sodic Soil (PH 9.7)	
Tolerant			
Usar-1	73.0	70.2	3.8
CSR-10	56.2	49.7	11.6
TCA88-10-1	70.0	54.1	22.7
NDR-80	66.0	61.5	6.8
Purple	58.0	46.3	20.2
NDRK-5003	94.0	65.7	30.1
Pokkali	63.7	43.3	32.0
Susceptible			
Pusa- 516	79.0	42.0	46.8
Rajshree	64.0	33.4	47.8
Kasturi	67.0	28.1	58.1
LSD(P0.05)	9.77	6.82	-

The literature frequently contrasts the central dilemma of ion toxicity versus water deficit (osmotic effect) in saline conditions (Flowers *et al.,* 1977 for halophytes and Greenway and Munns, 1980 for non-halophytes). Large quantities of salts are carried through the transpiration stream to the leaves which eventually leads to their death. NaCl accumulation in leaves is correlated with reduced photosynthetic activity and with ultrastructural and metabolic damage (Yeo and Flowers, 1986,1989) and there is now direct evidence that this is mediated by ayoplastic increase in salt concentrations in the expanded leaves (Flowers *et al.,* 1991). There is ample variability in salt susceptibility between (Yeo *et al.,* 1990) and within (Yeo *el al.,* 1988) varieties, differences in vigour accounting for much of the variation in the survival in salinity (Yeo *et al.,* 1990). Short term initial effects of salinity are primarily due to limitation of water supply, whereas long term effects are due to accumulation of salt within expanded leaves (Yeo *et al.,* 1991).

Table 7. Grain Yield and salt injury index in tolerant and susceptible rice genotypes.

Genotype	**Grain yield g/hill**		**Harvest index (%) at pH 9.7**	**Salt injury index**
	Normal Soil (pH 8.5)	Sodic Soil (pH 9.7)		
Tolerant				
Usar-1	24.7	22.0	31	0.11
CSR-10	26.0	20.7	44	0.20
CSR-11	26.9	22.2	33	0.17
TCA 88-10-1	24.3	20.0	37	0.17
NDR-80	26.1	22.6	37	0.13
Purple	24.7	21.9	43	0.11
NDRK-5003	24.5	19.9	30	0.19
Pokkali	22.1	15.5	34	0.29
Susceptible				
Pusa-516	23.5	12.2	23	0.48
Rajshree	34.2	10.1	30	0.71
Kasturi	21.1	8.4	30	0.60
LSD (P0.05)	3.96	3.00	4.55	

It is highly significant and important that individual plant variability in sodium uptake and in survival are negatively correlatcd. The presence of other ions may be expected to affect the absorption of Na^+ salts and the injury produced by them. It has long been known that Ca^{2+} antagonizes the injurious effects of Na^+ and this effect is largely due to decrease in cell permeability produced by Ca^{2+}. In contrast to decreased cell permeability to monovalent cations, Ca^{2+} also enhances the active uptake of some ions, particularly K^+ and P ions, the *"Viets effect".* NaCl, infact, induced a marked efflux of K from leafsegments of bean and barley, and this efflux was prevented by addition of 1 meq Ca^{2+} to the external solution (Marschner and Mix, 1973).

The importance of uptake of Na^+, K^+ and Ca^{2+} by rice plants and partitioning of these ions into different plant parts has been well emphasized. The observations presented in Table-10 indicate the role of beneficial ions like K^+ and Ca^{2+} in mitigating the detrimental effects of high internal Na^+. Almost all the salt tolerant genotypes invariably possessed higher K/Na and Ca/Na ratios than susceptible ones. A number of mechanisms for exclusion and sequestering/compartmentation of ions for mitigating the adverse effects of salinity/sodicity have been proposed by Flowers *el al.* (1977, 1991) and Yeo and Flowers (1984) including exclusion, sequestering of ions in roots, old leaves, or different cellular compartments or dilution by growth.

Table 8. Yield versus trait combinations in rice genotypes planted under sodic soil (pH 9.7).

Genotype	**Yield (g/hill)**	**Biol. Yield (g/hill)**	**HI (%)**	**Grain fertility (%)**	**EBT/hill**	**Salt injury index**
NDR-80	22.6	61.5	37	87	12	0.13
Usar-1	22.0	70.1	31	90	16	0.11
CSR-11	22.2	56.5	33	83	15	0.17
Purple	21.9	46.3	43	85	18	0.11
CSR-10	21.7	49.7	44	74	16	0.16
CSR-18	21.8	50.0	44	90	15	0.19
IET-12856	22.8	55.1	40	90	12	0.17
IET-12865	21.0	53.0	39	82	12	0.19
LSD (P0.05)	N.S.	3.10	4.66	8.15	4.95	-

Table 9. Harvest index versus trait combinations in rice genotypes planted under sodic soil (pH 9.7).

Genotype	**HI (%)**	**Yield (g/hill)**	**Biol Yield (g/hill)**	**Grain fertility (%)**	**EBT/hill**	**Salt injury index**
Usar-1	31	22.0	70.1	90	16	0.11
NDRK-5003	30	19.9	65.7	88	12	0.18
NDRK-5002	30	17.1	56.5	79	11	0.37
Rajshree	30	10.1	28.1	46	11	0.70
Kasturi	30	8.4	38.2	43	10	0.60
IET-13408	30	15.9	54.0	91	10	0.47
IET-11353	30	14.3	47.2	80	11	0.25
LSD (P0.05)	N.S.	3.68	2.85	6.67	2.71	–

Table 10. K/Na and Ca/Na ratios in salt tolerant and susceptible rainfed lowland rice genotypes.

Genotype	**K/Na ratio**			**Ca / Na ratio**		
	Leaf	Stem	Root	Leaf	Stem	Root
Tolerant						
Purple	2.4	1.9	1.1	3.0	4.1	2.1
CSR-10	3.0	3.0	3.1	2.0	2.5	2.2
CSR-5	2.5	3.1	2.5	2.1	2.5	2.2
CSR-18	0.8	1.6	2.1	2.6	-	-
Pokkali	1.5	1.7	1.7	1.3	1.8	1.7
TCA-88-10-1	1.9	1.6	1.5	1.3	2.8	1.7
IET-11351	16	1.2	1.2	2.5	1.8	1.6
Sajoo-52	1.6	1.4	-	2.9	2.2	-
Susceptible						
Pusa-516	1.1	0.9	0.7	0.9	1.0	0.9
Basmati-370	1.0	0.8	-	1.3	1.1	-
IET-13407	0.9	0.7	0.9	1.4	1.4	1.1

A distinction should be made between saline soils which contain enough Ca^{2+} to meet the nutritional requirements of the plants and sodic soils, in which very little available Ca^{2+} is present while the concentration of exchangeable sodium is greater than 15% and ample carbonate and bicarbonate ions are present leading to high pH of the soil solution. In salt affected soils, accumulation of Na^+ occurs in the stem and leaves of the plants which vary with plant species. Rice accumulated more Na and Ca than barley or wheat (George, 1967).

We have also observed a selective uptake and accumulation of Na^+, K^+ and Ca^+ by different rice genotypes. Tolerant genotypes usually showed higher K/Na and Ca/Na ratios in leaf, stem and roots than susceptible genotypes. These measurements may be used as selection criteria for screening rice genotypes for salt tolerance and should be included for environmental characterization as plant measurements (Table 1). Importance of vigour in salt tolerance of rice was emphasized which reduced actual ion concentration due to dilution and thus decreasing the adverse effects of salinity. Vigour parameters included for measurement are given in Table 1.

The mechanism of injury or tolerance to coastal and inland salinities may vary, as in the former case, the plants are exposed to intermittent high levels of salinity due to tidal inundations which often fluctuates. Inland salinity, though also fluctuates with other environmental factors like rainfall, temperature, humidity and light, but plants are exposed to a continuous stress, which enables them to adjust against slowly increasing ion concentrations within tissues. In both cases the slow build up of ions to inhibitory concentrations may explain why growth reductions over short exposure periods of salinity are less meaningful than growth or survival measured over several weeks (Yeo and Flowers, 1984; Akita and Cabuslay, 1986).

In rice growing areas, the inland saline soils especially in India and Pakistan are notorious due to associated alkalinity problems alongwith nutritional imbalances. Rice plants grown in saline-alkali or alkali soils are exposed to high pH, low to very low hydraulic conductivity, deficiency of nitrogen, zinc and iron, besides high soluble salts. These factors create an array of complex situations for plants growing therein. Neue *et al.* (1990), found that salinity tolerance scores for rice are significantly correlated to other stresses such as alkalinity and peatiness, P deficiency to alkalinity and zinc deficiency and Zn deficiency to Fe toxicity. Pokkali, one of the tolerant rice varieties to salinity could not match well to CSR-10, NDR-501 and TCA-88-10-1 in our rice screening programme for rainfed lowland salinity/alkalinity (Tables 6, 7). The reason is clear on the basis of the soil characterization since most of the saline soils are also highly alkaline (pH upto 10.5) and deficient in nitrogen, zinc and iron. This result contradicts the generalization that more vigorous and tall genotypes are tolerant to salinity (see also Tables 6 and 7). Dilution effect may be true over short term and needs to be evaluated further in long term experiments.

The complexities of saline environments, thus, render it difficult to characterize. The EC of the soil solution is the most important component to quantify the overall ions, and needs a careful monitoring during the experiment. The soil matric potential, water content, and nutrient status may also be given careful consideration. Soil pH, hydraulic conductivity, and the nature of $CaCO_3$ *hardpan* below root zone may essentially be measured in order to seggregate the plant responses to saline versus alkaline environments.

CONCLUSION

The forgoing discussions clearly indicate the importance of environmental characterization for drought, flood and salinity situations having enormous amount of variability across locations and seasons. Such measurements enable extrapolation of findings from one site to the other sites or locations in the rice growing countries.

REFERENCES

Akita S, Cabuslay C S (1986) Physiology of varietal response to salinity. II. Response to different salt concentrations. *Jap. J. Crop Sci.* **55** : Extra Issue 1:28-29.

Armstrong W (197l) Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. *Physiol. Plant.* **25:** 192–197.

Austin R B, Margin R B, Ford M A, Blackwell R D (1980) Contribution to grain yield from pre-anthesis assimilation in tall and dwarf genotypes in two contrasting seasons. *Ann. Bot.*. **45** : 309-319.

Balkrishna Rao, Biswas S (1979) Rainfed lowland rice in India(Pages 87-94). In : Rainfed lowland rice; Selected papers from 1978 International Rice Research Conference IRRI, Los Baños, Philippines.

Castillo E G, Buresh R J, Ingram KT (1992) Lowland rice yield as affected by timing of water deficit and nitrogen fertilizer. *Agron. J.* **84** : 152-158.

Chaturvedi G S, lngram KT (1988) Assimilate translocation of lowland rice in response to water deficit and shade. Paper presented at FCSSP Annual Meeting held at Davao City 27-30 April, 1988.

Chaturvedi G S, Misra C H, Singh O N, Pandey C B, Yadav V F, Singh A K, Dwivedi J L, Singh B B, Singh R K (1995) Physiological basis and screening for tolerance for flash flooding. Pages 79-96. In : Rainfed Lowland Rice - agricultural research for high risk environments. KT Ingram, ed., International Rice Research Institute, Los Banos, Philippines.

Crawford R M M (1992) Oxygen availability as an ecological limit to plant distribution. *Adv. in Ed. Res.* **23:** 93-185.

De Datta S K (1981) Principles and practices of rice production. John Wiley and Sons, New York, USA.

Dwivedi J L, Hille RisLambers, D (1991) Deepwater rices varietal improvement. IRRI, Los Banos, Philippines.

Ekanayake I J, De Datta S K, Steponkus P L (1989) Spikelet sterility and flowering response of rice to water stress at anthesis. *Annals Bot.* **63** : 252-264.

Flowers T J, Hajibagheri M A, Yeo A R (1991) Ion accumulation in cell walls of rice plants growing in saline condition: evidence for the Oertli Hypothesis. *Plant cell Environ.* **14** : 319-325.

Flowers T J, Trake P F, Yeo A R (1977) The mechanism of salt tolerance in halophytes. *Annu. Rev. Plant. Physiol.* **28** : 89-121.

Garrity D P, Oldeman L R, Morris R A, Lenka D (1986) Rainfed lowland rice ecosystems : Characterization and distribution. Pages 3-240. In : Progress in rainfed lowland rice IRRI, Los Banos, Philippines.

George L Y (1967) Accumulation of sodium and calcium by seedlings of some cereal crops under saline conditions. *Agron. J.* **59** : 297-299.

Greenway H, Munns R (1980) Mechanism of salt tolerance in non - halophytes *Annu. Rev. Plant Physiol.* **31:** 149-190.

Greenway H, Setter T L (1994) : Is there anaerobic metabolism in submerged rice plants? A View point (This proceeding).

Herdt R W, Barker R (1977) Multi-site test environments and breeding strategies for new rice technology. *IRRI Res. Pap. Ser,* 7. IRRI, Los Banos, Philippines, 32p.

Hille RisLambers D, Seshu D V (1982) Some ideas on breeding procedures and requirements for deepwater rice improvement. Pages 29-34. In.: Proceedings of 1981 International deepwater rice workshop. IRRI, Los Banos, Philippines.

Hsiao T C(1982) The soil-plant atmosphere continuum in relation to drought and crop production. Pages. 39-52. In: Drought resistance in crops with emphasis on rice. IRRI, Los Banos, Philippines.

Jackson M B, Drew M C (1984) Effects of flooding on growth and metabolism of herbaceous plants. Pages 47-128. In : Flooding and plant growth. T.T. Kozlowski ed. Academic Press, Orlando, Florida.

Jackson M L (1973) Soil Chemical analysis. Prentice Hall of India Pvt. Ltd., New Delhi.

Khush G S (1984) Terminology for rice growing environments. IRRI, Los Banos, Philippines.

Konings H, Jackson M B (1979) A relationship between rates of ethylene production by roots and the promoting or inhibiting effects of exogenous ethylene and water on root elongation. *Zeitschrift fur Pflanzenphysiologie* **92:** 385-397.

Levitt J (1980) Responses of plants to environmental stresses Vol. II. Water, radiation, salt and other stresses. Academic Press, New York, London, Toronto.

Marschner H, Mix G (1973) Effect of sodium chloride and mycostatin on the mineral content of leaf segments and on the fine structure of chloroplasts. *Z. Pflanzenermechi Bokenkd* **136:** 203-219.

Massoud F I (1974) Salinity and alkalinity as soil degradation hazards, FAO/UNEP expert consultation on soil degradation. FAO, Rome.

Mazaredo A M, Vergara B S (1982) Physiological differences in rice varieties tolerant of and susceptible to complete submergence. Pages 327-341. In. : Proceedings of the 1981 International deepwater rice workshop IRRI, Los Banos, Philippines.

Mercado B T, Malabayabas C A, Gumasing S R (1974) Growth of some rice varieties in NaCl salinated soils as affected by the season. *Philip. Agric.* **58:** 40-49.

Neue H U, Lantin R S, Cayton M T C, Autor N U (1990) Screening of rices for adverse soils tolerance. Pages 523-531. In: Genetic aspects of plant mineral nutrition. N.EI. Bassam *et al.,* eds. Kluwer Academic Publ, The Netherlands.

Ohwaki Y (1967) Growth of rice coleoptiles in relation to oxygen concentrations. Scientific reports of Johoku University, Series IV Biology 33 :I-5.

O'Toole J C, Baldia E (1982) Water deficits and mineral uptake in rice. Crop Sci. **22:** 1144-1150.

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

Palada M C, Vergara B S (1972) Environmental effects on the resistance of rice seedlings to complete submergence. Crop Sci. 12:209-212.

Pandey H K, Mitra B N, Ghosh B C (1979) Flood susceptibility of semi dwarf rices and their suitability for lowlying areas. Pages 185-195. In: Proceedings of 1978 International deepwater rice workshop. IRRI, Los Banos, Philippines.

Penning de Vries F W T, Jansen D M, Ten Barge H F M, Bakema A (1989) Simulation of ecophysical processes of growth in several annual crops. IRRI, Los Baños, Philippines.

Ponnamperuma F N, Bandyopadhya A K (1980) Soil salinity as a constraint on food production in the humid tropics. Pages 203-216. In: Soil related constraints to food production in the tropics. IRRI, Los Banos, Philippines.

Ram P, Ram P C, Singh B B (1988) Response of rice genotypes to water stress imposed at the tillering and boot stages of growth. *lndian J. Plant Physiol.* **31:** 308-311.

Raskin I, Kende H (1984) Regulation of growth in stem sections of deepwater rice. *Planta* 160:66-72.

Reyniers F N, Troung - Binh, Jacquinot L, Nicou R (1982) Breeding for drought resistance in dry land rice. Pages 273-292. In: Drought resistance in crops with emphasis on rice. IRRI, Los Banos, Philippines.

Senadhira D (1992) Abiotic stresses of rice, IRRI Rice Research Seminar, 30 January 1992 IRRI, Los Banos, Philippines.

Setter T L, Kupkanchanakul T, Kupkanchanakul K, Bhekasut P, Wiengweera A, Greenway H (1988) Environmental factors in deepwater rice areas in Thailand : O2, CO2 and ethylene. Pages 55- 66. In: Symposium of the 1987 International deepwater rice workshop. IRRI, Los Banos, Philippines.

Setter T L, Greenway H, Kupkanchanakul T (1989). Submergence of rice II. Adverse effect of low CO2 concentrations. *Aust. J. Plant Physiol.* **16:** 265-278.

Setter TL, Ingram K T, Tuong TP (1993) Environmental characterization requirements for strategic research in rice grown under adverse conditions of drought, flooding or salinity. Pages 3-18. In : Rainfed lowland rice– agricultural research for high-risk environments. KT Ingram, ed, IRRI, Los Banos, Philippines.

Setter T L, Ramkrishnayya G, Ram Maurya P C, Singh B B (1995) Environmental characteristics of floodwater in eastern India; Relevance to flooding tolerance of rice. *lndian J. Plant* Physiol. **38** : 34-40.

ShardaKov V S (1948) New field method for the determination of the suction pressure of plants. *Dold. Akad.* Nauk SSSR **60 :** 169–172.

Singh U S (1982) Deepwater rice in India : problems and prospects Pages. 355–362 In: Proceedings of 1981 International deepwater rice workshop. IRRI, Los Baños, Philippines.

Singh U, (1993) Systems approach to understanding and predicting nutrient response in rainfed lowland rice. Paper presented at Rainfed lowland Programme Meeting, 19-20 January. IRRI, Los Baños, Philippines.

Smith A M, ap Rees T (1979) Effects of anaerobiosis on carbohydrate oxidation by roots of *Pisum sativum. Phytochemistry* **18:** 1453–1458.

Taylor D L (1942) Influence of oxygen tension on respiration, fermentation, and growth of wheat and rice. *Amer.* J. of Bot. **29:** 721–738.

Vergara B S, Jackson B, De Datta S K (1976) Deepwater rice and its responses to deepwater stress. pages 301-320. In: Climate and Rice, IRRI, Los Baños,. Philippines.

Woopereis M C S, Kropff, M J, Bouma, J (1993). Soil data needs for systems approaches at different levels of detail and application of gas to predict water limited crop production. In Research programme on soil management for increased and sustainable rice production. Woopereis *et.al.* eds. IRRI, Los Baños, Philippines.

Yambao E B, Ingram K T (1988) Drought stress index for rice. *Phil. J. Crop Sci.* **13 :** 105–111.

Yeo A R, Flowers T J (1984) Mechanisms of salinity resistance in rice and their role as physiological criteria in plant breeding. Pages 151–170. In: Salinity tolerance in plants-strategies for crop improvement, R.C. Staples and G.A. Toenniessen, Eds. Wiley International, New York, USA.

Yeo A R, Flowers T J (1986) The physiology of salinity resistance in rice (*Oryza sativa* L.) and a pyramiding approach to breeding varieties for saline soils. *Australian J. Plant Physiology* **13:** 75–91.

Yeo A R, Flowers T J (1989) Selection for physiological characters- examples from breeding for salt resistance. Pages 217–234. In: Plants under stress, HG. Jones, T.J. flowers and M.B. Jones eds. Cambridge University Press, Cambridge, Great Britain.

Yeo A R, Yeo M E, Flowers T J (1988) Selection of lines with high and low sodium transport from within varieties of an inbreeding species, rice (*Oryza sativa* L.) *New Phytologist* **110 :** 13–19.

Yeo A R, Yeo M E, Flowers T J, Flowers S A (1990) Screening of rice (*Oryza sativa* L) genotypes for physiological characters contributing to salinity resistance and their relationship to overall performance. *Theoretical and Applied Genetics* **79:** 377–384.

Yeo A R, Lee K S, Izard P, Boursier P J, Flowers T J (1991) Short and longterm effects of salinity on leaf growth in rice (*Oryza sativa* L.) J. *Exp. Bot.* **42:** 881–889.

NUTRIENT UPTAKE BY ROOTS OF CEREALS IN OXYGEN DEFICIENT ENVIRONMENT

☐ *M .C. Drew*[1]

SUMMARY

Uptake and transport of nutrient ions by roots of higher plants is strongly dependent on oxidative phosphorylation in order to supply adequate ATP. When aerobic respiration is slowed down by O_{2-} deficiency in the rooting zone, roots become hypoxic or anoxic; mineral nutrition may be affected. In barley and wheat, phloem-mobile nutrients are reallocated from older, senescing leaves to the younger and growing ones; but the mineral nutrition of the plant as a whole is not sufficient and deficiency symptoms appear. Under saline conditions, Na^+ fails to be excluded by roots of maize and reaches leaves in injurious amounts. Uptake of Cl^- from low concentration, a thermodynamically active process is strongly inhibited by anoxia, even when roots are not totally depleted of ATP.

When cereals such as barley, wheat or maize develop aerenchymatous roots in response to O_2 deficiency, nutrient uptake can continue despite the loss of many cells in the root cortex. Internal transport of O_2 from the leaves improves the energy status of the root. In rice, and other aquatic plants that form an extensive aerenchyma, suberization and lignification of the root axes assists in O_2 conservation by minimizing radial leakage and loss to the rhizosphere. However, these structures sometimes act as barriers to radial, inward, transport of nutrient ions in other species, so that uptake probably depends largely on the formation of fine laterals that lack structural barriers.

INTRODUCTION

Most cereal crops are not well-adapted to wetland conditions, showing a variety of responses to a sudden excess of water in the rooting zone, including inhibition of leaf extension and tillering, precocious senescence of older leaves, stomatal closure and reduction of net photosynthesis, and finally in a drop in economic yield (Van't Woudt and Hagan 1957; Cannell and Jackson, 1981; Meyer *et al.,* 1985; Hodgson *et al.,* 1990). Such flooding symptoms are undoubtedly a consequence of the inadequate performance of the roots. In transiently flooded soil, dissolved O_2 is quickly depleted by the rapid respiration of roots and micro-oganisms when temperatures are high, *(Meyer et al., 1985; Hodgson et al., 1990)*

---

[1] Department of Horticultural Sciences, Texas A & M University, College Station, Texas 77843-2133, USA.

so that there is insufficient O_2 to maintain oxidative phosphorylation in the roots (Pradet and Bomsel, 1978).

Under these conditions the soil becomes reducing and there is an accumulation of metal ions, organic acids and volatile substances, including CO_2 and ethylene, that are injurious to plants, or exert distinct physiological responses (Ponnamperuma, 1972, 1984; Drew and Lynch, 1980). However, potential phytotoxins do not appear immediately in the soil solution following the onset of flooding, but rather accumulate over an extended period of time before they reach active concentrations. During that time, roots are exposed to O_2 deficient conditions which alone are sufficient to bring about many of the typical symptoms of flooding injury (Trought and Drew, 1980c).

This review briefly examines the overall changes in mineral nutrition in cereals that occur with flooding, and considers the mechanisms by which ion transport in roots is modified under conditions of restricted O_2 supply in the field and in the laboratory condition.

OXYGEN DEFICIENCY AND MINERAL NUTRITION

Transient flooding under field condition can result in a complex situation with respect to O_2 supply to roots. During the growing season, depending on soil temperature and respiration rate, dissolved O_2 in the rooting zone gradually declines towards zero over a period of hours to days. Within the roots particularly in the apical zones where respiration rates are highest, O_2 concentration gradients may develop more rapidly than in the surrounding soil (Armstrong and Beckett, 1987; De Willigen and Van Noordwick, 1989), and cells become hypoxic; that is, oxidative phosphorylation is slowed. Cell's interior to the endodermis, with less access to the diminishing O_2 concentration in the soil, quickly becomes anoxic, that is, oxidative phosphorylation becomes negligible relative to ATP production in fermentation (Pradet and Bomsel, 1978). Because of the very low K_m of a cytochrome oxidase for O_2 such anoxic cells are virtually anaerobic, or O_2-free. At the same time, for older root zones near the soil surface and close to the junction with the shoot, sufficient O_2 may enter by diffusion from the superficial, more oxygenated layer of soil, or through intercellular spaces (Saglio *et al.,* 1983). Such root zones may continue their physiological functions, although they would represent only a small fraction of the root system for a mature plant. In the field, further heterogeneity arises from the more rapid depletion of O_2 from within soil aggregates compared with the larger, drained pores between aggregates and peds (Greenwoood and Berry, 1962), or from pockets of O_2 trapped within the soil, such as occurs with a "perched" water table. Laboratory experiments cannot readily reproduce such situations.

Field observations, as well as those of plants in undisturbed soil in lysimeters (Belford, 1981) or in columns of remixed soil, (Leyshon and Sheard 1974; Drew and Sisworo 1979; Trought and Drew, 1980a), have all shown distinct changes in mineral nutrition of the shoot when the O_2 supply is restricted (reviewed by Drew, 1988, 1991; Drew and Lynch, 1980). Typically, N, E K, Ca and Mg all decrease in concentration in the shoots while Fe, Mn Na and Cu increase. What changes in the soil environment account for this? We investigated this question with barley (Drew and Sisworo, 1979) and wheat (Trought and Drew 1980a) grown in 7.5 cm diameter cylinders of a sandy loam soil (2% organic matter). After barley grew for 13 days (18°C day 16° C night) in a controlled environment the soil was water saturated and the changes in the composition of the soil solution as well as various plant parameters, were measured with time. The most significant change in the soil was the loss of dissolved O_2, which was essentially depleted in 24 h period. The initial symptoms of flooding damage to barley shoots, such as slow increase in fresh weight, inhibition of leaf extension, and chlorosis of the tops of the oldest (lower) leaves appeared in 2-4 days. After only 2 days, there was a marked decrease in concentration of N, P and K in shoots. At that stage, none of the potential toxins that accumulate, as the soil redox declines, had reached appreciable concentrations and there was still ample free nitrate. It was concluded that the early responses to flooding, including the lowering of mineral nutrient status, was the result at least in part of the inhibition of ion transport by roots through lack of O_2. The premature chlorosis or senescence of older leaves with flooding was accompanied by a rapid loss of N from those leaves, indicating a remobilization from older to younger leaves. With wheat in soil columns (Trought and Drew 1980b), flooding strongly inhibited net uptake of N, P and K into the shoots. Remobilization from older to younger leaves was found to include all three of these phloem - mobile nutrients.

Increased concentrations of Fe and Mn in shoots in the longer term accord with the much greater solubility in the soil water at low redox potentials, while Na^+ exclusion by roots fails under O_2-deficient conditions. If O_2-deficiency itself accounts for the early stages in flooding response in cereals, it seemed reasonable to expect that plants in de-oxygenated nutrient solution would respond similarly to those in flooded soil. Wheat was grown in nutrient solution for 13 days at 14°C in a controlled environment room, and then the mots were made suddenly O_2 deficient by sparging with N_2 gas (Trought and Drew, 1980c). Essentially all of the responses recorded with soil flooding occurred with plants in deoxygenated nutrient solution, where none of the potentially harmful products of low soil redox could accumulate.

Net uptake of nutrients into the shoot was almost eliminated with deoxygenation of the nutrient solution. The average concentration of nutrients in the xylem sap was calculated from measurements of the volume of water transpired and the net transfer of nutrients to leaves; for P, K, Ca and Mg these concentrations were equal to, or less than, those in the nutrient solution, indicating that mass flow of water through the roots to leaves could account for the small continuing transfer of nutrients. For N, the calculated concentration in the xylem sap exceeded that of NO_3 in the nutrient solution. It may be suggested that N might be remobilized from within the senescing root system, or be absorbed by the small number of aerenchymatous roots that were beginning to form at the shoot base and enter the nutrient solution toward the end of the experimental period.

If mineral deficiency of shoots is a contributory factor in flooding damage, might it be possible to overcome some of the symptoms by delivering additional nutrients to the shoots? It has long been recognized that under outdoor conditions, heavy dressings of N to the soil surface can help alleviate the detrimental effects of soil flooding (Van Hoorn, 1958; Belford, 1981). There is a variety of explanations for this, including the delaying effect of NO_3^- on the lowering of the soil redox potential (Ponnamperuma, 1972) and replacement of NO_3^- lost in denitrification (Gambrell and Patrick, 1978). However, with wheat we used a split root technique to show that as long as a small part of the root system was kept oxygenated and supplied with a full complement of nutrients, nutrient uptake and growth were comparable to that of aerobic control plants (Trought and Drew, 1981). A remarkable alleviation of flooding injury in soil columns was obtained with barley, simply by regular additions of Ca $(NO_3)2$ solution to the soil surface (Drew *et al.,* 1979). Here, presumably the hypoxic roots at the surface absorbed nutrients sufficiently rapidly to compensate for the disfunction of the remainder in the deeper soil. It seem as if mineral nutrition together with its interaction with the plants hormonal status can largely overcome the deleterious effects on the shoot.

It has been suggested that NO_3^- can act as an alternative electron acceptor to O_2 under anoxia, and thereby, permit regeneration of NAD from NADH to maintain glycolysis(Garcia-Novo and Crawford, 1973). In effect, a competition was envisaged between nitrate reductase and alcohol dehydrogenase (for NADH) such that anaerobic production of ethanol would be inhibited. However, experiments with rice roots (Reggiani *et al.,* 1985) failed to confirm this expectation. Moreover, with maize roots no evidence could be found that the presence of NO_3^- enhanced the energy status under strict anoxia (Saglio *et al.,* 1988); a more rapid provision of NAD might be expected to accelerate glycolysis and substrate- linked phosphorylations to yield ATP. Thus the effectiveness of 'nitrate respiration' in roots of higher plants remains in doubt.

ANOXIA AND ION TRANSPORT BY NON-AERENCHYMATOUS ROOTS

Absorption of cations and anions across the plasma membrane of root cells is linked directly or indirectly to the activity of H^+-translocating ATPases that pump protons out of the cell towards the external medium (Poole 1978; Serrano 1989; Sanders, 1990). The inward (passive) flux of protons, in co-transport with other ions is the initial step in the absorption of nutrient ions into the plant. After radial transport across the root, transport from xylem parenchyma into the xylem likewise depends on the activity of a similar H^+-pump (Hanson, 1978; Clarkson *et al.,* 1984).

Higher plant cells contain no reserves of ATP, which in metabolically active cells like those of the root apical zone, is sufficient to maintain metabolism for less than 60 seconds at room temperature (Roberts *et al.,* 1985). The immediate effect of sudden imposition of anoxia is thus to deplete cells of nucleotide triphosphates, and thereby arrest the activity of proton pumps. Depolarization of membrane potential is therefore an almost immediate response to the sudden imposition of anoxia (Cheeseman and Hanson 1979; Buwalda *et al.,* 1988), and presumably the dissipation of the H^+ gradient across the plasma membrane curtails active ion transport (Rao and Rains, 1976; Cheeseman and Hamon, 1979; Jacoby and Rudich, 1980). In anoxic maize roots, passive inward movement of K^+ could still continue because of a-100mv diffusion potential at the membrane (Cheeseman and Hanson, 1979), indicating that a general degeneration of membrane properties did not take place in the short term. This accords with other observations that the apical zone of maize mots, the zone most sensitive to anoxia, retains viability for 15-18 hours when anoxically shocked (Roberts *et al.,* 1984; Johnson *et al.,* 1989). However, the evidence suggests that anaerobic generation of ATP during fermentation is insufficient to energize ion transport in competition with all the other requirements for ATP in energy-depleted cells.

With long term anoxia, a seemingly generalized decline in plasma membrane properties takes place with loss of inorganic ions and organic solutes from roots of wheat (Greenway *et al.,* 1992). The concentrations of solutes remaining in the roots at 70 hours of anoxia, as a percentage of the initial values, were K^+5%, free amino acids 41%, soluble sugars 7%. However, in experiments with roots that had been aciclimated by exposure to solutions bubbled with about 6% O_2, losses at 20 hours of anoxia were measured for different mot zones. For the apical 1mm zone for those mot tips that had lost their elongation potential (i.e. were moribund), there was little retention of K^+, amino acids and sugars. Root tips that could still grow, and older mot zones (1-5mm and 10-20 mm) maintained similar concentrations of solutes as the controls. There was a close association between generalized solute leakage and loss of cellular viability of the root tips of wheat.

Subapical zones of hypoxically acclimated roots of wheat retain their ability to transport ions after 24 h of anoxia, when re- exposed to air (Greenway *et al.,* 1992). Evidently in these relatively anoxia-tolerant cells, which do not leak readily like anoxically shocked ones, the machinery for ion transport is not lost.

The effect of O_2-deficiency on ion transport to the xylem has long been a topic of interest. The hypothesis of Crafts and Broyer (1938) concerning the mechanism for ion transfer from xylem parenchyma cells to the xylem postulated that those cells bordering the xylem were leaky as a result of a deficiency of O_2 within the stele. Under most conditions of aeration, no such deficiency of O_2 occurs, and the 2-pump hypothesis is now widely accepted. However, when aeration becomes less than ideal, there is evidence that the stele in maize roots does become anaerobic (Thomson and Greenway, 1991) : for enzymes like pyruvate decarboxylase and alcohol dehydrogenase that are indicative of anaerobic, fermenting cells, there is induction in the stele but not the outer, more aerobic cortex.

OXYGEN DEFICIENCY AND SALINITY

Flooding of the soil with saline water represents a special situation of economic interest, because irrigated agriculture in arid and semi-arid climates is often associated with poor soil drainage and excess salts (Carter, 1975). In terms of root function, environments low in O_2 allow a greater transfer of Na^+ from roots to shoots. With adequate oxygenation, Na^+ is actively pumped out of the cytoplasm of root cells to the outer solution, and also sequestered by xylem parenchyma cells (Shone *et al.,* 1969), thereby depleting Na^+ in the ascending xylem sap. Such mechanisms are dependent on ATP and break down when deprived of O_2 (Drew and Lauchli, 1985; Drew et al., 1988). The additional flux of Na^+ to the xylem, together with inhibition of K^+ transport, can lead to extreme changes in the ratio Na : K entering the shoots. In one study by Drew et al. (1988) this ratio increased by a factor of 860 for O_2 deficient roots when the concentration of NaCl in the external solution increased from 1.0 to 50.0 mM. Absorption of $C1^-$ into roots is normally dependent on ATP for active transport, and O_2-deficiency strongly inhibits uptake at low to moderate concentrations (upto about 100mM) in maize (Ghosh and Drew, unpublished). However, at higher concentrations we found that passive transport was appreciable and perhaps as a result of depolarization of plasma membranes, $C1^-$translocation to the shoot was enhanced relative to aerobic controls. For salt sensitive species like rice and maize (Yeo *et al.,* 1988), root O_2-deficiency can thus greatly exacerbate the detrimental effects of excess salts.

NUTRIENT UPTAKE BY AERENCHYMATOUS ROOTS

The internal transfer of O_2 from shoots to roots within aerenchymatous cortical tissue is an important mechanism for complete or partial avoidance of O_2 deficiency in many cereal species. In rice, the system of interconnected gas spaces or lacunae is very well developed, as it is in many aquatics, so that roots can extend considerable distances into anaerobic soil (Armstrong, 1979), but the demand for O_2 is just as great as in non wetland species (Armstrong and Webb, 1985). The low porosity to O_2 of the hypodermis, other than in the apical zone, ensures rice roots to avoid loss of O_2 to the surrounding soil, but rather conserve it for respiration and for oxygenation of the rhizosphere in the tip zone. Additionally, the extension of prominent intercellular spaces into the apical meristem probably assists diffusion of gaseous O_2 to a group of cells with a very high respiratory requirement for O_2 (Armstrong, 1979). Non-wetland species are not so well-adapted, failing to form an impervious hypodermis, or such a prominent aerenchyma, or intercellular spaces in the meristem.

In non-wetland cereals, aerenchyma formation in the roots requires induction by hypoxia (Thomson *et al.,* 1990). Such conditions enhance ethylene biosynthesis and entrapment within root tissues, the ethylene in turn promoting lysis of cells in the cortex to form interconnected lacunae (Drew *et al.,* 1979; Jackson *et al,,* 1985a). Aerenchyma formation in rice is mostly constitutive, failing to demonstrate a clear signaling by ethylene (Jackson *et al.,* 1985 b).

What is the significance of such changes in root anatomy to radial ion transport to the xylem? In aerenchymatous roots of maize, radial transport of K^+ and Pi under well oxygenated conditions was not inhibited by the degeneration of many of the cortical cells Drew *et al,* 1980; Drew and Saker 1986). The remaining radial files of intact cortical cells, and radial cell wall remnants, appeared able to transport ions across the cortex without lowering the overall rate of transport (Drew and Fourcy, 1986). In situ, such aerenchymatous roots are sufficienctly well supplied with O_2 to maintain energy metabolism (Drew *et al.,* 1985), so that it seems reasonable to suppose that ion transport can continue.

In rice and other species with strongly suberized and lignified hypodermal layers (Clark and Harris, 1981), the question arises as to whether these act as barriers to ion transport (reviewed by Drew, 1987). In the sand sedge *(Carex arenaria),* the hypodermis becomes suberized within 2 to 5 cm of the root tip and becomes highly impermeable to water and inorganic nutrients (Robards *et al.,* 1979), so that uptake is confined to the finer lateral roots lacking such anatomical features. In maize, the permeability of the hypodermis depends on the humidity to which the mot has been exposed, with greater impermeability resulting from exposure to air (Ferguson and Clarkson; 1976; Peterson and Perumalla, 1984; Clarkson *et al.,* 1987). In sorghum exposed to dry soil, lignification and suberization of the hypodermis and endodermis occur unusually close to the mot tip, and the late maturing metaxylem vessels fail to lose their cross walls (Cruz *et al.,* 1992). The combined effect is to make such roots ineffective in water absorption. Relatively little work has been published on the precise zones along rice seminal and nodal roots that contribute to ion transport, so that the consequences of anatomical changes are less well understood. Such work is best done with radio-labeled tracers (Peterson, 1987), because although apoplastic fluorescent dyes provide useful evidence concerning changes in the resistance of potential pathways for flow of solutes and water, their larger molecular size is likely to become excluded where some passage of smaller molecules can continue.

CONCLUSION

For non-wetland species, oxygenation of the root system can greatly modify its function in plant mineral nutrition. Simultaneously, changes in permeability to water, and the synthesis of phytohormones and their transfer to the shoot, contribute to the symptoms of flooding damage. The ability of root cells to maintain viability under anoxia, together with the rapid formation of a new, aerenchymatous root system of a size that can replace the function of the original, damaged one, are features that assist greatly a plant's tolerance of transient flooding. Better understanding of the genetic mechanisms of anoxia-tolerance and anoxia-avoidance will help in further improvement of performance of flood-sensitive dryland cereals.

REREFENCES

Armstrong W (1979) Aeration in higher plants. *Adv. Bot. Res.* **7**:225-331.

Armstrong W, Beckett P M(1987) Internal aeration and the development of stelar anoxia in submerged roots: A multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. *New Phytol.* **105**:221-245.

Armstrong W, Webb T (1985) A critical oxygen pressure for root extension in rice. *J. Exp. Bot.* **36:**1573-1582.

Belford, R K(1981) Responseof winter wheat to prolonged waterlogging under outdoor conditions. *J.Agri. Sci. Camb.* **97:** 557-568.

Buwalda F, Thomson C J, Steigner W, Barrett-Lennard E G, Gibbs J, Greenway H (1988) Hypoxia induces membrane depolarization and potassium loss from wheat roots but does not increase their permeability to sorbitol. *J. Exp. Bot.* **39:**1169-1183.

Cannell R Q, Jackson M B (1981) Alleviating aeration stresses. Pages 141-192. In: Modifying the root environment to reduce crop stress. G.F. Arkin and H.M. Taylor, eds. American Society of Agricultural Engineering, Madison.

Carter D L (1975) Problems of salinity in agriculture. Pages 25- 35. In : Plants in saline environments. A Poljakoff-Mayber and J. Gale, eds. Springer Verlag, Berlin.

Cheeseman J M, Hanson J B (1979) Energy-linked potassium influx as related to cell potential in corn roots. *Plant Physiology.* 64: 842-845.

Clark L H, Harris W H (1981) Observations of the root anatomy of rice (*Oryza sativa* L.) *Amer. J. Bot.* 68:154-161.

Clarkson D T, Robards A W, Stephens J E, Stark M (1987) Suberin lamellae in the hypodermis of maize (*Zea mays*) roots; development and factors affecting the permeability of hypodermal layers. *Plant Cell Environ.* 10:83-93.

Crafts A S, Broyer T C (1938) Migration of salts and water into xylem of roots of higher plants. *Am. J.Bot.* 25:529-535.

Cruz R, Jordan W, Drew M C (1992) Structural change and associated reduction of hydraulic conductivity in roots of *Sorghum bicolor* L. following exposure to water deficit. *Plant Physiology.* 99: 203-212

De Willigen P, Van Noordwick M (1989) Model calculations on the relative importanceof internal longitudinal diffusion for aeration of roots on non-wetland plants. *Plant and Soil* 113: 111-119.

Drew M C (1988) Effects of flooding and oxygen deficiency on plant mineral nutrition. Page 115-159. Vol. 111 In : Advances in plant nutrition. A. Lauchli and P.B. Tinker, eds. Praeger, New York.

Drew M C (1987) Function of root tissues in nutrient and water transport. Pages 71-101. In : Root development and function effects of the physical environment. P J Gregory, J V Lake and A H Rose eds. Cambridge University Press, Cambridge-London.

Drew M C (1991) Oxygen-deficiency in the root environment and plant mineral nutrion. Pages 303-316. In : Plant life under oxygen deprivation. M.R. Jackson, D. D. Davies, and H. Lambers, eds. SPB Academic Publishing; The Hague, The Netherlands.

Drew M C, Chamel A, Garrec J P, Fourcy A (1980) Cortical air spaces (aerenchyma) in roots of corn subjected to oxygen stress, structure and influence on uptake and translocation of ^{86}Rb ions. *Plant Physiology.* 65:506-511.

Drew M.C., Fourcy A(1986) Radial movement of cations across aerenchymatous roots of *Zea mays* measured by electron probe X-ray microanalysis. *J.Exp. Bot.* 37: 823-831.

Drew M C, Guenther J, Lauchli A (1988) The combined effects of salinity and root anoxia on growth and net Na^+ and K^+ accumulation in *Zen mays* L. (cv Pioneer 3906) grown in solution culture. Ann. Bot. 61:41-53.

Drew M C, Jackson M B, Giffard S (1979) Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays L. Planta.* 147:83-88.

Drew M C, Lauchli A(1985) Oxygen dependent exclusion of Na^+ by roots of *Zea mays* (cv. Pioneer 39060) in relation to salinity damage. *Plant Physiology.* 79:171-176.

Drew M C, Lynch J M (1980) Soil anaerobiosis, micro-organisms and root function, *Ann. Rev. Phytopath.* 18:37-66.

Drew M C, Saglio P, Pradet A (1985) Higher adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. *Planta* 165:51-58.

Drew M C, Saker L R (1986) Ion transport to the xylem in aerenchymatous roots of *Zea mays. J. Exp. Bot.* 37:22-33.

Drew M C, Siworo E J (1979) The development of waterlogging damage in young barley plants in relation to plant nutrient status and changes in soil properties. *New Phytol.* ***82***:301-314.

Drew M C, Sisworo E J, Saker L R (1979) Alleviation of waterlogging damage to young barley plants by application of nitrate and a synthetic cytokinin, and comparison between the effects of waterlogging, nitrogen deficiency and root excision. New Phytol. ***82:*** 315-329.

Ferguson I B, Clarkson D T (1976) Ion uptake in relation to the development of a root hypodermis. *New Phytol. 77*:11-14.

Gambrell R P, Patrick W H (1978) The chemical and microbiological properties of anaerobic soils and sediments. Pages 375-424. In : Plant life in anaerobic environments. D.D. Hook and R.M.M. Crawford, eds. Ann.Arbor.Science, Ann. Arbor, Michigan.

Garcia-Novo F, Crawford R M M (1973) Soil aeration, nitrate reduction and flooding tolerance in higher plants. *New Phytol. 72*:1031-1039.

Greenway H, Waters I, Newsome J (1992) Effect of anoxia on uptake and loss of solutes in roots of wheat. Aust. J. *Plant Physiol.* ***19***:233-247.

Greenwood D J, Berry G (1962) Aerobic respiration in soil crumbs. *Nature* ***195***:161-163.

Hanson J B (1978) Application of the chemi-osmotic hypothesis to ion transport across the root. *Plant Physiology.* ***62***:402-405.

Hodgson AS, Constable G R, Duddy Daniells I G (1990) A comparison of drip and furrow irrigated cotton on a cracking clay soil 2. Water use efficiency, waterlogging, root distribution and soil structure. *Irrig. Sci.* ***11***:143-148.

Jackson M B, Fenning T M, Drew M C, Saker L R (1985a) Stimulation of ethylene production and gas-space (aerenchyma) formation in adventitious roots of *Zea mays* L. by small partial pressures of oxygen. *Planta.* ***165***:486-492

Jackson M B, Fenning T M, Jenkins W (1985b) Aerenchyma (gas- space) formation in adventitous roots of rice (*Oryza sativa* L.) is not controlled by ethylene or small partial pressures of oxygen. *J. Exp. Bot.* ***36***:1566-1572.

Jacoby B, Rudich B (1980) Proton-chloride symport in barley roots. *Ann. Bot.* ***46***:493-498.

Johnson J, Cobb B G, Drew M.C. (1989) Hypoxic induction of anoxia tolerance in roots of *Zea mays. Plant Physiology.* ***91***:837-841.

Leyshon A J, Sheard R W (1974) Influence of short-term flooding on the growth and plant nutrient composition of barley. *Can. J. Soil Sci.* ***54***:463-473.

Meyer W S, Barrs H D, Smith R C G, White N S, Heritage A D, Short D L (1985) Effect of irrigation on soil oxygen status and root and shoot growth of wheat in a clay soil. *Aust. J. Agri Res.* ***36***:171-185.

Peterson C A(1987) The exodermal casparian band of onion roots blocks the apoplastic movement of sulphate ions. *J. Exp. Bot.* ***38***:2068-2081.

Peterson C A, Perumalla C J (1984) Development of the hypodermal casparian band in corn and onion roots. *J. Exp. Bot.* ***35***:51-57.

Ponnamperuma, F N (1972) The chemistry of submerged soils. *Adv. Agron.* ***24***:29-96.

Ponnamperuma, F N(1984) Effects of flooding on soils. Pages 9-45. In : Flooding and plant growth. T.T. Kozlowski, ed. Academic Press, Orlando, Florida.

Poole R J (1978) Energy coupling for membrane transport. *Annu. Rev. Plant Physiology.* ***29***:437-460.

Pradet A, Bomsel J L (1978) Energy metabolism in plants under hypoxia and anoxia. Pages 89-118. In : Plant Life in anaerobic environments. D.O. Hook and R.M.M. Crawford, eds. Ann. Arbor, Michigan.

Rao K P, Rains D W (1976) Nitrate absorption by barley: 1. Kinetics and energetics. *Plant Physiology.* ***57***:55-58.

Reggiani R, Brambila U, Bertani A (1985) Effect of exogenous nitrate on anaerobic metabolism in excised rice roots: 1. Nitrate reduction and pyridine nucleotides pools. *J. Exp. Bot.* ***36***:1193-1199.

Robards A W, Clarkson D T, Sanderson J (1979) Structure and permeability of the epidermal/hypodermal layers of the sand sedge (*Carex arenario* L.) *Planta* ***101***:331-347.

Roberts J K M, Lane A N, Clark R A, Nieman R H (1985) Relationships between the rate of synthesis of ATP and the concentrations of reactants and products of ATP hydrolysis in maize root tips, determined by ^{31}P nuclear magnetic resonance. *Arch. Biochem. Biophys.* ***240***:712-722.

Roberts, J K M, Callis J, Jardetsky O, Walbot V, Freeling N(1984) Mechanism of cytoplasmic pH regulation in hypoxic maize root tips and its role in survial under hypoxia. *Proc. Nat. Acad. Sci.* USA ***81***:3379-3383.

Saglio P H, Drew M C, Pradet A(1988) Metabolic acclimation to anoxia induced by low (2-4 kPa partial pressure) oxygen pretreatment (hypoxia) in root tips of *Zea mays. Plant Physiology.* ***86***:61-66.

Saglio P H, Raymond P, Pradet A (1983) Oxygen transport and root respiration of maize seedlings. A quantitative approach using the correlation between ATP/ADP and the respiration rate controlled by oxygen tension. *Plant Physiology* ***72***:1035-1039.

Sanders D (1990) Kinetic modeling of plant and fungal membrane transport systems. *Annu. Rev. Plant Physiology.* ***42***:77-107.

Serrano R(1989) Structure and function of plasma membrane ATPase. *Annu. Rev. Plant Physiology.* **40**:61-94.

Shone M G T, Clarkson D T, Sanderson J (1969) The absorption and translocation of sodium by maize seedlings. *Planta.* ***86***:301-314.

Thomson C J, Greenway H(1991) Metabolic evidence for stelar anoxia in maize root exposed to low O_2 concentrations. *Plant Physiology.* ***96***:1394-1301.

Thomson C J, Armstrong W, Waters L Greenway H(1990) Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. *Plant Cell Environ.* ***13:*** 395-403.

Thomson C J, Greenway H(1991) Metabolic evidence tor stelar anoxia in maize roots exposed to low O_2 concentrations. *Plant Physiology* ***96***:1294-1301.

Trought M C T, Drew M C (1980a) The development of waterlogging damage in wheat seedlings *(Triticum aestivum* L.) L. Shoot and root growth in relation to changes in the concentration of dissolved gases and solutes in the soil solution. *Plant and Soil.* ***54***:77-94.

Trought M C T, Drew M C (1980b) The development of waterlogging damage in wheat seedlings *(Triticum aestivum* L.).II. Accumulation and redistribution of nutrients by the shoot. *Plant and Soil* ***56***:187-199.

Trought M C T, Drew M C (1980c) The development of waterlogging damage in young wheat plants in anaerobic solution cultures. *J. Exp. Bot.* ***31*** : 1573-1585.

Trought MC T, Drew MC (1981) Alleviation of injury to young wheat plants in anaerobicsolution cultures in relation to the supply of nitrate and other inorganic nutrients. *J. Exp. Bot.* ***32***:509-522

Van Hoorn J W (1958) Results of a ground water level experimental field with arable crops on clay soil. *Neth. J. Agric. Sci.* ***6***:1-10.

Van't Woudt B D, Hagan R M (1957) Crop responses to excessively high soil moisture levels. Pages 514-611. In : Drainage of agricultural lands, J. N. Luthin. ed, : American Society of Agricultural Engineering, Madison, Wisconsin.

Yeo A R, Yeo M E, Flowers T J(1988) Selection of lines with high and low sodium transport from within varieties of an inbreeding species; rice (*Oryza sativa* L.). *New Phytol.* ***110***:13-19.

RESPONSE OF FLOODING IN GOGORANCAH RICE AND MOISTURE STRESS EFFECT AT REPRODUCTIVE STAGE IN WALIK JERAMI RICE

☐ *Didiek Setio Budi and*
Bambang Suprihatno[1]

SUMMARY

The effect of time of flooding and reproductive -stage moisture stress on crop productivity was studied at the Jakenan experimental station during 1989-90 wet season, and 1991 and 1992 dry seasons. The soil is classified as Planosol with a sandy loam texture. Three separate field experiments were conducted in split plot design with four replications. Time of flooding treatments consisted of flooding at, a) 4 wk, b) 5 wk, c) 6wk, d) 7wk, e) 8 wk and f)9 wk after seeding. The reproductive stage moisture stress treatments consisted of, a) continuous field saturation, b) noirrigation from panicle initiation (PI) to heading and c) no irrigation from heading to harvest. The rice genotypes used were Dodokan and Cikapundung for the gogorancah experiment and IR64, IR36, Ciliwung, IR39357 - 71-1-1-2-2, IR 39422-18-1-2-2, IR45912-9-1-2-2, IR48563-11-2-2-3, S969b-265-1-4-1, S400b-55-2 for the walik jerami experiment (dry season).

The results showed that flooding at 7 week after seeding was very important for gogorancah rice in achieving higher yields. Without rainfall during walik jerami growing period, the moisture stress imposed from panicle initiation to heading reduced grain yield up to 50%. When the moisture stress was imposed from heading to maturity, yield reduction was around 70%. The results of 1991-92 experiment failed to detect any of the effects of reproductive stage moisture stress on grain yield because the rainfall was well distributed during the treatment period. In greenhouse experiment the -50 cb moisture stress from panicle initiation to heading reduced grain yield of IR64 by 50%. However, Ciliwung variety was relatively stable under various stages of moisture stress. IR 39357-71-1-1-2-2 showed the intermediate tolerance to the reproductive stage moisture stress and was also suitable for gogorancah crop, particularly when the rainfall was uneven during the early part of the growing season.

INTRODUCTION

In Pati district, rainfed rice area occupies about two-third of the total wetland rice areas (irrigated rice 20,598 ha; rainfed rice 39,383 ha), and comprises 11% of the total rainfed rice concentrated in Jaken, Jakenan, Winong and Puncakwangi sub-districts.

---

[1] SURIF, Jakenan Experiment Station, Jakenan, Pati. Central Java, Indonesia

The traditional cropping pattern at Jaken sub-district is gogorancah (dry seeded bunded)during wet season, followed by walik jerami rice (minimum tillage, transplanted) in dry season I and dryland crops in dry season II.

The average yield of gogorancah is around 6.0 t/ha under normal conditions. However, variation in the onset and lack of rainfall before and after sowing are serious production constraints for gogorancah rice. Drought often occurs in the beginning of wet season, therefore, the farmers delay tillage and sowing. Drought stress during reproductive stage poses a major problem for the walik jerami rice also and so the yield often falls as low as 2.0 t/ha. The proportion of the length of dry and wet periods during gogorancah growing season determines growth and yield performance.

Little information is available on the time of flooding for gogorancah, although many studies on the effect of moisture stress at different growth stages on rice have been conducted. However, the results varied with location, season and variety. These variations are attributed to the effect of climatic, soil and hydrological factors on yield components and root growth and development.

The present study was conducted to (1) know the effect of time of flooding on the yield of gogorancah rice in order to determine the most crucial time of flooding for it and (2) to understand the reaction of varieties or breeding lines to water stress at reproductive stage in walik jerami rice.

MATERIALS AND METHODS

Experiment 1. Effect of time of flooding on the yield of gogorancah rice.

A field experiment was conducted during 1988-84 wet season at the Jakenan Experimental Station on the planosol soil with sandy loam texture, pH 5.6, organic matter 0.6296, total N 0.07%, CEC 5.3 meq per 100 g soil, extractable P 18.0 mg Kg^{-1} and exchangeable K 0.04 meq per 100 g. soil,

A split plot design with four replications was used. Time of flooding was studied on the sub-plot and variety on the main-plot. A very early maturing rice variety Dodokan and an early variety Cikapundung were used. Time of flooding consisted of flooding at, a) 4wk, b) 5wk, c) 6wk, d)7wk and e) 8wk and f) 9 wk after seeding. Watering was from the rainfall through a water collector located near the experimental site.

Rice seeds were dibbled at @ three seeds per hole, with 20 x 20 cm spacing. The plot size was 4.0 x 5.0 m. All plots were fertilized at the rates of 112 kg N, 45 kg P_2O_5 and 40 kg K_2O ha^{-1}. Nitro en fertilizer (Urea) was applied in splits, 40kg N ha^{-1} at seeding time, 40kg N ha^{-1} 3 wk after seeding and 32 kg N ha^{-1} at panicle initiation (PI). Total amount of Potassium (KCI) and Phosphorus (triple superphosphate; TSP) were given at seeding time together with the first nitrogen application. Weeds, pest, and diseases were controlled intensively.

Observations were made for root dry mass, yield components and grain yield. Root mass was sampled by a core method for determining the root mass density.

Yield Components and yield were recorded at harvest. Yield was obtained from 5 m^2 harvest area and then adjusted to ton per hectare at 14% moisture content. Five plants per plot were used to characterize the yield components.

Soil matric potential was measured by tensiometers' installed at 10 cm depth, whereas perched water table was measured with piezometer inserted at the 75 cm depth. Daily rainfall data were taken from a weather station located 50 m away from the experimental site.

Experiment 2. Study on the effect of soil-water stress at reproductive stage on grain yield in walik jerami rice.

Field experiments were conducted at the Jakenan Experimental Station during 1991 and 1992 dry seasons. A split plot design with three replications was used for both experiments. In 1991, five rice genotypes IR 393557-71-1-1-2-2, IR39422-181-22, lR459129-1-22,lR48563-11-2-2-3 and Dodokan were used as subplot and three levels of soil water stress as the main-plot factor. The soil moisture stress treatments were : a) continuous field saturation, b) no irrigation from panicle initiation(PI) to heading, and c) no irrigation from heading to maturity. In 1992 rice, the genotypes used were:IR36, IR39357-71-1-1-2-2, S969b-265-1-4-1 and S400b-55-2.

The 21-d-old seedings were transplanted at 2 seedlings/hill with 20 x20 cm spacing. Land was ploughed twice by hoeing and harrowing. The plot size was 4 x 5 m and each plot received Urea), TSP and KC1 with the rates 135 kg N, 45 kg P_2O_5 and 50 kg K_2O ha^{-1} , respectively. Nitrogen fertilizer (Urea) was applied in three equal splits of 45 KgN ha^{-1} each, at transplanting/ at 3 weeks after transplanting, and at panicle initiation. All of KC1 and TSP were applied as basal. Weeds, pests and diseases were controlled intensively.

Observations were made for yield components and yield. Four plants per plot were used to characterize yield components. Grain yield was obtained from 8 m^2 harvest area and calculated as ton per hectare at 14% seed moisture content.

Soil moisture status at 0-15 cm depth was determined by gravimetric method and expressed as per cent oven dry weight (%ODW).

Experiment 3. Greenhouse study on the effect of soil water stress at different growth stages on the yield of lowland rice.

This experiment was conducted at the Sukamandi Experimental Station during 1989 dry season using Ultisol soil with silty clay texture. A split plot design with four replications was used. Four levels of soil water stress were used as sub-plot factor i.e.: a) continuous flooding, b) water stress imposed from 10 DAT to panicle initiation, c) water stress imposed from panicle initiation to heading and d) water stress imposed from heading to maturity. Two varieties were used as main plot factor i.e. a) IR64 and b) Ciliwung. The soil moisture stress was allowed to reach -50 cb and measured by tensiometer at 10 cm depth. The water stress was imposed by not watering the pots. After reaching the stress level, pots were reirrigated until field saturation. The 21-d old seedlings were transplanted to each pot with 4 hills per pot.

Grain yield data were obtained from each pot and expressed in gram per hill at 14% moisture content.

Crop data were analyzed using the methods for the split plot design and Duncan's Multiple Range Test was employed if F-test showed significance.

RESULTS AND DISCUSSION

The results of the effect of time of flooding on the yield components and grain yield for gogorancah rice are presented in Table 1. Panicle length, 1,000–grain weight and grain yield were affected by time of flooding. Flooding at four to six weeks after seeding was important period to achieve higher yields. There was a tendency of decline in grain yield when the flooding was applied more than six weeks after seeding. Spikelet number per panicle and filled-spikelet percentage were not affected by time of flooding treatments. There were significant differences in spikelet number per panicle, filled- spikelet percentage and 1,000- grain weight but not in grain yield between Dodokan and Cikapundung cultivars.

The decline in yield at, or above seven weeks after seeding might be due to low supply of water and nutrients particularly nitrogen to the crop. Ismunadji (1985) stated that the form and availability of nutrients are directly related to moisture supply in the soil.

The effect of time of flooding on the mot mass density for the gogorancah rice is illustrated in Figures 1 and 2.

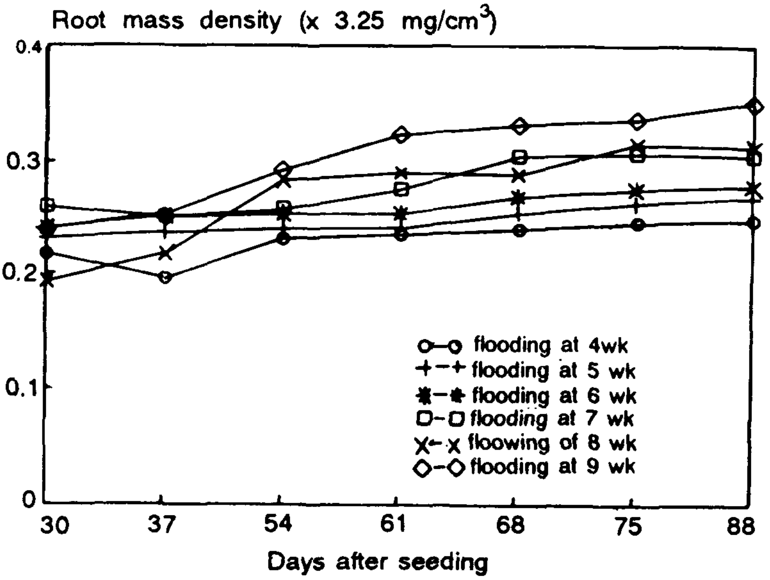


Fig. 1 : Root growth of Dodokan variety at the 0-5 cm soil depth as affected by time of flooding, Jakenan, 1988-89 WS.

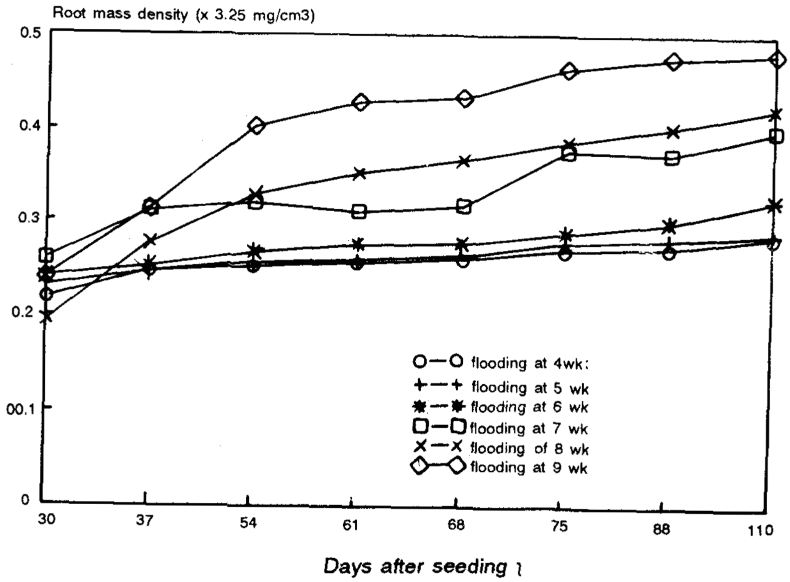


Fig. 2 : Root growth of Cikapundung variety at the 0-5 cm soil depth as affected by time of flooding, Jakenan, 1988-1989 WS.

Table 1. Effect* of time of flooding and cultivars on the yield components and grain yield for gogorancah rice, Jakenan, 1988-89 WS.

Treatments	Yield components				Grain yield (t/ha)
	Spikelet/ panicle (nos)	Filled spikelet (%)	1,000 grain wt (g)	Panicle length (cm)	
Cultivars (C)					
Dodokan	84.3 b	75.0 a	24.7 a	22.3 b	4.17 a
Cikapundung	119.4 a	69.5 b	23.5 b	23.1 a	3.95 a
Time of flooding (F) Weeks after seeding (WAS)					
4 WAS	105.4 a	74.4 a	25.1 a	23.4.a	4.54 a
5 WAS	98.3 a	73.5 a	24.5 ab	22.9 ab	4.24 ab
6 WAS	103.0 a	70.7 a	24.2 abc	22.9 ab	4.10 ab
7 WAS	105.1 a	71.9 a	23.8 bc	22.4.b	4.05 bc
8 WAS	101.5 a	71.1 a	23.3 c	22.3 b	3.81 bc
9 WAS	97.6 a	72.0 a	23.6 a	22.3 b	3.63 c
CV (C):	5.3%	4.7%	3.3%	3.9%	18.9%
CV (F):	7.8%	4.5%,	3.8%	3.3%	10.0%

* In a column, means followed by a common letter are not significantly different at the 5% level by DMRT

There was gradual increase in root mass density from 37 to 88 days after seeding. The rooting characteristics were influenced by water regime and type of cultivars. Longer dry period relative to wet period tended to increase the root mass density at 0-5 cm depth.

Apparently Cikapundung had higher root mass density at 0-5 cm depth than Dodokan, particularly when flooding was done at nine weeks after seeding. Rooting depth of both the varieties was deepest when grown under dryland condition.

An aerobic soil favours deep root growth and rice varieties differ markedly in their rooting habits, both laterally and vertically (Yoshida and Hasegawa, 1982). The fluctuations in soil matric potential and piezometric water level during gogorancah growing season are illustrated in Figures 3 and 4.

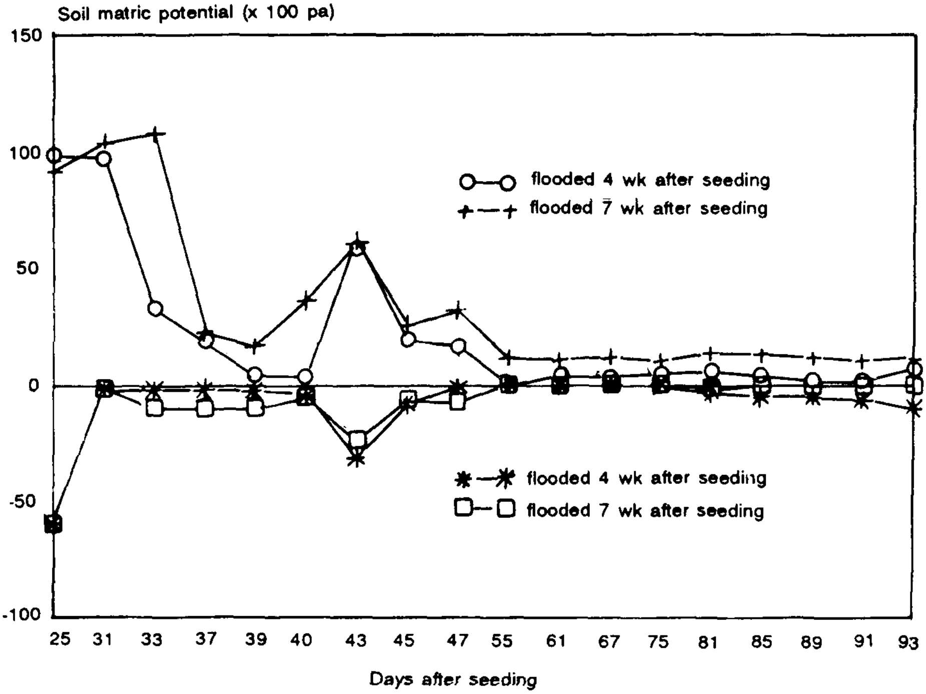


Fig. 3 : Fluctuation of the soil matric potential at the 10 cm soil depth and piezometric water level for the two time of flooding of Dodokan. Jakenan, 1988-1989 WS.

High fluctuation in soil matric potential occurred from 25 to 40 days after seeding and was subsequently relatively stable. The piezometic water level was close to the soil surface from 45 days after seeding till harvest.

The dynamics of soil matric potential and the depth of piezometric water level are partly controlled by rainfall. Weekly rainfall well distributed was from 45 days afterseeding until harvest (Fig.5) and therefore, the soil matric potential and perched water table were found stable.

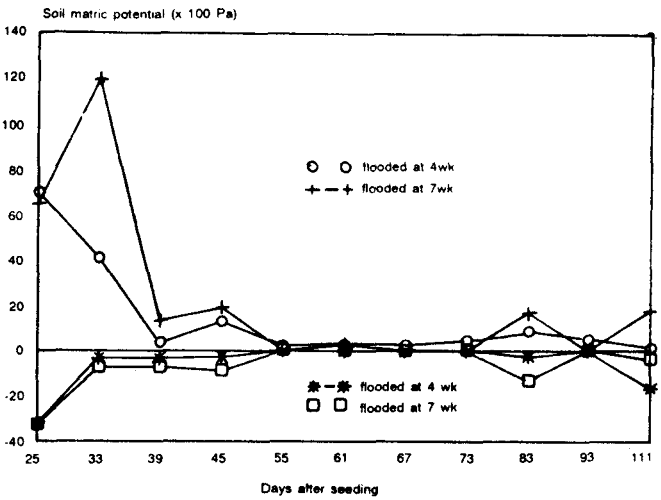


Fig. 4 : Fluctuation of the soil matric potential at the 10 cm soil depth and piezometric water level for the two time of flooding of Chillwung, Jakenan, 1988-1989 WS.

The effect of rice genotypes and soil water stress at the reproductive stage on the yield components and yield are presented in Tables 2 to 5. The results of genotype x water stress interaction on the number of spikelets per panicle are presented in Table 2. Dodokan and IR3922-18-1-2-2 were found to have stability in number of spikelets per panicle under reproductive moisture stress.

Table 2. Interactive effect between rice genotypes and soil water stress at reproductive stage on the number of spikelets of rice, Jakenan, 1991 DS.

Treatment **Rice genotypes (C)**	**Reproductive stage soil water stress (S)** Continuous saturation (no stress)	 Primordia to heading	 Heading to maturity
	Spikelet/panicle (no)*		
IR393537-71-1-1-2-2	96.7 a	74.4 b	78.1 a
IR39422-18-1-2-2	69.4 b	99.9 a	82.7 a
IR45912-9-1-2-2	51.7 c	60.7 c	62.0 b
IR48563-11-2-2-3	56.3 c	68.4 bc	64.0 b
Dodokan	80.5 b	89.9 a	75.9 a
CV(C):		12.07%	
CV(S):		9.3%	

- In a column, means followed by a common letter are not significantly different at the 5% level by DMRT

The number of spikelets per panicle were shown to be reduced by reproductive-phase drought (De Datta, 1981). The effects of moisture stress at the reproductive stage on the yield components and yield are presented in Table 3.

Table 3. Yield components and grain yield as affected by rice genotypes and soil water stress at reproductive stage, Jakenan, 1991 DS.

Treatment	Yield Components*		
	Filled spikelets (%)	1,000 grain wt (g)	Grain yield (t/ha)
Soil water stress (S)			
Continuous saturation	65.8 a	26.6 a	1.96 a
PI to heading	47.8 b	26.0 a	0.97 b
Heading to maturity	24.7 c	23.1 b	0.36 c
Rice genotypes (C)			
IR393537-71-1-1-2–2	51.3 a	25.9 a	1.20 a
IR39422-18-1-2-2	52.0 a	22.8 b	1.19 a
IR45912-9-1-2-2	40.8 b	25.6 a	0.99 b
IR48563-11-2-2-3	44.4 b	25.6 a	0.97 b
Dodokan	42.1 b	26.3 a	1.13 ab
CV(S):	16.0%	5.3%	–
CV(C):	13.4%	5.0%	–

* In a column, means followed by a common letter are not significantly different at the 5% level by DMRT.

During the growing season of walik jerami rice, occurrence of moisture stress from panicle initiation to heading and from heading to maturity, significantly influenced the filled spikelet percentage and grain yield. Moisture stress from panicle initiation to heading and from heading to maturity reduced yield by 50% and 72%, respectively. However, moisture stress from heading to maturity significantly influenced the 1,000 grain weight.

Moisture stress in the early reproductive stage (panicle initiation to heading) resulted in a decreased grain yield through Education in number of spikelets. Moisture stress during reproductive phase has been shown to reduce filled spikelet number per panicle (IRRI, 1990). However, it had no influence on the panicle number per hill, 1,000 grain weight and yield of walik jerami rice during the dry season of 1992 (data not shown).

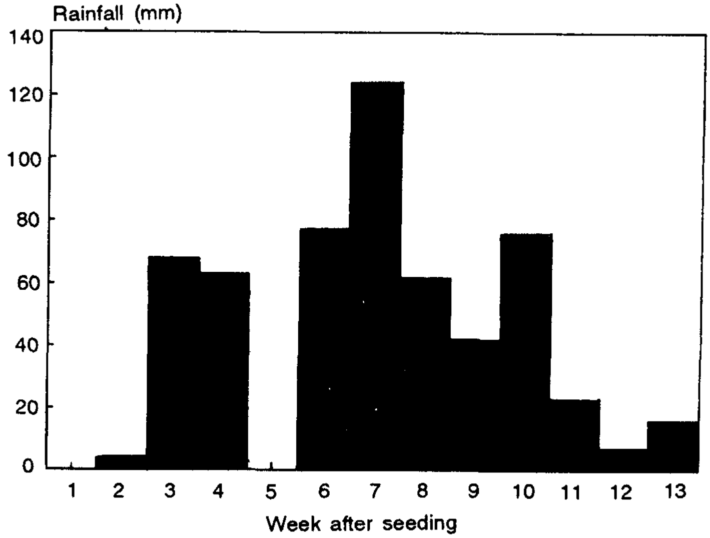


Fig. 5 : Weekly rainfall distribution in gogorancah rice growing season, Jakenan, 1988-1989.

The genotype IR36 exhibited greater spikelet sterility under both the continuous saturation and reproductive moisture stress situation. Apparently, soil water stress from heading to maturity induced the spikelet sterility (Table 4).

Table 4. Interactive effect of rice genotypes and soil water stress at reproductive stage on the spikelet sterility of rice, Jakenan, 1992 DS.

Rice genotypes (C)	**Soil water stress (S)**		
	Continuous saturation	Panicle initiation to heading	Heading to maturity
		Spikelet Sterility (%)*	
IR36	15.8 a	34.3 a	41.0 a
IR393537-71-1-1-22	13.3 a	23.9 ab	28.8 b
S969b-265-1-4-1	10.2 a	16.2 c	17.2 b
S400b-55-2	18.7 a	23.0 ab	19.5 b
CV (C) :	29.6%	-	-
CV (S) :	31.0%	-	-

* In a column, means followed by a common letter are not significantly different at the 5% level by DMRT

The rice genotypes grown in 1992 walik jerami did not show any significant differences in grain yield. Water stress treatments at reproductive stage had no effect either. The average yield ranged from 2.2-2.6 t/ha. The genotypes IR36, however, exhibited a tendency to yield higher (though not significant) than other breeding lines (data not presented). The rainfall distribution was optimum during the stress-treatment periods and hence the soil moisture status reached above field capacity. This is considered as critical level of soil moisture for rainfed lowland rice (Fagi, 1986), below which significant yield differences could be expected.

A comparison between two genotypes (grown in 1989) to moisture stress tolerance revealed that the level of yield of Ciliwung was lower than IR64. However, it was found to be more tolerant to moisture stress at various growth stages. IR64 was more sensitive to moisture stress from panicle initiation to heading than other phases of moisture stress, as evidenced by a drastic reduction in grain yield (Table 5).

Table 5. Interactive effect of rice cultivars and soil water stress at different growth stages on the grain yield (g/ hill), Sukamandi Greenhouse, 1989 DS.

Soil water stress (S)	**Cultivar (C)**	
	IR64	Ciliwung
	grain yield* (g/hill)	
Continuous flooding	20.82 a	17.26 a
10 DAT to Panicle initiation	18.82 a	15.71 a
PI to Heading	10.31 b	15.04 a
Heading to maturity	19.90 a	17.25 a
CV (C) :	3.0%	
CV (S) :	10.7%	

* In a column, means followed by a common letter are not significantly different at the 5% level by DMRT

CONCLUSION

In Pati district, the optimum time of flooding in gogorancah rice is in the range of four to six weeks after seeding to obtain higher yield. The moisture stress from panicle initiation to heading was found to be critical in walik jerami rice. The genotypes Ciliwung and TR39357-71-1-1-2-2 were found, having potential to be planted as Walik jerami rice.

REFERENCES

De Datta S K (1981) Principles and practices of rice production. John Wiley & Sons.

Fagi A M (1986) Efficient use of water for rainfed lowland rice. In : Progress in rainfed lowland rice. IRRI, Los Banos, Philippines.

IRRI (1990) Program report for 1989. International Rice Research Institute., Los Banos, Philippines.

Ismunadji M (1985) Effect of sulphate application on the performanceof IR36 rice variety under submerged and dryland condition. *Indonesian Journal of Crop Science* l(1) : 1-64.

Yoshida S, S Hasegawa (1982) The rice root system, its development and function. In : Drought resistance in crops with emphasis on rice. IRRI, Los Banos, Philippines.

ANAEROBIC TOLERANT RICE SEEDLING GROWTH AND ITS POTENTIAL IN THE TROPICAL RAINFED LOWLAND ECOSYSTEMS

☐ *M. Yamauchi*[1], *A.M. Aguilar*[1], *J.L Padilla*[1]
D.V Aragones[1] *and U. Singh*[2]

SUMMARY

Rice seedling establishment in wet direct seeding is erratic because farmers sow seeds on the soil surface. Anaerobic- tolerant cultivars that grow vigorously in flooded or water- saturated soil were identified. These cultivars developed longer coleoptiles than non-tolerant controls, suggesting that they can transport 0_2 in the air or water to the seeds in anaerobiosis efficiently. The superiority of tolerant cultivars in seedling survival and growth persisted even when grown in the dark, although their growth increased under light. Temperatures between 15 and 35°C had little effect on difference in seedling survival between tolerant and control cultivars, although seedling growth of both types of cultivars was reduced at 15°C.

The growth of a tolerant cultivar in flooded soil was equivalent to that of a control grown in drained soil. Thus, the use of anaerobic cultivars may make sowing in flooded or water-saturated soil similar to that in freely drained soil. The potential of its applicattion to rainfed lowland ecosystems was tested in Tarlac, Philippines, during 1993 wet season. Rice seeds soaked in water for 24 h were dibble-sown into water-saturated soil under zero tillage. There was little difference between anaerobic-tolerant and control cultivars in crop establishment, presumably due to soil dryness (there was no rainfall after seeding). The tolerant cultivars outyielded the controls: the six anaerobic cultivars had a mean grain yield of 3.2 t/ha at 0-180 kg N/ha, whereas the control cultivars had 2.4 t/ha. Further agronomic and physiological studies are needed to adapt anaerobic-tolerant cultivars in heterogeneous rainfed lowland soils.

INTRODUCTION

Crop establishment

A rice crop is established either by transplanting or by dry or wet direct seeding. Transplanting is mostly practiced in irrigated lowland rice and is an established technology. Dry seeding is also well studied and is practiced where

---

[1] International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines

[2] International Fertilizer Development Center-IRRI cooperative Program

soil is dry. Rice plants adapted to irrigated lowland and upland ecosystems are bred for transplanting and dry seeding, respectively, in Asia.

Wet seeding technology, however, has not been well developed. Germinated seeds are sown on the surface of drained, water- saturated puddled soil or flooded soil surface (water seeding). Crop establishment by wet seeding seems to be more unstable and inconsistent than that by dry seeding. In dry seeding, seeds are covered with aerobic soil and protected from birds, rodents, and rain splashing; in wet seeding, seeds are sown on puddled soil surface and exposed to these disturbances. The condition of the puddled soil surface changes according to intensity of puddling, climate, and time after land preparation. In water seeding, seedlings not only drift due to poor anchorage but are also destroyed by snails and fish.

Rice seedlings grown by wet seeding are exposed to soil anaerobiosis, although this is not a constraint in transplanted and dry seeded rice. Because there are no cultivars raised and adapted for wet seeding, farmers currently use cultivars developed specifically for transplanting.

Anaerobic seeding is proposed to improve the wet seeding process (Yamauchi *et al.,* 1993a). Germinated seeds are sown under the surface of puddled soil with or without standing water so that seeds are protected from the disturbances occurring on the soil surface. In addition, seeds get better anchorage in water seeding. Because seeds are exposed to soil anoxia, cultivars tolerant of anoxia are preferable for this seeding method.

The process of crop establishment in wet seeding could be divided into survival (which can be measured by percentage seedling establishment) and growth (which can be characterized by leaf development, seedling height, and shoot and root weights). Mesocotyl elongation is an important factor in raising the apical meristem to the upper soil layer when seeds are sown deep into the soil (Takahashi, 1984).

Germplasm selection

A screening system to find rice germplasm suitable for anaerobic seeding was developed (Yamauchi *et al.,* 1993a). Seeds that germinated for 2 d were planted 25 mm deep in seedling trays. The trays were then submerged in water to a depth of 30-50 mm. Seedling establishment was evaluated by analyzing leaf development, seedling height, and percentage establishment (survival) 15 d after planting.

Rice germplasm tolerant to soil anoxia were identified in traditional cultivars and also in breeding lines with improved plant type. Screening for anaerobic-tolerant rice germplasm was conducted using 256 accessions from conserved germplasm from the International Rice Germplasm Center (IRGC) and 404 accessions from the International Network for Genetic Evaluation of Rice (INGER), IRRI (Yamauchi *et al.,* 1993 a). IRGC germplasm represented broad genetic diversity, and INGER germplasm involved desirable agronomic characters. Eight percent of the IRGC germplasm and 2% of those from INGER were identified statistically as tolerant of soil anoxia. Among the anaerobic germplasm were those from northeast India and Bangladesh which were adapted to deepwater and early summer rainfed lowland cultures.

In vitro growth characteristics

Germinated seeds were placed in vials or erlenmeyer flasks with distilled water and exposed to various degrees of hypoxia. The anaerobic-tolerant cultivars had longer coleoptiles than the control cultivars in the gas flow of N_2 and air, and underhypoxia in closed flasks in the dark (Yamauchi and Herradura, 1993; Yamauchi *et al.,* 1994). Although ethylene stimulated coleoptile elongation of tolerant and control cultivars was at the same degree, mesocotyl and shoot (leaf and sheath) elongations of tolerant cultivars were more stimulated by ethylene compared with those of control cultivars. The tolerant cultivars produced more ethylene per plant than did the control cultivars; at times, however the same amount of ethylene were produced. Although the *in vitro* seedling growth of tolerant cultivars was more than that of control cultivars, the fundamental mechanism underlying the vigorous growth is unknown.

Growth characteristics in soil

Seedling establishment may be partly controlled by some factors related to soil properties and soil management. In the Philippines, crop establishment was better in upland soil than in lowland soils, presumably due to higher redox potential in the upland soil when the soils were flooded (Yamauchi *et al.,* 1993b).

The presence of chloroplasts in the coleoptile was demonstrated by Kordan and Ashraf (1990), suggesting that photosynthetically produced O_2 in the coleoptile may be involved in the process of seedling survival and that assimilated carbohydrates may accelerate seedling growth. Because the coleoptile is the first organ to reach the surface of the flooded soil, it may be important to confirm if photosynthesis is involved in the process of seedling establishment.

Because temperature controls the catabolism of seed reserves, it may have an effect on seedling survival and growth. The growth of anaerobic-tolerant cultivars in aerobic soil has not been compared with the growth in anaerobic soil. Characterizing anaerobic seedling growth as a function of temperature and water may help to determine the rice ecosystem in which anaembic-tolerant cultivars may be adopted.

Anaerobic seeding in irrigated lowlands

Rice seeds sown under the surface of puddled soil can successfully establish seedlings particularly when anaerobic- tolerant cultivars are used. Broadcast seeds can be placed under the soil surface when sowing is done immediately after puddling. Anaerobic drill seeding is practiced by using a seeder. Anaerobic broadcast seeding and drill seeding were successfully conducted in the Philippines during dry and wet seasons in two locations (Aragones *et al.,* 1993, 1994). The most serious constraint identified in this study was the destruction of seedlings by freshwater snails (*Pomacea* sp.) (Mochida, 1988). Anaerobic broadcast seeding was also successfully conducted in the Mekong Delta (Chau and Yamauchi, 1994) and in Hanoi (Chuong and Yamauchi, 1994) in Vietnam. Anaerobic seeding in irrigated lowland is feasible.

The yield potential of anaerobic tolerant cultivars with improved plant type was equivalent to or higher than that of high-yielding local check cultivars when grown under direct seeding. In yield trials at Los Baños, Philippines, the anaerobic-tolerant cultivar IR52341-60-1-2-1 had the same high yield as check IR72 (8.4 t/ha). At Muñoz, IR52341-60-1-2-1 yielded more than IR 72 (9.8 vs 7.0 t/ha). In the Mekong Delta, anaerobic-tolerant cultivar BR1870-67-1-3 yielded 5.8 t/ha, whereas check MTL103 yielded 5.1 t/ha during the 1993 wet season (Chau and Yamauchi, 1994). IR52341-60-1-2-1 yielded 5.2 t/ha in Hanoi with check CN2 yielding 4.5 t/ha during the 1993 wet season (Chuong and Yamauchi, 1994).

Wet seeding in the rainfed lowland ecosystem

Because soil water conditions in rainfed lowland fields vary according to location in toposequence, rainfall, and time after the onset of the wet season, farmers choose dry seeding, wet seeding, or transplanting in order to establish the crop successfully and economically. Drought is a serious constraint in rainfed lowland rice culture. Early planting by direct seeding advances the plant developmental stage, thus avoiding drought at the termination of rainfall at the end of the wet season. Direct seeded plants have both seminal and nodal roots, whereas transplanted plants have only nodal roots. In addition, seminal roots might develop deeper than nodal roots at the early growth stage. Thus, direct seeded rice might be more tolerant of drought at the early stage than transplanted rice.

Compared with dry seeding, wet seeding is less commonly practiced in the rainfed lowland fields, presumably due to the instability of crop establishment. Success in wet seeding depends on the characteristics of the dry-to-wet transition period at the onset of the monsoon and on adequate surface drainage (Morris and Zandstra, 1979). Water seeding is practiced where drainage is difficult. Introducing anaerobic seeding in the rainfed lowlands would stabilize crop establishment in wet seeding, and thus may interest farmers to follow direct seeding.

Seedling growth of anaerobic-tolerant cultivars in flooded soil is characterized here in terms of light and temperature, and in comparison with growth in drained soil in controlled environments. We also studied the crop establishment and grain yield of rice plants in rainfed lowland fields with water- saturated soil under zero tillage to identify the contraints in adoption of anaerobic seeding.

MATERIALS AND METHODS

Anaerobic seedling growth under continuous light and darkness

Seeds of three anaerobic-tolerant cultivars (CO25 [percentage germination, 93.4%; rate of germination, 1.00], ASD1 [99.6; 1.001, and Taothabi [98.3; 1.001 and three control cultivars IR36 [96.5; 1.00 IR50 [95.2; 0.951, and IR74 [91.7; 0.99]) were germinated in petri dishes for 2 d at 30°C, and then sown in sieved (mesh 40) upland (Maahas clay) soil placed in a container (300 x 240 x 110 mm). Rate of germination was measured according to Krishnasamy and Seshu (1989). The container was filled with soil up to a height of 80 mm. Seventeen seeds were sown for each cultivar per container. The soil was then submerged under 30 mm of water. Eight containers were placed in a growth chamber (30°C, 70% relative humidity) under continuous darkness or light (30 k lux). Plants in four containers (replications) were sampled 7 and 11 d after seeding.

Seedling growth was characterized by measuring emergence score (0=no emergence, 1=coleoptile emerged, 2=lst leaf emerged, 3= 2nd leaf emerged, ...) ; seedling height; and mesocotyl length of the individual plant; and shoot, mot, and seed weights as a bulk sample per replication after drying at 80°C. Percentage of seedlings established was calculated to estimate seedling survival.

Effect of temperature on anaerobic seedling growth

Seeds of six cultivars (CO25 [percentage germination, 93.7%; rate of germination, 0.991, ASDl [l00; 1.001, Taothabi [97; 0.941, IR 36 [95.5; 0.981, IR50 (93.3; 0.931, and IR74 [91.3; 0.991) were germinated and planted using the method described above. The containers were placed in temperature-controlled glass rooms (outdooor growth chamber) (under natural light) using the set of 15, 20 and 30°C or 25, 30, and 35°C. One container represented one replication. Four containers (replications) were placed in each glass room. Plants were sampled 14 d after seeding and their growth and survival analyzed.

Seedling growth in flooded and drained soils

Seeds of IR36 (percentage germination, 96.8%; rate of germination, 0.98) and Taothabi (98.9; 0.97) were similarly germinated and sown, except that the plastic containers were replaced by 3.8-liter pots. The soil in the pot was flooded at a depth of 5 cm or freely drained, Seventeen seeds of the cultivar were sown per pot. The pots were placed in a temperature- controlled (29/2lºC day/night) glass room (phytotron) under natural light . Plants were sampled 4, 6, 8, 10, 12, and 14 d after seeding and their growth was measured. Root length (from the tip of seminal root to the base of plant) was measured. The experimental design was a randomized complete block with four replications (pots).

Performance in rainfed lowlands

Seeds of six anaerobic-tolerant cultivars (IR341996-50-2-1-3 [percentage germination, 99.3; rate of germination, 1.00], IR52341-60-1-2-1 [100; 1.00], IR50363-61-1-2-2 [99.3; 0.991, IR31802-48-2-2-2 [100; 1.00], BR1870-67-1-3 [98.5; 0.89], and BR736- 20-3-1 [100; 1.00]) and two controls (PSBRC10 and IR72) were dibble-sown under zero tillage in a rainfed lowland field at Masalasa, Tarlac, Philippines, during 1993 wet season. All seeds were produced during 1993 dry season; dormancy was broken by keeping seeds at 50°C for 5 d.

After dry-season harvest, the remaining straw was removed from the field. The seeds were soaked in water for 1 d, then dibbled manually at 5-10 seeds per hole at a depth of 25-30 mm at 20x 20cm spacing. Soil was saturated with water at sowing and dried after 1 wk. Weeds were removed by hand. Fertilizer was applied at the rate of 0, 60, 120, and 180 kg N/ha in four splits (15 and 35 d after emergence, 5 d before panicle initiation, and flowering). Experimental design was a randomized complete block with four replications. Plot size was 6 x 4 m.

Crop establishment was measured 25 d after seeding by counting the number of seedlings in a 0.8 m^2 area per plot. Seedling dry weight, mesocotyl length, and emergence scores were taken from the plants, using 4 hills/plot. Grain yield was measured from a 5m^2 area.

RESULTS AND DISCUSSION

Anaerobic seedling growth under continuous light and darkness

This study was conducted to clarify how light affects anaerobic seedling growth and if light reaction is involved in the mechanism of cultivar difference in the tolerance for soil anoxia. Seedling growth was enhanced in the light presumably due to photosynthesis (Fig. 1).

Emergence score, seedling height, and shoot and root weights were greater under light than under darkness. On the other hand, seedling survival was not affected by light. Means of percentage seedling establishment of control and anaerobic cultivars were 67.2 and 94.4% under light and 71.6 and 94.9% under darkness, respectively. This indicates that light reaction is not involved in the process of seedling survival.

The percentage seedling establishment at 7 d of IR36 under light and of IR50 and IR74 under darkness decreased at 11 d; those of the others were not changed. This suggests that seedling establishment had been determined before 7 d and that some seedlings established at 7 d died later. Lack of photosynthesis is not the cause of seedling death.

Regardless of light conditions, there were significant differences between control and anaerobic-tolerant cultivars in percentage seedling establishment, emergence score, seedling height, shoot and root weights, and mesocotyl length (Fig.1). The results suggest that light is not involved in the mechanism of cultivar difference.

Effect of temperature on anaerobic seedling growth

This study was conducted to determine the effect of temperature on seedling survival and growth. The percentage of seedling establishment was less affected by temperature than was seedling growth, which was measured by shoot weight and height (Fig.2). Growth significantly diminished at 15°C but was highest at 30°C.

The difference in seedling growth between the control and anaerobic-tolerant cultivars diminished at 15°C, whereas the difference in survival was little affected by the change in temperature. These results suggest that the factors controlling seedling growth may be different from those controlling seedling survival.

Crop establishment in the field is determined by biomass production per unit land area, which is the product of the number of seedlings per unit area (determined

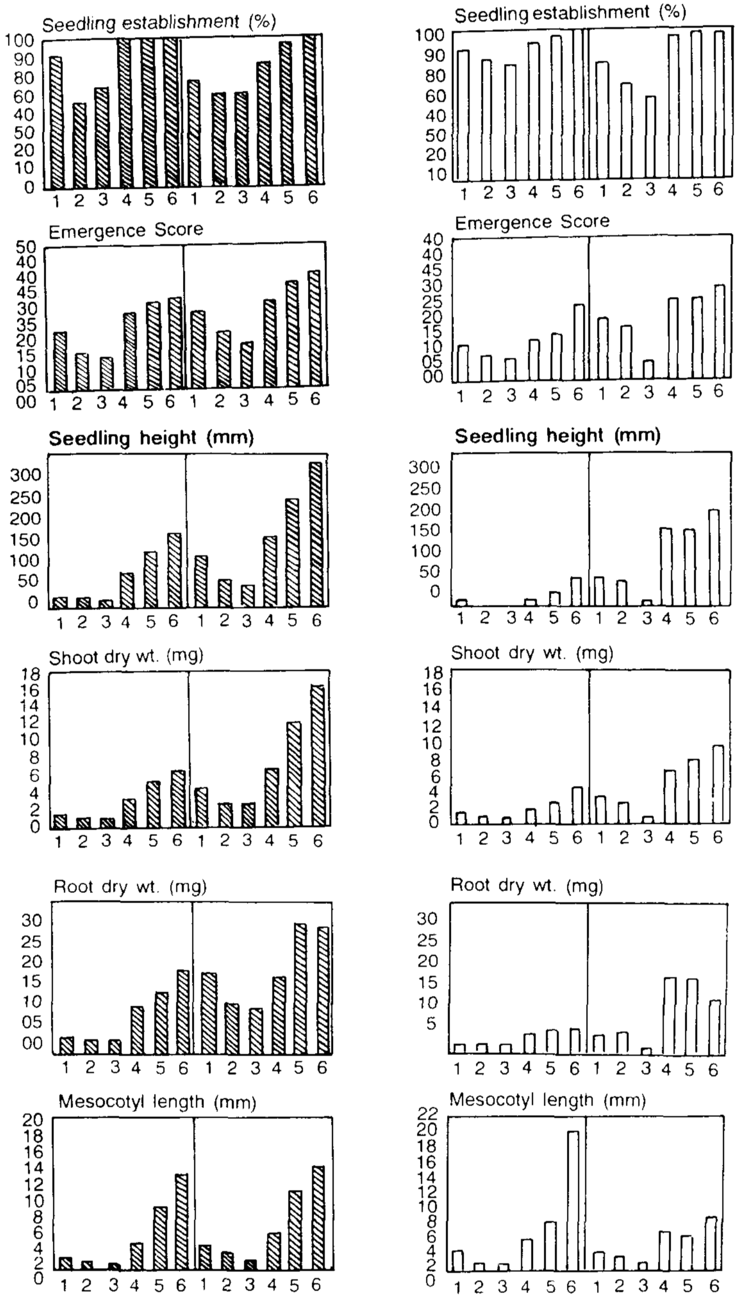


Fig. 1. Rice seedling growth in flooded soil under continuous light and darkness at 30°C. Seedling growth was measured at 7 and 11d after seeding. Bars having a common letter (under light or dark condition at 7 or 11d) are not significantly different at the 5% level by DMRT. Number denotes cultivar names: 1=IR36; 2=IR50; 3=IR74; 4=CO25; 5=ASD1; 6=Taothabi. The shaded and closed bars indicate the light and dark conditions, respectively.

by seed rate and seedling survival) and single-seedling weight. Therefore, crop establishment may be low at lower temperatures and the highest at 30°C.

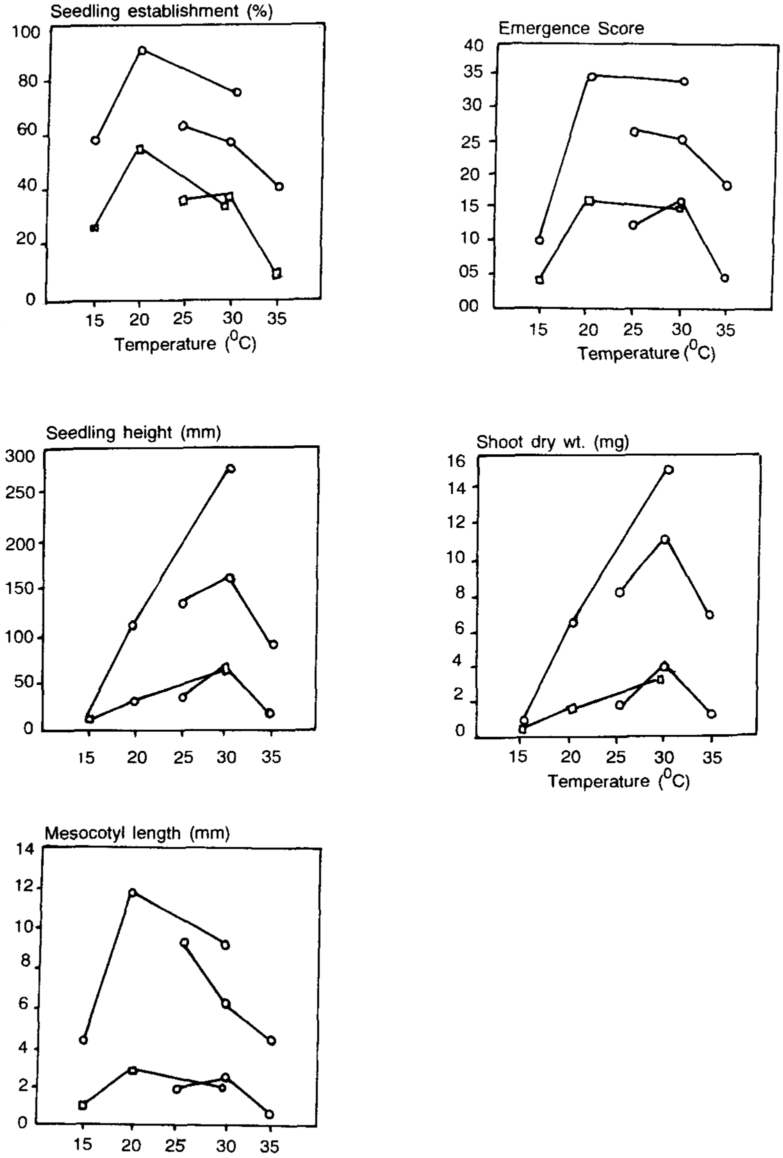


Fig. 2. Effect of temperature on rice seedling growth under natural light condition. Growth was measured 14d after seeding. Experiments were conducted 2 times with the temperature combinations of 15, 20, and 30°C (closed symbols) and 25, 30 and 35°C (open symbols). Values are the means of control (IR36, IR50. and IR74) (□) and anaerobic tolerant cultivars (CO25, ASD1, and Taothabi) (O). The difference in each character between control and tolerant at each temperature was significantly different at the 1% level (even at 15°C for seedling height and shoot dry weight).

Seedling growth in flooded and drained soils

This study was conducted to compare growth of the control and anaerobic-tolerant cultivars in drained and flooded soils. Taothabi was superior to IR36 in terms of seedling height, shoot weight, and mesocotyl length. Emergence of IR36 was inhibited in the flooded soil, whereas Taothabi was not (Fig.3), an indication of its anaerobic character.

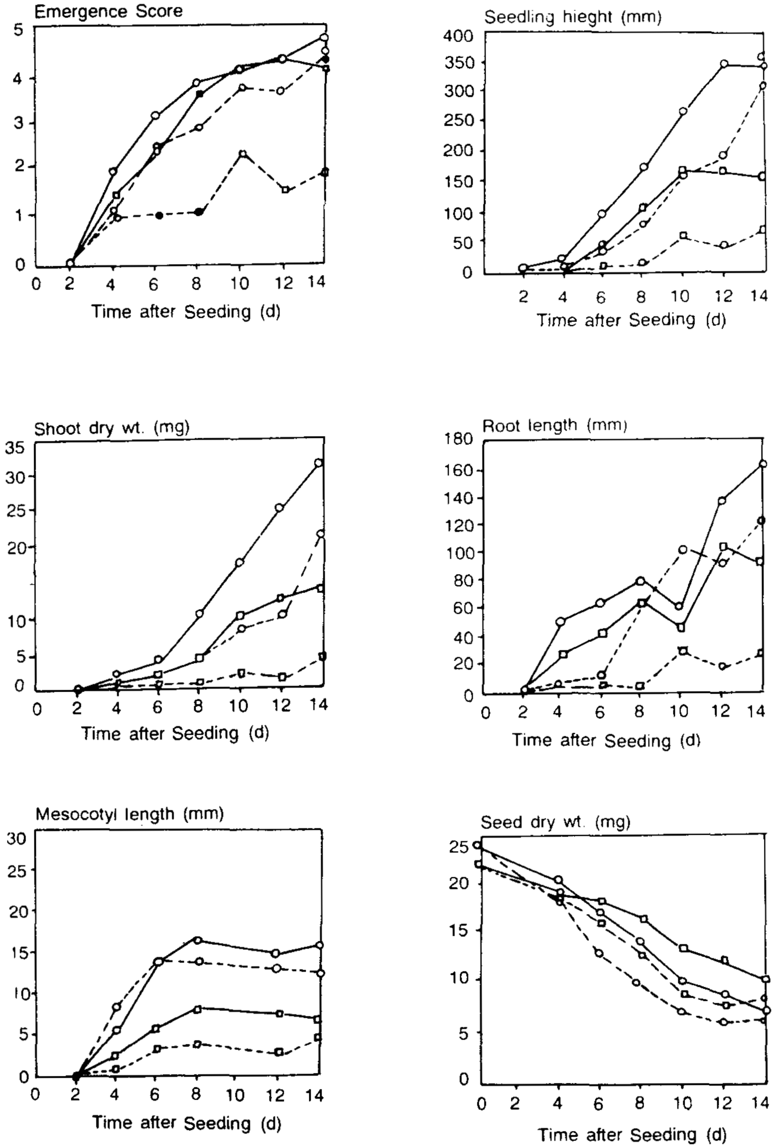


Fig. 3. Seedling growth and seed weight of rice cultivar IR36 (control) (□) and Taothabi (anaerobic) (O) in flooded (closed) and drained soils (open). Values having a common letter at each day are not significantly different at the 5% level by DMRT.

Development in shoot weight and seedling height suggested that, although growth in drained soil was superior to that in flooded soil, the growth of Taothabi in flooded soil was equivalent to that of IR36 in drained soil. The root length of Taothabi in flooded soil was inhibited until 6 d after seeding, but the roots started to grow later. After 8 d, root length of Taothabi was the same as that of IR36 in the drained soil. It could be presumed that in Taothabi, which was grown in flooded soil, the O_2 in the atmosphere was transported from the shoot to the root between the 6th and 8th d and then was utilized to develop the roots (since emergence score was more than 2 (1st leaf emerged) at 6 d).

The decrease in seed weight, which may indicate the catabolism of the seed reserved material for use in energy production in the tissue, was larger in drained soil than in flooded soil. The larger decrease in seed weight in Taothabi than in IR 36 in drained or flooded soil suggests rapid metabolic turnover in Taothabi.

Performance in rainfed lowland field

This field experiment was conducted to analyze yield potential of anaerobic-tolerant cultivars and to identify the constraints in growing them under the rainfed lowlands. After harvesting the dry-season rice crop, the rain started and soil was saturated with water. The land was too wet to conduct dry seeding, although it did not have enough standing water to puddle the soil for transplanting. Under these field conditions, farmers generally waited for more rainfall and thus planting gets delayed. Delayed planting increased the chance for plants to encounter drought because rain often stops at the late growth stage. Introduction of zero-tillage wet seeding may advance the time of planting over transplanting. We assumed that sowing anaerobic-tolerant cultivars using zero tillage may be possible because they can survive and establish seedlings even with heavy rains and even if fields were flooded after sowing.

There was no heavy rainfall aftersowing. Soil dried up and a crust was formed. There was no significant difference between anaerobic-tolerant and control cultivars in terms of plant density (Table 1). Similarly, no significant differences in emergence score, seedling height, shoot weight per unit area, and mesocotyl length were observed.

Grain yield of anaerobic-tolerant cultivars was higher than controls irrespective of the dose of N application (Table 1). IR4 1996-50-2-1-3 produced the highest yield (3.0 t/ha) among the cultivars tested at 0 kg N/ha while BR736-20-3-1 showed highest yield (4.6 t/ha) at 180 kg N/ha. The percentage increase in grain yield by the introduction of anaerobic tolerant cultivars was 79% at 0 kg N/ha and 23-30% at 60-180 kg N/ha.

IR72 is a high-yielding cultivar in irrigated lowlands. Hence, the low yield of IR72 (1.5-2.9 t/ha) demonstrates that the yield potential was hindered by unidentified stresses and that the anaerobic-tolerant cultivars were more tolerant to such stresses than IR72. Therefort, it could be presumed that anaerobic-tolerant cultivars have the tolerance for the unidentified stresses. The screening system should be able to select rice germplasm tolerant not only of soil anoxia but also of unidentified stresses. The results suggest that stress tolerance in rainfed lowland rice is important in increasing the yield.

Table 1. Crop establishment* and grain yield* of 6 anaerobic tolerant and 2 control cultivars in rainfed lowlands, Masalasa, Tarlac, Philippines. 1993 wet season.

Cultivars	Crop establishment**				Grain yield (t/ha)			
	Plant density (no./m²)	Shoot dry wt. (g.m²)	Height (mm)	Mesocotyl length (mm)	N levels (kg/ha)			
					0	60	120	180
IR41996-50-21-3	124bcd	10.5	216	5.4	3.0a	3.3ab	3.7a	3.3bc
IR52341-60-1-2-1	147ab	12.9	169	5.4	2.4abc	2.9abc	3.3ab	4.0ab
IR50363-60-1-2-2	116cd	8.1	170	5.0	2.1bcd	2.9abc	3.5a	3.4bc
IR31802 48-2-2-2	143abc	12.3	181	7.3	2.0cd	3.5a	3.6a	3.8ab
BR1870-67-1-3	96d	7.2	149	5.1	2.8ab	3.0abc	3.7a	3.3bc
BR736-20-3-1	102d	9.3	191	7.1	2.0bcd	2.9abc	3.5a	4.6a
PSBRC10 (Control)	169a	12.6	177	6.9	1.1e	2.6bc	3.1ab	2.9c
IR72 (Control)	123bcd	12.5	176	6.6	1.5de	2.3c	2.7b	2.9c

* In a column, means followed by a common letter are not significantly different at the 5% level by DMRT.

** Measured 25 d after seeding.

RESEARCH NEEDS

The results presented here demonstrated that anaerobic-tolerant cultivars had superiority in seedling establishment over a wide range of environmental conditions : light, temperature, drained/flooded soil. In addition, they were more tolerant to the unidentified stresses in the rainfed lowland field in the Philippines, producing more grains than the non-tolerant controls. Introducing anaerobic cultivars into rainfed lowlands would increase not only the stability of wet seeding but also the grain yield. Systematic research is needed to develop wet seeding technology in the rainfed lowlands, in as much as crop establishment and grain yield are influenced by many factors-- climate, soil, seed vigor, and cultivar:

- * The mechanism of the superiority in seedling survival and growth and high grain yield of anaerobic-tolerant cultivars need to be clarified.
- * The data base of available anaerobic-tolerant germplasm for use in agronomic and breeding studies should be developed.
- * Breeding of high-yielding anaerobic-tolerant cultivars is necessary. Genetic studies including RFLP analysis will be useful.
- * There is a need to search for germplasm with multiple stress tolerance because of exposure of germinating seeds to anoxia and drought in the rainfed lowland ecosystem.
- * There is a need to develop proper agronomic practices of crop establishment for the transition time between dry seeding and transplanting to maximize use of the potential of cultivar traits. Zero-tillage wet seeding technology should be studied to enable early planting of rice.

REFERENCES

Aragones D V, Casayuran P R, Asis C A, Aguilar A M, Sta Cruz P C, Yamauchi M (1993) Evaluation of crop stand establishment by anaerobic seeding technology at two locations in the Philippines. *Philip. J. Crop Sci.* **18:**36 (suppl. 1).

Aragones D V, Casayuran P R, Cruz R T, Yamauchi M (1994) Direct seeding technology: drill seeding using anaerobic cultivars. *Philip. J. Crop Sci.* **19:** 21 (suppl. 1).

Chau N M, Yamauchi M (1994) Performance of anaerobically direct seeded rice plants in the Meakong Delta of Vietnam. *Int. Rice Res. Notes* **19:**6.

Chuong P V, Yamauchi M (1994) Anaerobic direct seeding of rice in Northern Vietnam. Paper presented at the Wet Seeded Rice Workshop, 31 May-3 June 1994, Bangkok, Thailand.

Kordan H A, Ashraf M (1990) Environmental anoxia is unnecessary for inhibiting chloroplast photomorphogenesis in rice coleoptile (*Oryza sativa* L.). *J. Exp Bot.* **41:** 435-440.

Krishnasamy V, Seshu D V (1989) Seed germination rate and associated characters in rice. *Crop Sci.* **29:** 904-908.

Mochida O (1988) Non-seed borne rice pests of quarantine importance. Pages 117-129 In :Rice seed health. Internattional Rice Research Institute, P.O. Box 933, Manila, Philippines.

Morris R A, Zandstra H G (1979) Land and climate in relation to cropping patterns. Pages 255-274 In : Rainfed lowland rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Takahashi N (1984) Seed germination and seedling growth. Pages 71-88 In : Biology of rice. S. Tsunoda and N. Takahashi, eds. Japan Science Society press, Tokyo.

Yamauchi M, Aguilar A M, Vaughan D A, Seshu D V (1993a) Rice (*Oryza sativa* L.) germplasm suitable for direct sowing under flooded soil surface. *Euphytica* **67:** 177-184.

Yamauchi M, Aguilar A M, Sta Cruz P S (1993b) Anaerobic seeding with suitable germplasm. *Int. Rice Res. Notes.* **18:**36.

Yamauchi M, Herradura P S (1993) Superior coleoptile elongation of rice varieties suitable for anaerobic seeding. *Int. Rice Res. Notes.* **18:**37-38.

Yamauchi M, Herradura P S, Aguilar A M (1094) Genotype difference in rice postgermination growth under hypoxia. *Plant Sci. Lett.* (in press)

CARBOHYDRATE STATUS OF RAINFED LOWLAND RICES IN RELATION TO SUBMERGENCE, DROUGHT AND SHADE TOLERANCE

☐ *G.S. Chatuverdi*[1], *P.C. Ram*[1], *A.K. Singh*[1], *P.Ram*[1]
K T. Ingram[3], *B.B. Singh*[1], *R.K. Singh*[1] *and V.P. Singh*[2]

SUMMARY

Rice accumulates significant amount of carbohydrate in different plant parts especially in the culm which has an important role when plant experiences drought and flooding at various stages of crop growth. Carbohydrate status of rainfed lowland rice vis-a-vis mechanism of submergence tolerance at seedling stage, drought at flowering stage and shade at reproductive stage has been discussed with experimental evidences. Tolerance to submergence at seedling stage, and drought at flowering was closely associated with higher levels of carbohydrates (total water soluble carbohydrate and starch). Hydrolytic enzyme, alpha amylase activity had positive correlation with seedling survival at initial stage of submergence and was negatively correlated during submergence. Yield of rice under water deficit at booting or flowering was directly related to carbohydrate content, apparent translocation rate (ATR) and apparent contribution rate (ACR). Chemical desiccation method for screening flowering stage drought resistance has been discussed. Histochemical analysis technique for screening for flowering stage drought tolerance in rice has also been discussed. Adaptive features of wild rice species **Oryza australiensis** in relation to drought has been discussed which include reduced tiller and leaf area, more carbohydrate in culm and rhizomes.

INTRODUCTION

Rainfed lowland rice represents one of the major rice ecosystems of South and South-East Asia. About one-fourth of the world rice area falls under this category and contributes 19% of total rice grain yield. In India, approximately 14 million hectare rice lands are rainfed lowland, of which major area (60%) comes from Eastern India. Eastern Uttar Pradesh constitutes about 66% of rainfed lowlands in the state (Table 1).

The productivity of rainfed lowland rice is low and averages around 1.0-1.5 t/ha which, though is higher than upland and deep water rice, but much lower than that of irrigated ecosystem. Productivity of rainfed lowland is about 48% of value product per hectare of irrigated rice (ADB, 1989). Among the general causes of poor productivity of rainfed lowland are (i) poor establishment of seedlings due to

---

[1] N.D.University of Agriculture and Technology, Kumarganj, Faizabad, U.P., India.
[2] International Rice Research Institute, P.O. Box 933, Manila, Philippines
[3] Peanut CRSP Management Office, University of Georgia, Griffin, Georgia, USA.

partial to complete submergence (Chaturvedi *et al.,* 1993; Vergara, 1985), (ii) late season drought/anthesis drought (Chaturvedi and Ingram, 1989, (iii) low light stress in wet (*Kharif*) season (Murty and Sahu, 1987; Venkateswarlu and Srinivasan, 1978), (iv) accumulation of toxic substances in ill-drained soils (Ponamperuma, 1984), (v) soil factors such as salinity/alkalinity and zinc deficiency (Rao and Biswas, 1979), (vi) cold stress at panicle initiation (Nanda and Coffman, 1979) and (vii) severe occurrence of diseases and pests etc. Among the causes mentioned above, submergence and drought are the most prevalent stresses to reduce yield, and account for about 70% and 25% of yield loss, respectively in rainfed lowland rice area (Widawsky and O'Toole, 1990). Thus evaluating and screening cultivars for submergence at initial stage and for drought at later stages of crop growth become an important pre-requisite to improve overall productivity of rainfed lowland rice. Besides, there is a need to screen for salt, shade and cold tolerance for location-specificity.

Table 1 . Total rice and rainfed lowland rice area by regions

Region	Total Rice Area (000 HA)	Rainfed Lowland Rice Area (000 HA)
World	146400	37950
Asia	131000	36200
India	41000	14601
Eastern India	24000	8880
Uttar Pradesh	5500	2245
Eastern U.P.	2661	1415

Limited studies have been done on the morphological, physiological, biochemical and anatomical bases of submergence tolerance (Levitt, 1980; Singh, 1982; HilleRisLambers and Seshu, 1982. Vergara, 1985; Setter *et al.,* 1989 a & b; Chaturvedi *et al.,* 1993), flowering stage drought resistance, and shade tolerance in rice (Murty and Sahu, 1987; Venkateswarlu, 1977; Chaturvedi and Ingram, 1989).

In the present paper, the aim is to review and discuss one of the physiological factors i.e. carbohydrate status of rainfed lowland rice vis-a-vis mechanism of submergence tolerance at seedling stage and drought at flowering stage. Experimental results of rainfed lowland rice research consortium, conducted at Masodha Faizabad, India and of flowering stage drought stress behaviour, observed at IRRI, Manila, Philippines are discussed.

A REVIEW

Carbohydrate status and stress tolerance

Most of the carbohydrates are produced by green leaves and other green tissues of plants and are either translocated as sugar or stored temporarily as sugar, starch or fructans. Later in the dark, sugar is resynthesized and translocated from the leaf. In most plants, sucrose is translocated via phloem to carbohydrate sinks for cell growth, metabolism, respiration or storage. Growing cells act as carbohydrate sinks but later they may act as source when they become photosynthetically active. At subcellular level chloroplast may act as carbohydrate source and mitochondria of same cell act as sink (Kozlowski, 1992).

Growth and grain yield depend on both current photosynthesis and stored assimilates. If current photosynthesis is limited by environmental stresses such as water deficit (Marshall *et al.,* 1989 Bunce, 1982: Blum *et al.,* 1983; Chaturvedi and Ingram, 1988), low temperature (Hilliard and West, 1970; Chatterton *et al.,* 1972), nutrient deficiency (Lenhert *et al.,* 1979), or submergence (Setter *et al.,* 1989 a and b; Chaturvedi *et al.,* 1993), the remobilization of stored assimilates is accelerated and plant is forced to depend on stored assimilates. Stored assimilates also enhance recovery of plants after stress (Wardlaw and Eckhardt, 1987).

Stored carbohydrates have important role in metabolism, growth, development or stress tolerance, defense and survival (Kozlowski, 1992). It is therefore, also called reserve carbohydrate (RC) and is particularly sensitive to late season stress and management practices. It is also essential for survival when photosynthesis is low or is stopped. Among stored carbohydrates, starch is the most important reserve carbohydrate. Starch accumulates whenever high level of sugars build up and starch is transformed into sugars when sugars are low (Kozlowski and Keller, 1966). Among soluble carbohydrates, sucrose is the major translocable and storage carbohydrate. Reserve carbohydrates are also important in preventing invasion by certain plant pathogens and insect attacks.

Carbohydrate status and submergence tolerance

Rice crop suffers from partial to complete submergence in rainfed lowland areas. Complete submergence occurs during short- term flash flooding, varying upto 15 days, near river valleys and riverlets. Characteristics of flood water vary at different locations and the nature depends upon light intensity under water, turbidity and concentration of dissolved gases such as O_2, CO_2 and C_2H_4. Partial submergence of rice is quite common in low lying areas.

Complete submergence of rice leads to low concentration of carbohydrates and reduced growth and finally death of tissues (Palada and Vergara, 1972). It is partly due to low rate of photosynthesis (Trought and Drew, 1980; Rai and Murty, 1979), which is directly associated with slow diffusion of CO_2 in water (Setter *et al.,* 1989 a). Other factors which contribute to slow growth are (i) acceleration of photorespiration, (ii) anaerobiosis leading to breakdown of CHO and carbon loss as CO_2 and ethanol, (iii) high ethylene production disturbing membrane integrity and chlorosis, (iv) leakage of CHO, amino acids and ketones, (v) ABA accumulation and decreased supply of cytokinins which lead to stomatal closure and (vi) reduction of RUBP carboxylase activity. Complete submergence reduces level of carbohydrates but in partial submergence the reduction depends on proportion of leaves below the water (Setter *et al.,* 1989). Submergence reduces concentration of soluble sugars and starch in all plant parts of rice by 4-12 fold (Setter *et al.,* 1989).

Amount of carbohydrate in plant parts correlates positively with submergence tolerance (Palada and Vergara, 1972; Emes *et al.,* 1987; Chaturvedi *et al.,* 1993). Older seedlings which have greater submergence tolerance, also contain more carbohydrate (Vergara, 1985; Chaturvedi *et al.,* 1993). Decreasing seedbed soil nitrogen level increases seedling carbohydrates and submergence tolerance as well (Vergara, 1985). Emes *et al.* (1987) observed that under submerged condition, the culm of submergence-tolerant varieties accumulated higher levels of starch and at a more rapid rate than did varieties with low submergence tolerance. Culms of submergence tolerant plants contained starch even after being submerged for 7 days, whereas the starch reserve of submergence susceptible varieties was exhausted during the same period. Plant may use reserve starch stored in the culm during submergence, and the ability to survive for longer periods may be related to continued availability of carbohydrates. Chaturvedi *et al.* (1993) showed that levels of total water soluble carbohydrates and starch were positively correlated with tolerance to complete/partial submergence. Tolerant genotypes had lower rate of reduction of CHO during submergence and higher recovery after 30 days. Slow rate of reduction in tolerant genotypes makes the substrate available for regeneration of growth after releasing the submergence. Alpha- amylase activity was also higher before submergence and after recovery in tolerant genotypes. In contrast, under partial submergence condition, leaf sheath plays the major role in carbohydrate distribution. High carbohydrate depletion rate (CDR) in leaf sheath was observed in tolerant than susceptible genotypes under partial submergence condition.

Submergence for 3 days under continuous light led to mobilization of 65% of the starch from the regions of rice internodes which has been formed prior to submergence and disappearance of starch was accompanied by a 70-fold enhancement of amylolytic activity (Raskin and Kende, 1984). Submergence also caused 26-fold increase in the translocation of newly synthesized photosynthate assimilate from leaves to internodes and younger regions of culms. Tops of rice contain significantly larger amounts of starch than those of submerged plant (Yamaguchi, 1973). Amylase activity increases in rice leaves and internodes during submergence (Yamaguchi and Sato, 1963).

Carbohydrates status and drought tolerance at reproductive stage

Substantial quantities of carbohydrates are accumulated in different parts in rice (Perez *et al.,* 1971) which are of paramount importance when plant experiences water deficit at flowering (Rahman and Yoshida, 1985; Chaturvedi and Ingram, 1988, 1989). Pre-anthesis assimilates stored in stem and leaf sheath tissue appear to contribute substantially to grain filling under water stress (Akita, 1987; Cock and

Yoshida, 1972; Chaturvedi and Ingram, 1989). In rice, translocation of assimilates increases under stress (Reyniers *et al.,* 1982). Pre-anthesis assimilates in wheat are also known to contribute to grain filling when drought occurs in the later stages of growth (Gallagher *et al.,* 1976).

Water stress causes reduction in the pool size of sucrose in many crop species (Lawlor and Fock, 1978). This reduction is not due to decrease in the level of enzymes but due to overall changes in the direction of metabolic fluxes. More organic carbon is sequestered for the production of amino acids such as glycine, serine and glutamine.

Water stress reduces net photosynthate availability by reducing leaf area and increasing stomatal resistance. This is followed by a decrease in activity of enzymes such as RUBP Carboxylase and in the photochemical activity of chloroplast (Sinha *et al.,* 1982; Marshall *et al.,* 1980).

Maintenance of functional integrity and survival under stress depends upon the capacity of plant for osmoregulation (Turner and Jones, 1980; Hanson and Hitz, 1982). This is commonly associated with starch breakdown and concomitant increase in low molecular weight solutes. Major contributing solutes to osmoregulation comprise soluble sugars, free amino acids, organic acids, betains and inorganic ions and polyols (Morgan, 1984). Genetic differences exist in degree of osmotic adjustment in sorghum genotypes (Ackerson *et al.,* 1980).

Translocation of photosynthates within the plant is more tolerant to water stress than growth and photosynthesis (Boyer, 1976). The relative importance of translocation in supplying carbohydrates to grain increases when stress develops (Hunt, 1979; Austin *et al.,* 1980). Varieties differ for stored stem carbohydrates and their rate of translocation into the grain increases under stress. Upto 31% of rice grain yield under stress was accounted for by the translocation of stem reserves. Differential ability of genotypes to sustain translocation-based grain growth under stress by destroying the photosynthetic source at the grain filling stage was assesed in wheat (Blum *et al.,* 1993 a, b; Regan *et al.,* 1993). This was done by spraying field plots with chemical dessicants (magnesium chlorate, atrazine and KI solution) that kill leaf blades, awns and glumes. Injury by late season water stress was correlated with injury by chemical dessication.

Carbohydrate status and shade tolerance

Reduced light is one of the major constraints to the productivity of rainfed lowland rice due to prevalent clouds in monsoon season, as it is mostly grown during wet season (July to December). Low light during primordial initiation (PI) to flowering, or flowering to harvest, reduces grain development considerably (Venkateswarlu, 1977; Kato, 1986), while low light at anthesis leads to high spikelet sterility and low harvest index. Under low light at flowering, carbohydrate decreases and GA and soluble N in panicle increase, leading to a high spikelet sterility. Greater accumulation of carbohydrate in shoots at flowering relates to tolerance to low light stress (Murty and Sahu, 1987). Under low light, stored carbohydrates contribute substantially to grain filling (Janardhan *et al.,* 1980). Under shade, total sugars (mostly non reducing sugars and starch) are markedly reduced in all plant parts. Total soluble N and amino N are enhanced in susceptible varieties. Higher sterility is ascribed to disturbed N metabolism and accumulation of soluble N in the panicle which is toxic to normal grain setting (Murty *et al.,* 1983).

EXPERIMENTAIRESULTS

Submergence tolerance

Submergence tolerance in rice is not governed by a single factor. Our previous results (Chaturvedi *et al.,* 1993) indicated that elongation and submergence tolerance are two independent traits. Attempt has been made to combine these two traits in one genotype (Raysaha *et al.,* 1993). Submergence tolerance is a dominant character and additive gene effects appear to be operative in the control of this trait (Mohanty and Khush, 1985).

From our three years (1991-1993) data, it is clear that initial high carbohydrate level in the tissues is one of the adaptive traits of submergence tolerance. Higher levels of initial carbohydrate (water soluble sugar and insoluble starch) act as buffer stock and its continued availability during submergence is critical for the survival and growth of rice. Metabolic energy needed by the plant during submergence is primarily supplied from stored carbohydrates present in the tissue.

Tolerant genotypes had higher total initial carbohydrate content and starch before submergene and had lower rate of depletion during submergence than the susceptible (Fig. 1 & 2). Susceptible genotypes had poor accumulation of CHO and showed faster rate of depletion during submergence. Slow rate of depletion of CHO in tolerant genotypes seems to be one of the adaptive traits to withstand submergene due to continuous availability of substrate for energy for a longer period. In susceptible plants, drastic reduction of CHO leads to high rate of anaerobic fermentation and production of ethanol at toxic level. Setter *et al.* (1989b) also proposed the accumulation of end products to toxic levels in their model on response of rice to submergence.

Carbohydrate status of plant changes with the type and nature of submergence, plant age and exposure to water phase (Setter *et al.,* 1989b). In one of the experiments, plants were completely submerged and both shoots and roots were under water, carbohydrate depletion occurred and it was more in susceptible than in the tolerant genotypes.

Tolerant genotypes had higher recovery of total carbohydrate and starch 30 days after releasing submergence stress than the susceptible ones. The alpha amylase activity was higher before as well as after releasing stress (Fig. 3). Higher alpha amylase activity in leaf and culm seemed important for longer submergence duration tolerance in tolerant genotypes. In general, older seedlings (45- day old) had better survival than younger seedling (15, 30-day old) and it was due to higher level of stored CHO in older seedlings. Vergara (1985) also observed higher level of CHO before submergence which decreased at low rate during submergence.

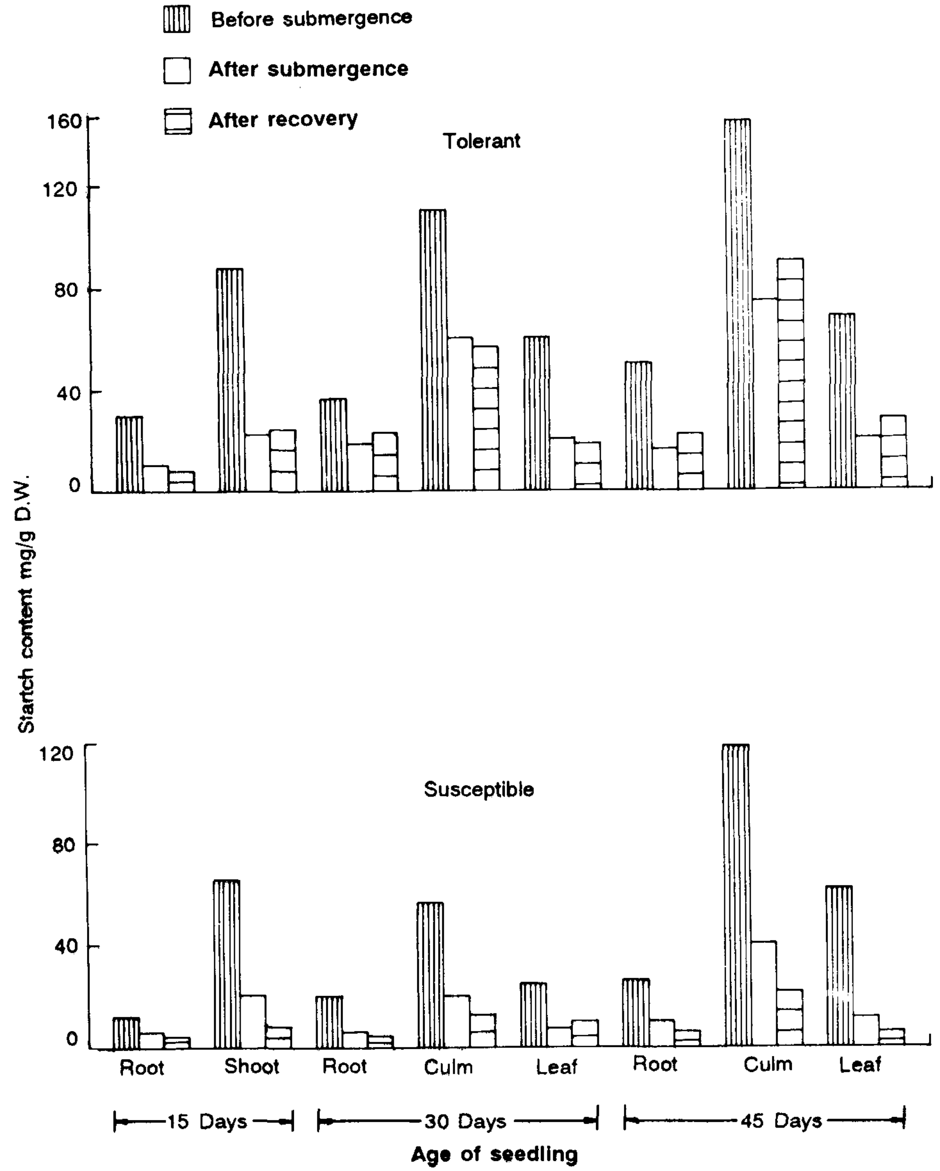


Fig. 1. Changes in starch content of tolerant and susceptible genotypes in complete submergence (15 days). Pooled data of 1992-93.

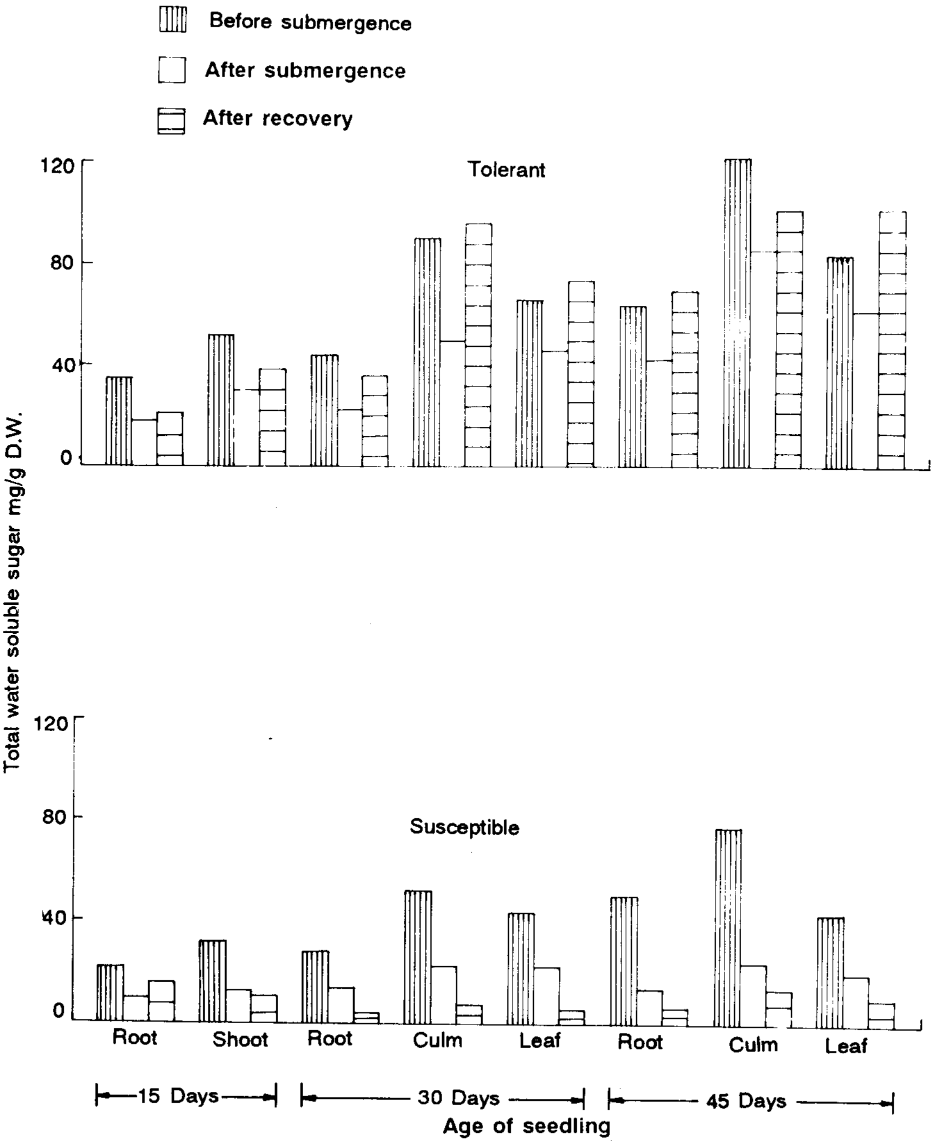


Fig. 2. Changes in total water soluble sugar (WSS) in tolerant and susceptible genotypes in complete submergence (15 days). Pooled data of 1992-93.

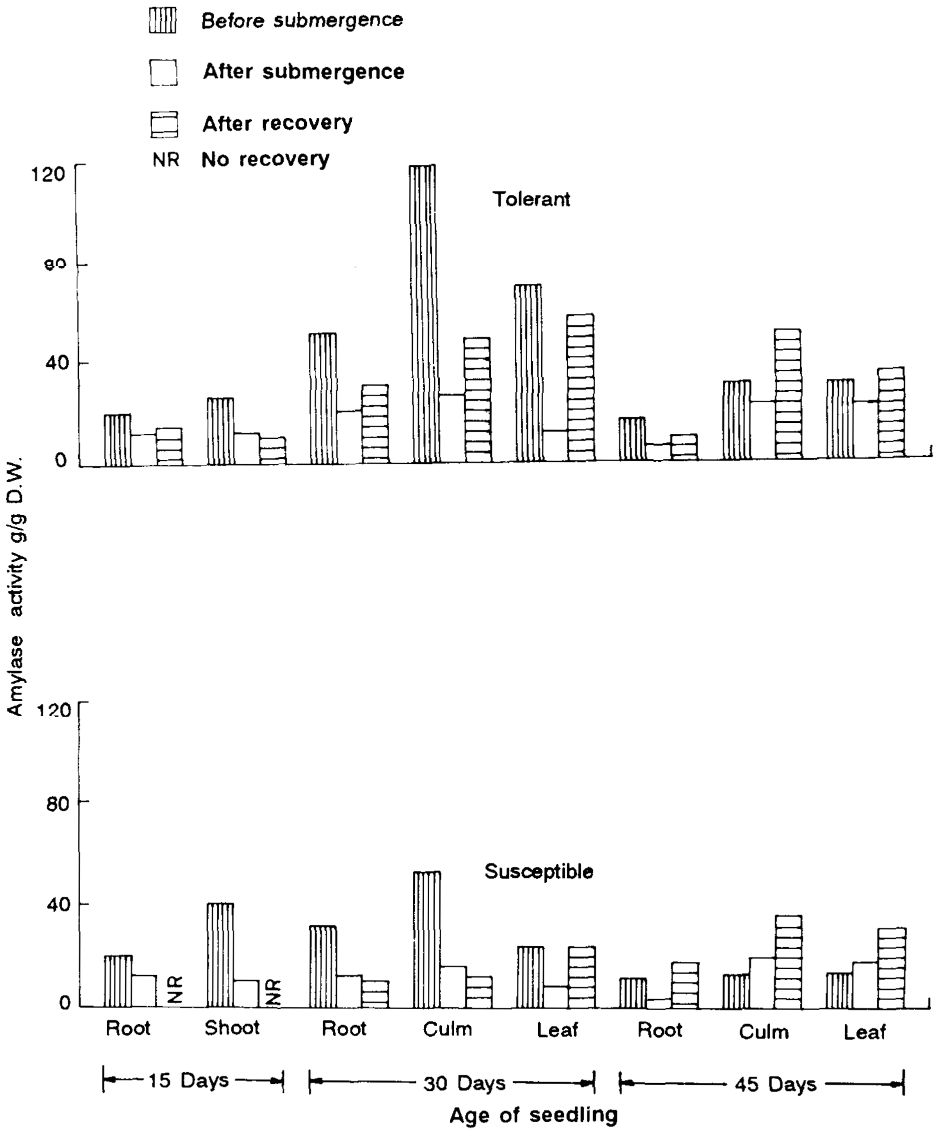


Fig. 3. Changes in a amylase activity in tolerant and susceptible genotypes in complete submergence (15 days). Pooled data of 1992-93.

Contrarily, in deep water rice, Emes *et al.,* (1987) reported that culms of submergence tolerant varieties maintained higher levels of starch, and its accumulation was more rapid than the less tolerant type. Raskin and Kende (1984) working with deep water rice variety-Habibganj Aman from Bangladesh, found that starch disappearence was acompanied by 7-fold enhancement of amylolytic activity. Internodes of air grown rice plants contained large amounts of starch (about 10% DW) which disappeared upon submergence in water under continuous light. This indicates that carbohydrate status and its remobilization alter with the status of plant in water.

Correlation studies showed that survival of rice was positively correlated with the level of total water soluble sugar and starch in the culm, before submergence, after submergence and after recovery (Table 2). Strong positive correlation was found in shoot (culm) after submergence stage rather than before and after recovery. There was a negative correlation between alpha amylase and survival in both mot and shoot after submergence.

Table 2. Correlation values between survival and starch, survival and total water soluble sugar and survival and alpha amylase activity in different plant parts. 30 d old seedling, 11 d submergence. Pooled data of 1992-1993.

Character	Relationship	r value*		
		B.S.	A.S.	A.R.
Survival and starch				
	Root	N.S.	N.S.	0.99**
	Shoot	0.95**	0.99**	0.96**
Survival and total water soluble sugar				
	Root	N.S.	N.S.	N.S.
	Shoot	O.80**	0.76**	0.92**
Survival and alpha-amylase activity				
	Root	0.85	-0.90	N.S.
	Shoot	0.94	-0.99	N.S.

* BS=Before Submergence ; AS=After Submergence ; AR=After Recovery

Drought tolerance

Rice accumulates significant amount of carbohydrates before heading and there exists wide variability among genotypes. Improved rices have higher contents of total non-structural carbohydrate at heading than do the low yielding traditional varieties (Weng *et al.,* 1986). Previous experiments have shown that when water deficit occurs during flowering or grain filling, grain growth derives a greater proportion of substrates from stored assimilates than when no stress occurs. Assimilates accumulated prior to anthesis are of paramount importance when plant experiences water deficit at later growth stages.

In general, cultivars which had higher levels of CHO before flowering, also had higher yields under both normal and water deficit conditions. A strong positive correlation was observed between flowering stage CHO in all plant parts and yield (Table 3). A non-significant relationship was found between tissue CHO at tillering and yield. Carbohydrate contents of different plant parts were positively correlated with filled grains/hill at flowering stage (Table 3). Leaf blade carbohydrate had greater affinity for increasing filled grain, as evidenced by high r value (0.78).

Table 3 : Correlation coefficient between filled grain/hill and carbohydrate content and yield and carbohydrate content of different plant parts (stress and control data combined).

	Time of water deficit		
Plant Parts	Tillering	Booting	Flowering
	Filled grain/hill versus carbohydrate content		
Leaf blade	0.23	0.42*	0.78**
Leaf sheath	0.20	0.49*	0.51*
Culm	0.14	0.19	0.46*
	Yield versus carbohydrate content		
Leaf blade	0.21	0.47	0.85**
Leaf Sheath	0.20	0.41*	0.66**
Culm	0.20	0.46*	0.52**

* and ** significant at p 0.05 and 0.01, respectively.

Yield was inversely Correlated with apparent translocation rate (ATR). Among cultivars, yield was directly correlated with maximum ATR under stress condition, and cultivar IR-46 maintained better translocation under stress than did the other cultivars (Table 4).

One of the goals of plant breeders is to produce germplasm with stable yields, and a measure of yield stability is the slope of ATR vs yield regression, the smaller the slope, the more stable the yield. Variety IR-64 had the greatest slope and high crop susceptibility (cs) factor.

Table 4. Apparent translocation rate (ATR) and apparent contribution rate (ACR) in lowland rices in response to water deficit.

Cultivars	Time of water deficit	ATR	ACR	Yield g/plot	Crop sucesptibility
IR64	Control	0.10	0.13	19.4	-
	Tillering	0.17	0.21	16.7	0.13
	Booting	0.24	0.34	12.8	0.34
	Flowering	0.29	0.39	11.9	0.38
IR46	Control	0.14	0.16	22.3	-
	Tillering	0.21	0.26	19.2	0.06
	Booting	0.31	0.44	15.7	0.22
	Flowering	0.42	0.51	14.7	0.23
Mahsuri	Control	0.08	0.11	15.9	-
	Tillering	0.15	0.16	13.2	0.17
	Booting	0.19	0.26	11.1	0.31
	Flowering	0.25	0.32	09.8	0.39
Salumpkit	Control	0.08	0.11	14.3	-
	Tillering	0.13	0.16	11.8	0.17
	Booting	0.22	0.31	10.1	0.29
	Flowering	0.31	0.42	11.1	0.22
IR54	Control	0.12	0.14	20.3	-
	Tillering	0.19	0.22	18.3	0.13
	Rooting	0.27	0.37	13.8	0.25
	Flowering	0.36	0.40	11.8	0.31
LSD 0.05		0.04	0.05	0.6	0.05

In the histochemical studies also, it was observed that tolerant genotypes had higher level of starch localization at flowering in non-stress environment than susceptible genotypes. Histochemical observation of CHO localization was very close to the observation recorded by quantitative method (Tables 5-7). Under stress, carbohydrate is remobilized relatively faster in tolerant than in susceptible genotypes as also evident by carbohydrate depletion rate (CDR) (Table 6). It is evident from Table 7, that yield of tolerant cultivar IR 46 was relatively higher under stress condition than that of susceptible variety IR 52. Higher level of sugar acts as osmotic agent to maintain higher leaf area and dry weight. Poor yield in susceptible cultivar IR 52 was mainly due to its poor storage of CHO and poor translocatory behaviour which was reflected in its poor dry weight and, leaf area, and more unfilled spikelets (64%) in comparison to tolerant ones (30%).

Table 5. Culm carbohydrate content in three genotypes at flowering under well-watered, (without stress), during stress, and after recovery.

Cultivars	Culm CHO mg/pot		
	Without stress	During stress (80 kPa)	After recovery
IR-46	3000	1390	580
N-22	2230	900	420
IR52	2300	1200	840
LSD0.05	470	281	136

Table 6. Culm carbohydrate depletion rate (CDR) in three rice genotypes subjected to water deficit (80 kPa SMT) at flowering.

Cultivars	Culm CHO (mg/pot)	
	Control	Stress (80 kPa SMT)
IR-46	40	80
N-22	38	64
IR52	28	34
LSD0.05	14	

Table 7. Yield and yield attributes of three rice genotypes under well-watered (C) and water-deficit (WD) conditions (80 kPa) at flowering.

Cultivars	Grain yield (g/pot)		Spikelet/ panicle		Individual grain weight (mg)		Unfilled grain (%)	
	C	WD	C	WD	C	WD	C	WD
IR46	20.6	14.0	105	83	23	20	16.5	30.5
N-22	16.4	12.4	87	71	19	18	20.0	30.5
IR52	17.9	9.0	107	87	24	19	19.7	63.8
LSD 0.05	1.1		3.0		1.1		3.1	

Among wild species too, variation existed in carbohydrate accumulation and remobilization (Table 8). Wild species *Oryza nivara* had higher accumulation of CHO in leaf blade, while *Oryza australiensis* had higher accumulation of CHO in culm and leaf sheath.

Table 8 . Total carbohydrate content and carbohydrate depletion rate (CDR) of wild rices under well watered and water deficit (80kPa) at flowering.

Wild rices	Water treatment	CHO (mg/pot) Leaf	Culm	Root	CDR mg/pot/day
Oryza australiensis	Control	1500	3600	1080	40
	Stress	1050	2340	646	60
Oryza officinalis	Control	1800	3000	780	30
	Stress	1530	2400	585	35
Oryza nivara	Control	2400	2560	750	40
	Stress	2160	2048	600	48
LSD0.05		430	570	375	

All wild species showed rhizomatous characters, full of starch, but *Oryza austruliensis* had higher starch localization and remobilization than other wild species as evident by histochemical and quantitative analysis. This was reflected in higher yield under stress condition. *Oryza nivara,* which produced higher dry matter, did not produce enough yield under stress. Among 3 wild species, *Oryza australiensis* showed more adaptive traits like reduced tiller and leaf area, and more carbohydrate content before stress and faster remobilization during stress. Higher intensity of starch localization in rhizomes is a strong indicator of tolerance behaviour under stress.

In one of the experiments, a chemical dessicant was used as an agent for simulating drought to identify genotypes for drought tolerance at flowering. Carbohydrate depletion rate in vegetative tissue gives a relative estimate of CHO remobilization to panicles. Except for roots, IR 46 had the highest CDR in all plant parts. Thus, drought tolerant IR 46 had both the traits of accumulation and remobilization of CHO. Both traits together confer tolerance to water deficit or chemical dessication at flowering. Cultivar N22 had the highest CDR in its roots. High root and culm CDR may explain renewed tiller production at the expense of grain production. Our results are in close agreement with the work on wheat done by Blum *et al,* (1983) and in rice by Chaturvedi and Ingram, (1991). Submergence tolerant cultivar had minimum CDR value, and therefore showed that faster remobilization is not a feature of submergence tolerance.

All cultivars responded similarly to water deficit and chemical dessication with respect to CHO distribution, leaf area, dry matter, and yield and yield components. Injury index by drought was more closely related to injury index by chemical dessication at 5 days after panicle emergence (DAPE) than at 10 days before panicle emergence (DBPE). The results showed that chemical dessicant had an effect on rice yield similar to that of water deficit, with the common effect, that of forcing the plant to rely on previously accumulated assimilates for grain growth. Chaturvedi and Ingram (1991) also found that low concentration of atrazine (0.05 kg a i/ha) in a non-stress environment, was a potential simulator of drought.

Shade tolerance

In general, shade reduced CHO in all plant parts relative to unshaded control. The greater reduction in CHO however, was observed when shaded at 5-20 DAPE than 10-25 days after panicle initiation (DAPI) in both wet and dry seasons. Reduction in CHO by shading was also reported by Eaton and Ergle (1954), and Kemp (1981).

Table 9 . Correlation coefficient of grain yield and carbohydrate content of various plant parts at different stages of growth in lowland rice under wet and dry treatments.

Stage	Treatment	Leaf blade	Culm	Leaf sheath
10 DAPI	WET	0.79**	0.72	0.53
	DRY	0.75*	0.73	0.62
25 DAPI	WET	0.45	0.34	0.59
	DRY	0.35	0.36	0.62
5 DAPE	WET	0.78**	0.76*	0.52
	DRY	0.76*	0.80**	0.61
20 DAPE	WET	0.48	0.29	0.09
	DRY	0.22	0.25	0.02
HARVEST	WET	0.49	0.07	0.37
	DRY	0.13	0.07	0.10

* and ** Significant at P 0.05 and 0.01, respectively.

Grain yield was positively correlated with CHO in leaf blades and culm at 10 DAPI and 5 DAPE (Tables 9 and 10). The culm was the greatest source of translocated CHO for grain growth is supported by ACR. The results indicate that under water deficit, grain growth depended on previously accumulated assimilates. Grain yield and ATR were negatively correlated, but correlation was positive with maximum ATR value. Our results are similar to those of Reyniers *et al.* (1982) who also reported higher ATR values under water deficit. Translocation in supplying CHO to grain increases when plant experiences stress (Austin *et al.,* 1980). Upto 31% of rice grain yield under stress was accounted for by translocation of stem reserves. Among the cultivars, IR 64, IR 46 and Mahsuri had similar ATR values with no shade but IR 46 had more CHO coupled with high ATR and ACR under both shade and water deficit conditions. Thus, IR 46 had the best CHO accumulation and translocation to confer stress tolerance.

Table 10. Effect of water and shade on yield, apparent translocation rate (ATR), and apparent contribution rate (ACR) in lowland rice.

Variety	Treatments	**Wet season**			**Dry season**		
		Yield	ATR	ACR	Yield	ATR	ACR
IR 46	No shade	4.0	5	20	3.9	13	20
	Shade 10-25 DAPI	3.1	10	21	3.1	22	23
	Shade 5-20 DAPE	2.8	24	35	2.8	34	40
IR 64	No shade	4.6	6	24	4.4	8	24
	Shade 10-25 DAPI	3.6	12	26	3.5	23	28
	Shade 5-20 DAPE	3.4	28	45	3.3	40	46
Mashuri	No shade	3.0	4	21	2.9	6	20
	Shade 10-25 DAPI	2.1	10	22	2.0	12	25
	Shade 5-20 DAPE	1.8	20	36	1.7	25	38
LSD 0.05		0.1	-	-	0.1	-	-

Reduction of rice grain yield by shade was also reported by Murty and Sahu, 1987; Venkateswarlu, 1977; Jadhav, 1987; Patro and Sahu, 1988). Yoshida (1973) found that shade, particularly at reproductive and ripening phases reduced rice yields by 40 to 78 compared to unshaded controls. Additive effects of shade and water deficit were observed in the dry but not in wet season trials. It was concluded that IR 46 had the greatest shade and drainage tolerance during panicle emergence and flowering owing to its ability to form and set spikelets using accumulated assimilates (Chaturvedi and Ingram, 1989).

CONCLUSION

- Submergence tolerance at seedling stage is closely associated with higher levels of water soluble carbohydrate and starch in the tissues. Survival of seedlings was positively correlated with the levels of WSC and starch before and after stress as well as after recovery.
- Slow rate of depletion of CHO during submergence appears to be a desirable trait for tolerance. This will help the plant to continue its growth for a longer period of submergence.

- * Submergence tolerance and elongation ability are not related. Most elongating genotypes are not submergence tolerant with exception to a few genotypes which showed high submergence tolerance alongwith moderate elongation ability.
- * Hydrolytic enzyme-alpha amylase-activity seems crucial in the remobilization of assimilates, and had positive correlation with seedling survival at initial stage and was negatively correlated during submergence stage.
- * Culm is the major organ which accumulates higher stored carbohydrate. Carbohydrate level in plant is significantly correlated with survival.
- * Higher CHO at anthesis plus high ATR appear useful traits to select cultivars for drought tolerance at flowering.
- * Yield of rice under water deficit at booting or flowering was directly related to the level of CHO, ATR and ACR.
- * Yield was directly correlated with maximum ATR under stress condition.
- * Drought tolerant IR 46 culm had higher intensity of starch staining before stress and faster remobilization, during and after stress, than drought susceptible cultivar IR 52.
- * Spray of a chemical dessicant, magnesium chlorate (4%), had similar effects on CHO remobilization, yield components and yield as that of water deficit.
- * Injury index by drought and chemical dessicant were significantly and strongly correlated at 5 DAPE. Dessication method can be used to screen large number of genotypes where water deficit is difficult to be imposed.
- * IR46 had relataively more shade and drainage tolerance during flowering stage owing to its ability to form and set spikelets using accumulated assimilates.
- * Histochemical analysis of starch localization and remobilization is quick and reliable method and can be used as a tool of CHO qualitative analysis in breeding programme.
- * Wild species *Oryza australiensis,* showed more drought adaptive traits like reduced tiller, leaf area, more carbohydrate in culm and rhizomes before stress and faster remobilization during stress.

REFERENCES

Ackerson R C, Krieg D R, Sung F J M (1980) Leaf conductance and osmoregulation of field grown sorghum genotypes. *Crop Sci.* **20:** 10-16.

ADB (1989) Rainfed Agriculture in Asia and pacific. Asian Development Bank Manila, Philippines. 644p.

Akita S (1987) Physiological aspects for improving yield potential in tropical rice cultivation. Paper presented at International Rice Research Conference 21-25 September 1987, IRRI, Manila, Philippines.

Austin R B, Morgan R B, Ford M A, Blackwell R D(1980) Contribution to grain yield from pre-anthesis assimilation in tall and dwarf genotypes in two contrasting seasons. *Ann. Bot..* ***45:*** 305-319.

Blum A, Poiarkova H, Golan A, Mayer J (1993) Chemical dessication of wheat plants as simulator of post-anthesis stress. I.Effects on translocation and Kernel growth. *Field Crops Res.* ***6:*** 149-155.

Boyer J S (1976) Post-anthesis at low water potential.*Phils. Trans Royal Soc. Lond. Ser.* B. ***273*** : 501-512.

Bunce J A (1982) Effect of water stress on photosynthesis in relation to diurnal accumulation of carbohydrate in source leaves. *Can. J. Bot.* ***60:*** 195-200.

Chaturvedi G S, Misra C H, Singh O N, Pandey C B, Yadav V P, Singh A K, Dwivedi J L, Singh B B, Singh R K (1993) Physiological basis and screening for tolerance for flash flooding. Pages 78-96. In: Rainfed lowland rice-agricultural research in high risk environments. KT Ingram, ed., International Rice Research Institute, Los Banos, Philippines.

Chaturvedi G S, Ingram K T (1991) Effect of atrazine and moisture stress on translocation of assimilates in rice. *Plant Physiol. and Biochem. India* ***18*** (1) 40-42

Chaturvedi G S, Ingram KT (1989) Growth and yield of lowland rice in response to shade and drainage. *Philip. J. Crop Sci.* ***14***(2) 61-67.

Chaturvedi G S, Ingram KT (1988) Assimilate translocation of lowland rice in response to water deficit and shade. Paper presented at the 4th FCSSP annual meeting. 27-30 April, 1988, Davao city, Philippines.

Chatterton N J, Carlson G E, Hungerford W E, Lee D R (1972) Effect of tillering and cool nights on photosynshesis and chloroplast starch in Pangola. *Crop Sci.* ***12:*** 206-208.

Cock J, Yoshida S (1972) Accumulation of C14 labelled carbohydrate before flowering and its subsequent redistribution and respiration in rice plant. *Proc. Crop Sci. Soc.* Japan ***41*** : 226-234.

Eaton F M, Ergle D R (1954) Effects of shade and partial defoliation on carbohydrate level, growth, fruiting and fiber properties. *Plant Physiology.* ***29:*** 39-49.

Ernes M J, Wilkins C P, Smith P A, Kupkanchanakul K, Hawker K, Charlton T W A, Cutter E G (1987) Starch utilization by deep water rice during submergence. In : Proceeding of International Deep Water Rice Workshop, 26-30 Oct, 1987, Thialand.

Gallagher J N, Biscoe P V, Hunter B (1976) Effect of drought on grain growth. *Nature* ***264*** : 541-542.

Hanson A D, Hitz W D (1982) Metabolic responses of mesophytes to plant water deficits. *Annu. Rev. Plant Physiol.* ***33*** : 163- 203.

HiIle Ris Lambers D, Seshu D V (1982) Some ideas on breeding procedures and requirements for deepwater rice improvement. Page 29-44. In :Proceedings of the 1981 International Deepwater Rice Workshop, IRRI, Los Banos, Philippines.

Hilliard J H, West S H (1970) Starch accumulation associated with growth reduction at low temperature in a tropical plant. *Science* ***168*** : 494-496.

Hunt L A (1979) Stem weight changes during grain filling in wheat diverse sources. Pages 923-929. In : Proc. 5th International Wheat Genetics Symposium, Delhi, India.

Jadhav B B (1987) Effect of partial shading on the yield of rice. *Indian J. Agric. Sci.* ***57 (7) :*** 515-516.

Janardhan K V, Murty K S, Das N B (1980) Effect of lowlight during ripening period on grain yield and translocation of assimilates in rice varieties. *Indian J. Plant Physiol.* ***23:*** 163-168.

Levitt J (1980) Excess water or flooding stress. Pages 213-280. In : Response of plants to environmental stresses, Vol-II Academic press Inc. New York.

Kato K (1986) Effects of the shading and rachis branch clipping on the grain filling process of rice cultivars differing in the grain size. *Japan J. Crop Sci.* ***56:*** 173-174.

Kemp D R (1981) The growth rate of wheat leaves in relation to the extension zone sugar concentration manipulated by shading. *J. Expt. Biol.* ***32:*** 141-160.

Kozlowski T T (1992) Carbohydrate sources and sinks in woody plants. *Bot. Rev.* ***58* (2):** 107-222

Kozlowski T T, Keller T (1966) Food relations of woody plants *Bot. Rev.* ***33:*** 293-382

Lawlor D W, Fock H (1977) Water stress changes in the amounts of some photosynthetic assimilation of products and respiratory metabolites of sunflower leaves. *J. Expt. Bot.* ***28:*** 329-337.

Lenhert H J, Vieweg G H, Rongine D E (1979) Starch accumulation in leaves from maize and *Zebrina pendula* Schnizl, dependent on nitrogen and phosphorus deficiency. Z. *Pflazenphysiol.* ***92:*** 163-169.

Marshall B, Sedgley R H, Biscoe P V (1980) Effect of water stress on photosynthesis and respiration in wheat ears. *Aust. J. Agric. Res.* ***31:*** 857-871.

Mohanty H K, Khush G S (1985) Diallel analysis of submergence tolerance in rice *(Oryza sativa) Theoret. Appl. Genet.* ***70*** : 467-473.

Morgan J M (1984) Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.* ***35:*** 299-319.

Murty KS, Sahu G (1987) Impact of low light stress on growth and yield of rice. Pages 93-101 In :"Weather and Rice" Proc. International Workshop on Impact of Weather Parameters on Growth and yield of Rice IRRI, Los Banos, Philippines.

Murty P S S, Rao V R, Charvulu, Murty K S (1983) Relation between spikelet sterility and accumulation of soluble nitrogen (15N) in rice (*Oryza sativa* L). *J. Nuclear Agril. Biol* ***12:*** 17-19.

Namuco O S, Hsio T C, O' Toole J C (1980) Water stress sensitivity of rice at flowering. Paper presented at the 11th Annual meeting of Crop Science Society of the Philippines, Manila, Philippines.

Nanda J S, Coffman W R (1979) Alternative plant types and other agronomic characteristics for rainfed lowland rice. In :Rainfed Lowland Rice : Selected papers from the 1978 Internatiional Rice Research Conference, IRRI, Manila, Philippines.

Palada M C, Vergara R S (1972) Environmental effects on the resistance of rice seedlings to complete submergence. *Crop Sci.* ***12:*** 209-212.

Patro R, Sahu A (1988) Effects of low light intensity at different growth stages of crop in sink size. *Oryza* ***23:*** 123-125.

Perez C M, Palmiano E P, Baun C L, Julliano B O (1971) Starch metabolism in leaf sheaths and culm of rice. *Plant Physiology.* ***47:*** 404-408.

Ponnamperuma F N (1984) Effects of flooding on soils. Pages 9-45. In: Flooding and Plant Growth. T. T. Kozlowski ed. Academic press, London.

Rahman M S, Yoshida S (1985) Effect of water stress on grain filling in rice. *Soil Sci. Plant Nutr.* ***31* (4)** : 497-511.

Rai V R S, Murty K S(1979) Note on the effect of complete submergence on RUBP carboxylase activity of rice seedlings. *Indian J. Agric. Res.* ***13:*** 61-63.

Rao M J V, Riswas S (1979) Rainfed low land rice in India. In : Rainfed low land rice : Selected papers from the 1978 International Rice Research Conference. IRRI, Manila, Philippines.

Raakin I, Kende H(l984) Effect of submergence on translocation, starch content and amylolytic activity in deep water rice. Planta ***162:*** 556-559.

Raysaha P K, HilleRisLambers, Tepora N M (1993) Combination of stem elongation ability with submergence tolerance in rice. *Euphytica* ***68:*** 11-16.

Regan K L, Whan B R, Turner N C (1993) Evaluation of chemical dessicants as a selection technique for drought resistance in dryland wheat breeding programme. *Austr. J. Agril. Res.* ***44:*** 1683-1691.

Reyniers F N, Troung Binh, Jacquinot L, Nicou R (1982) Breeding for drought resistance in dryland rice. Pages 273-292. In : Drought resistance in crops with emphasis on rice. IRRI, Manila, Philippines.

Setter T L, Waters I, Wallace I, Wiengweera A, Bhekasut P, Greenway H (1989 a) Submergence of rice. I Growth and photosynthetic response to CO_2 enrichment of flood water. *Austr. J. Plant Physiol.* 16: 251-263.

Setter T L, Jackson M B, Waters I, Wallace I, Greenway H (1989 b) Flood water carbondioxide and ethylene concentrations as factors in chlorosis development and reduced growth of completely submerged rice. In : Proceedings of 1987 International Rice Workshop, Thailand.

Singh U S (1982) Deep water rice in India : Problems and prospects. pp 355-362 In : Proceedings of International Deep Water Rice Workshop, 1981. IRRI, Manila, Philippines.

Trought M C T, Drew M C (1980) The development of waterlogging damage in wheat seedlings *(Triticum aestivum)*. Shoot and root growth in relation to changes in the concentration of dissolved gases and solutes in soil solutions. *Plant and Soil* 54:77-94.

Turner N C, Jones M M (1980) Turgor maintenance by osmotic adjustment : a review and evaluation. Pages 87-103. *In:* Adaptation of plants to water and high temperature stress. N C Turner and P J Kramar eds. John Wiley and sons. London.

Venkateswarlu B (1977) Influence of lowlight intensity on growth and productivity of rice (*Oryza sativa* L). *Plant and Soil* 46: 713-719.

Venkateswarlu B, Srinivasan T E (1978) Influence of lowlight intensity on growth and productivity in relation to population pressure and varietal reaction in irrigated rice. *Indian J. Plant Physiol.* 21: (2) 162-170.

Vergara B S (1985) Growth and development of the deep water rice plant. *IRRI Research Paper series* 103: 1-38.

Wardlaw IF, Eckhardt L (1987) Assimilate movement in lolium and sorghum leaves IV. Photosynthetic response to reduced translocation and leaf stage. *Aust. J. Plant Physiol.* 14: 573-591.

Weng J H, Agata W, Takeda T (1986) Studies on dry matter and grain production of rice plants IV. Varietal differences of total carbohydrate content of heading stage. *Japanese J. Crop Sci.* 55 (2): 201-207.

Widawsky D A, O' Toole J C (1990) Prioritizing the rice biotechnology research agenda for Eastern India. Pub. The Rockfeller Foundation.

Yoshida S (1973) Effect of temperature on growth of rice plant (*Oryza satival*) in a controlled environment. *Soil Science Plant Nutr.* 19: 299-310.

Yamaguchi T (1973) Studies on the floating rice III. Effects of raising water level on the growth and carbohydrate contents of the tops. *Proc. Crop Sci. Soc. Japan* 42: 29-34.

Yamaguchi T, Sato T(1963) Studies on floating rice II. The effect of water level treatment upon carbohydrate content and the amylase invertase activities. *Proc. Crop Sci. Soc. Japan* 31: 357-361.

STRESS PHYSIOLOGY IN RELATION TO BREEDING FOR DROUGHT RESISTANCE : A CASE STUDY OF RICE

☐ *S. Fukai and M. Cooper*[1]

SUMMARY

Drought is a major problem for rice grown under rainfed lowland and upland conditions, but progress in breeding for drought resistance has been slow. This paper reviews genotypic variation in stress-related traits in rice, and suggests how stress physiology can contribute to plant breeding programmes that aim to improve yield under water-limiting environments.

There are several putative traits which confer drought resistance in rice. The most important is the correct phenology which matches crop growth and development to the water environment. A deep-root system and some other drought avoidance mechanisms are useful in upland conditions. However, their usefulness is not known for rainfed lowland rice where the development of a hard pan prevents deep root penetration and where transpiration is a small proportion of total water loss from the system. Drought tolerance mechanisms appear to offer more scope for the genetic improvement of drought resistance in the rainfed lowland systems. Osmotic adjustment is promising, as it can counteract the effects of a rapid decline in leaf water potential and there is large genotypic variation for this trait. Green leaf retention appears to be a useful character for a prolonged drought, but is affected by plant size and this complicates the use of this as a selection criterion for drought resistance.

A major reason for the slow progress in breeding for drought resistance in rice is the complexity of the drought environment, which often results in the lack of clear identification of the target environment(s). Then. is a need to identify the relative importance of the three common drought types; early stress which often causes delay in transplanting, mild-intermittent stress which can have a severe cumulative effect, and late stress which affects particularly the late maturing varieties in rainfed lowland rice aerobic and anaerobic soil.

INTRODUCTION

Plant breeding aims to produce new cultivars suitable for a pre- defined target populations of environments. Often the outcome is improved crop yield by

---

[1] Department of Agriculture, The University of Queensland, Brisbane. Queensland, Australia, 4072

exploiting specific adaptation through minimising adverse effects of biotic factors, improving broad adaptation across environments or by increasing potential yield where crop growth is not affected by water or nutrient limitation. Generally advanced lines from breeding programmes are tested at a number of locations within the target geographical region for a number of years before their release as new cultivars. Traditional plant breeding takes time, and strategies to improve the efficiency of plant breeding programmes are continually sought. One major reason for the slow progress is the incidence of large genotype by environment (GxE) interactions, which result from a combination of differences in genotypic adaptation and the heterogeneous mixture of environments within the target area. The environmental variability is generally observed as year-to-year and site- to-site variation. A consequence of GxE interactions is that particular lines often do not perform well under all conditions encountered in the target population of environments. The biological reasons for these interactions are often unknown.

Rice is a semi-aquatic plant and commonly grown under flooded conditions. However, about a half of the rice area in the world not have sufficient water to maintain flooded conditions and rice yield is reduced to some extent by drought, a period of no rainfall or irrigation (Hanson *et al.,* 1990). The total area of upland rice is much smaller than rainfed lowland rice, though drought research has been concentrated mostly on upland rice, and only recently has a coordinated research effort for rainfed lowland rice commenced.

A wide range of water stress environments take place in the rice growing area as drought conditions differ in both the timing and intensity of water deficits. Therefore, the target population of drought environments for the rice growing area is a highly complex mixture of different types of water stress environments. In general the composition of this mixture is poorly understood. However, developing a picture of this mixture is critical to the success of translating drought physiology research into successful crop improvement strategies. Stress physiology has elucidated both responses of different physiological and morphological traits to water stress and genotypic defferences in these traits under specific drought conditions. Putative traits have been identified which may confer drought resistance in some crops, for example, for sorghum (Ludlow and Muchow, 1990). In rice also a large number of traits have been considered to affect grain yield under drought conditions (O’ Toole, 1982). Some traits appear more important than others, and their usefulness has been confirmed under some drought conditions. However, despite our increased understranding of stress physiology, development of drought resistant cultivars, i.e. cultivars which produce higher yield than others in drought conditions, is slow in rice, as it is for other crops, at least partly because of the lack of our understanding of GxE interactions.

This paper reviews some of the problems associated with GxE interactions in physiological studies of drought resistance, examines factors which cause GxE interactions for rice grown in water-limiting conditions, discusses several putative traits for improving drought resistance, and suggests ways of improving the efficiency of plant breeding programmes by adopting physiological research strategies which are appropriate for the target population of environments. The focus will be on rice, but work from other crops is included to make a comparison with rice.

G X E INTERACTION AND SELECTION FOR DROUGHT RESISTANCE

Genotype by environment (GxE)interactions are expressed as a change in the relative performance of genotypes in different environments. These interactions complicate selection of superior genotypes when they are large relative to genotypic variation and particularly when they result in a change in the rank of genotypes across environments (Haldane 1946; Baker, 1988a). The incidence, size and nature of GxE interactions are commonly investigated by conducting multi-environment trials (METs), where a sample of genotypes is evaluated at a number of sites in a number of years. Statistical models and methodology for the analysis and interpretation of such series of experiments have been widely discussed in the literature (Comstock and Moll, 1963; Baker, 1988b; Eisemann *et al.,* 1990; Nyquist, 1991; Cooper *et al.,* 1993; Cooper and De Lacy, 1994). Such analysis allows an evaluation of the size of GxE interaction variation relative to genotypic variation for the plant traits studied. The objective here is not to review GxE interactions in general but to consider some aspects of how they can complicate interpretation and extrapolation from the results of physiological experiments which concentrate on genotype adaptation to water stress and/or genotype by water-stress (GxE) interaction in rice grown under water limiting conditions. The two aspects which will be considered here are (i) definition of targeted environments for the breeding programme concerned and (ii) the relevance of particular types of physiological experiments to the target population of environments. The salient principles are developed by first considering a traditional statistical model used by plant breeders to analyse the results of genotypic adaptation in METs. This is then re-defined in terms of environmental factors which impinge on the results of drought resistance research on rice.

Where genotypes are tested at a series of sites in a number of years, a linear model which explicitly considers the cross- classification structure of sites and years is often used to analyse the results of the experiments. This model may be formlly defined as:

$$P_{ijkl} = \mu + g_i + s_j + y_k + (sy)_{jk} + (gs)_{ij} + (gy)_{ik} + (gsy)_{ijk} + {}^{e}ijkl, \quad (1)$$

where P_{ijkl} is observation 1 on genotype i at site j in year k and $i=l, ..., n_g$, $j=1, ..., n_s$, $k=l, ... n_y$, $l=1, ..., n_r$ with n_g, n_s, n_y and n_r the number of genotypes, sites, years and replicates, respectively; μ is the grand mean of all observations; g_i is the effect of genotype i; s_j is the effect of site j; y_k is the effect of year k; $(sy)_{jk}$, $(gs)_{ij}$, $(gy)_{ik}$, $(gsy)_{ijk}$ are the interaction effects associated with the main-effects; and ${}^{e}ijkl$ is the random error effect 1 associated with genotype i at site j in year k. Generally data on quantitative traits such as grain yield collected from METs are analysed in relation to this model. From this model the relative importance of genotypic and GxE interaction effects can be estimated for the traits analysed. Two deficiencies of such an analysis are (i) that there is no definition of what aspects of the environment are important in discriminating among the genotypes and (ii) there is no understanding of the physiological attribute to the differences in adaptation expressed among the genotypes (Eisemann *et al.,* 1990). Consequently where GxE interaction is large many questions remain unanswered, e.g. were water stress environments sampled in the METs? What types of water stress environments were sampled? Were the high yielding genotypes adapted to water stress? How important was GxW interaction? Was there genotype by water-stress by other (eg. nutrition, disease) environmental factor interaction?. Clearly these questions will continue to remain unanswered unless additional information is obtained on the physiological basis of genotypic variation and the causes of GxE interaction.

While the influence of GxE interactions is an important consideration for some breeding programmes, the model given in equation (1) is not directly applicable to many physiological experiments. Often these more detailed experiments concentrate on one type of water stress environment or a restricted range of water stress environments. In such experimental studies of drought resistance, we consider that there is a critical question which must be considered, i.e. how does the type of water stress generated in the experiment relate to those encountered in the mixture of environments which comprise the target population of environments?. This question of relevance can be re-phrased to consider its applicability to specific experimental situations. We do this below for two types of experiments.

Experiment 1. Where a restricted range of water stress environments is considered and other environmental factors (eg. nutrition, management, disease, insects etc.) are held constant, how does this influence the capacity to make inference from the experiments to the target population of environments? An example of this type of experiment would be where line-source sprinklers are used to consistently generate a range of water-stress environments with other inputs held constant (e.g. Puckridge and O' Toole, 1981). Environments at a research station, particularly of high soil fertility, may be quite different from the target environment where fertilizer input would be low.

Experiment 2. Where a single specific water stress environment is considered in addition to the assumption of other environmental factors being held constant, how does this influence the capacity to make inference from the experiments to the target population of environments? An example of this type of experiments would be a specific single environmental screen for drought resistance such as a dry season, upland experiment using young seedlings in which rainfall occurrence is very low (e.g. De Datta *et al.,* 1988).

These types of experimental situations are widely encountered in physiological-genetical studies of drought resistance in rice. However, it is rare for the questions we have posed to be asked and even more unusual for an answer to be sought.

To develop a theoretical famework to answer the question of relevance for experiments 1 and 2 above, we can express the statistical model given in equation (1) in a form more familiar to the elements of a physiologial experiment. As a first step, instead of site-to-site and year-to year variation we may consider that different water stress levels (refer to these by the symbol W for water-stress) are encountered in different experiments. Other environmental factors such as temperature, nutritional deficiencies and toxicities and biotic stresses (refer to these by the symbol 0 for other) will also influence the performance of the genotypes and these may vary among experiments. Therefore, the model can be redefined as:

$$P_{ijkl} = \mu + g_i + w_j + o_k + (wo)_{jk} + (gw)_{ij} + (go)_{ik} + (gwo)_{ijk} + e_{ijkl} \quad (2)$$

where P_{ijkl} is observation l on genotype i under water-stress j and influenced by other environmental factor k and i=l, ..., n_g, j=1, ..., n_w, k=1, ..., n_o, l=1, ..., n_r with n_g, n_w, n_o and n_r the number of genotypes, water-stress environments, other environmental factors and replicates, respectively; m is the grand mean of all observations; g_i is the effect of genotype i; w_j is the effect of water-stress type j; o_k is the effect of other environmental factor k; $(wo)_{jk}$, $(gw)_{ij}$, $(go)_{ik}$, $(gwo)_{ijk}$ are the interaction effects associated with the main-effects; and e_{ijkl} is the random error effect 1 associated with genotype i under water- stress j and other environmental facror k. Clearly this is a simplified model relative to that which would generally apply to the target production-system. However, it applies to experimental situations where we can evaluate genotype in a factorial combination of water stress regimes and other environmental factors. This model is applicable to the sorts of physiological experiments commonly conducted to investigate the physiological basis of drought resistance such as our experimental types 1 and 2 above. An important difference between models (1) and (2) is that developing and analysing series of experiments in terms of model (2) asks specific questions about the nature of drought resistance of genotypes in relation to types of water stress. However, to allow such an analysis it is necessary to be able to identify types of water-stress environments and generate these within the experiments. A model-based answer to the question of relevance posed for experiment types 1 and 2 can be obtained by considering the experimental scenarios posed in context with model (2). This is achieved by placing the appropriate restrictions on the effects in the model and assessing how the components of model (2) are confounded (Nyquist, 1991). The two experimental types are considered in turn.

For experiment 1, where a range of water-stress environments is considered but other environmental factors are held constant, n_o=1 and therefore k=1 in model (2). Here estimates are obtained for genotypic effects across the water-stress regimes and for GxW interaction. In this situation model (2) becomes:

$$P_{ij1l} = [\mu + o_1] + [g_i + (go)_{i1}] + [w_j + (wo)_{j1}] + [(gw)_{ij} + (gwo)_{ij1}] + e_{ij1l} \quad (3a)$$

In this presentation of the model the square brackets surround the effects of model (2) which are confounded. In this case the estimates of the genotypic effects are confounded with the genotype by other- environmental-factor (GxO) interactions and the genotype by water-stress (GxW) interaction effects are confounded with the genotype by water-stress by other-environmental-factor (GxWxO) interactions. Therfore, as the GxO and GxWxO interactions increase within the target production-system, the capacity to predict the relative drought resistance of genotypes and expression of GxW interactions in the target production-system from this type of experiment will decrease. However, it should be emphasised that where GxW interactions are the major component of the GxE interaction complex and both GxO and GxWxO interactions are small, the results from these types of experiments will allow good prediction of the relative drought resistance of genotypes in the environments of the target production-system.

For experiment 2, where only one type of water-stress environment is considered and other environmental factors are held constant, $n_o=l$ and $n_w=l$ and therefore j=k=l in model (2). Here estimates are obtained for genotypic effects only and no interaction effects can be estimated. In this situation model (2) becomes:

$$P_{i11l} = [\mu + w_1 + o_1 + (wo)_{11}] + [g_i + (gw)_{i1} + (go)_{i1} + (gwo)_{i11}] + e_{i11l} \quad (3b)$$

In this case the estimates of the genotypic effects are confounded with all three components of the GxE interaction complex. Therefore, in this type of experiment there is no separation of the genotypic effects from the GxE interaction complex and as any one of the GxE interaction components increases, the predictive value of the specific environmental screen for the target production-system will decrease. Again it is important to emphasise that while prediction to many of the environments which comprise the target production system may be unsuccessful, if the specific drought resistance screen matches one type of target-environment in the production-system then the screen will provide good prediction to that target environment. The additional question which must be asked in this situation is what is the frequency of occurrence of the particular target environment. For example, a seedling screen in a dry season may be useful for identifying rice genotypes which perform relatively well under early water stress conditions in a wet season, again assuming negligible GxO and GxWxO interactions. If this form of water-stress occurs with high frequency in the target production- system then the specific screen would be relevant. However, if this environment only occurs at a low frequency then while the screen may have good predictive capacity, its relevance would be decreased.

From the above consideration of screening genotypes for drought resistance it is argued that a critical component of studying drought resistance is a clear definition of the relevant target environments within the crop-production system. Where the objective is to select genotypes or identify physiological components which contribute to drought resistance, consideration must be given to the relative contribution of GxW, GxO, and GxWxO interactions in relation to the target environments. Without due consideration of the relevance of types of experiment, the success of a particular drought resistance screen, putative drought resistance trait or plant ideotype is likely to be poor in its contribution to plant breeding strategies and progress in breeding for drought resistance will continue to be slow. At present little is known of the size and causes of GxE interactions in rice production under water limitation. Given the ubiquitous nature of GxE interactions in other crop production systems (Delacy *et al.,* 1990) and the diverse nature of the types of environments in which rice is grown it may be anticipated that GxW, GxO and GxWxO interactions will be large for quantitative traits such as grain yield. In the following sections we consider putative drought resistance traits which have been studied in rice and assess their possible contribution to drought resistance for various types of drought conditions. Specific attention is given to the incidence and influence of GxE interactions on the role of these putative traits in drought resistance.

THE PHYSIOLOGICAL BASIS OF INTERACTING FACTORS

There are a number of reasons for the genotype by drought environment interactions discussed above. One reason is that yield potential under favourable water conditions varies among genotypes but yield under water limiting conditions may be similar. This interaction is not of interest here as we try to understand yield differences in water limiting conditions.

Timing of drought development in relation to a genotype's phenology is important for GxE interaction. It is well known that panicle development to anthesis is the most critical stage for water stress in rice. Our work (Boonjung *et al.,* 1994b) with rice indicates that grain yield is lowered at the rate of 2% per day as a 15-day stress period (dawn leaf water potential less than -1.0 MPa) later during panicle development is delayed (Fig. 1). Unfilled grain number increases sharply with stress during late panicle development. Water stress reduces assimilate production and this causes reduction in yield components such as panicle number per plant, spikelets per panicle, filled grain percentage, and individual grain mass. However, unfilled grain number appears most susceptible to reduced assimilate availability.

Assuming the reduction of 2% grain yield per day with the delay in termination of 15 days stress, a 20-day difference in flowering time between two cultivars would cause a grain yield difference of about 40% if they have the same yield potential under non-limiting conditions. Thus, it is likely that the cultivars with a difference in phenology will react differently to a drought, depending on the timing of stress development (Maurya and O'Toole, 1986). Phenology is important in determining grain yield response also because quick maturing cultivars often escape from severe stress, while late maturing cultivars may be affected by a terminal stress. These results suggest that genotypes should be compared for their drought resistance / susceptibility within the same phenology group, or at least genotypic variation in phenology should be corrected statistically before genotypic difference in drought tolerance is estimated (Bidinger *et al.,* 1987a, b). Alternatively it is possible in some experiments to implement a strategy of staggered planting of different varieties so that they would flower at about the same time (Lilley and Fukai, 1994b).

In addition to timing of drought in relation to crop phenology, duration and severity of drought can also affect genotypic response to drought. For example, genotypic responses to mild, intermittent stress may be quite different from those to prolonged stress.

Another reason for GxE interactions among drought environments is that drought affects crop growth indirectly through contributing to the incidence of another adverse condition. For example, certain diseases in rice tend to develop under dry conditions. Dry conditions may not always induce the disease in the same manner. Thus, where there is genotypic variation in resistance to the disease in some dry years, some lines appears to be doing well relative to others but not in other

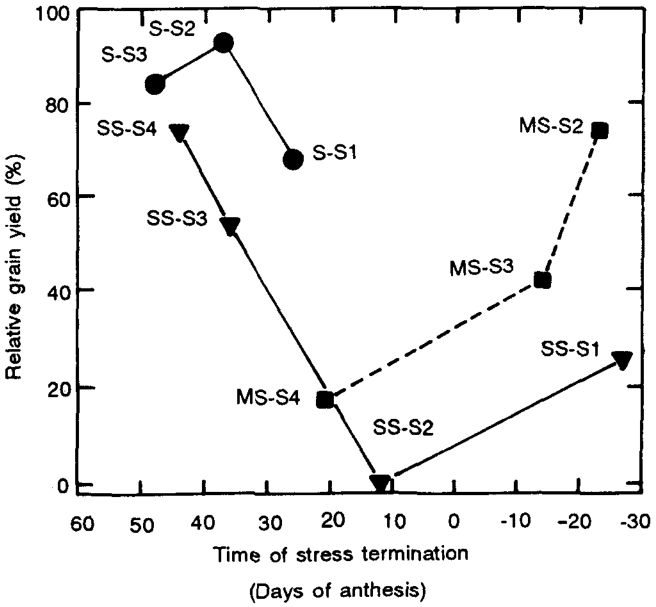


Fig. 1. Relationship between grain yield under water stress conditions, relative to the corresponding sowing in the irrigated trial, and the time of water stress termination expressed in days to anthesis, of three trials. Experiment 1 (0, Exp 1), Severe stress (▼, SS) and mild stress (☐ MS) trials in Experiment 2. S1- S4 indicate time of sowing. (Boonjung *et al* 1994b).

dry years, depending on the pattern of disease development. Under these situations the specific drought resistance response is confounded with the presence of the other factor, a disease in this case, and the large GxWxO interactions (see equations (3a) and (3b) complicate interpretation of drought resistance responses. It is then necessary to identify the presence of the disease in the experiment and screening methods for drought resistance need to consider the complications generated by this other factor. Where the disease occurs widely with drought, the direct selection against the disease may be more appropriate than attempting to develop cultivars with drought resistance per se.

Rainfed lowland rice has a unique nature of alternating aerobic and anaerobic soil conditions during the crop growth cycle and this is likely to be another major source of the GxE interactions, particularly GxO and GxWxO interactions. During a flooded period, rainfed lowland rice may perform similarly to irrigated lowland rice, but often growth is reduced as water level recedes to below the soil level. Our recent experience in Northeast Thailand indicates that the rice plants do not show typical water stress symptoms of leaf rolling and leaf death immediately after the flood water has disappeared from the soil surface. In some cases these symptoms were never seen, but grain yield was generally low in the sites where there was no flooding water during the latter part of the growing season. This may be related to phosphorus becoming less availabe in the aerobic soil, or to a loss of nitrogen during alternating periods of aerobic and anaerobic soil conditions (Patrick and Wyatt, 1964). It is also possible that loss of standing water results in increased acidity of soil water, as in many cases the soil is strongly acidic. With standing water the acid soil is unlikely to cause a problem. Rice is known to be susceptible to manganese and aluminium toxicity and reduced pH of the soil solution may induce the toxicity within a short time period.

Genotypes may differ in their response to the manganese or aluminium level in the soil as found in some crops. If experiments are conducted at different locations with soils of various pH levels, there could be strong GxE interactions in dry seasons and between wet and dry years.

Where the objectives is to study drought resistance, the incidence of the above complex mixture of these and other types of environment in rice production systems and their potential for generating GxE interactions strongly suggests (i)the importance of identifying the types of stress environments sampled in the traditional METs conducted in plant breeding programme and (ii) more focussed screening of lines under relevant target environment conditions. In both of the areas there is scope for stress physiology research to contribute to plant breeding strategies.

PUTATIVE TRAITS FOR IMPROVING DROUGHT RESISTANCE

This section evaluates the evidence for a number of putative traits which may confer drought resistance in rice. The use of putative traits to improve grain yield is a classic example of indirect selection in plant breeding. In this case the objective is to indirectly increase grain yield, or stability of grain yield by selecting for putative drought resistance traits, or for a combination of yield and the traits. The indirect response to selection($\Delta G_{y/x}$) for character y (yield) from selection for character x(putative draught resistance trait) is described by the equation :

$$\Delta G_{y/x} = i_x h_x h_y r_{gxy} \sigma_{py} \quad (4)$$

where i_x is the standardised selection differential applied to the putative drought resistance trait x; hx and hy are the square root of the heritability of the putative traits x and y, respectively; rgxy is the genetic correlation between traits x and y; and σ_{py} is the square root of the phenotypic variation for character y. This equation may be expressed in different forms and a detailed treatment of the principles of indirect selection can be found in Falconer (1989) and in the review by Gallais (1984). The component of equation (4) which determines whether there is scope for indirect improvement of yield via the putative trait (s) is the genetic correlation between the two traits. Genetic correlations are a result of either linkage or pleiotropy. For a high chance of successful indirect selection, identification of a putative trait which is pleiotropic for yield is desirable. Linkage relationships can change with time and between populations due to recombination. Recently Aastveit and Aastveit (1993) considered the impact of GxE interactions on genetic correlations between traits. In general, the presence of unpredictable GxE interactions will reduce the heritability of traits and the reliability of genetic correlations between traits measured in individual experiments and thus reduce the indirect response to selection equation (4).

Where a putative trait is advocated as a selection criterion for a plant breeding programme it should at the very least be evaluated in relation to the components of equation (4) in relevant target environments. Information on the heritability of the trait and the genetic correlation with yield would allow an objective assessment of the indirect response to selection for yield. The putative trait could be prioritised in context with the many other traits that are selected for within the breeding programme. The slow progress which has been observed for the improvement of grain yield of rice under water limiting conditions suggests that the heritability of yield is low. In our recent work in Thailand, preliminary information suggets that genetic variations for yield exists and reasons for the low heritability include large G x E interactions and experimental errors. Therefore, there appears to be scope for indirect improvement of yield if the cause of the G x E interations could be better understood and suitable drought resistance traits could be identified. Here we consider a number of putative drought resistant traits in rice following a review by O'Toole (1982), and evaluate the evidence for these as suitable indirect selection criteria in relation to the components of equation (4).

Molecular marker technology has been identified as a powerful tool for selection of traits which are otherwise difficult to screen. O'Toole (1989) discussed the use of molecular marker technology for selection of drought resistance traits in rice. Where molecular markers are linked to genes controlling the expression of drought resistance traits, there is scope to select for the genes without subjecting breeding lines to a drought screen. Therefore, given the difficulty in identifying and conducting a reliable drouhgt resistance screen, there are opportunities for improving the efficiency of selection for drought resistance via the use of molecular markers. Work is currently under way in rice and some aspects of this will be discussed.

Root system

Under upland condition, rice, maize and sorghum have similar root length, density and water extraction pattern down to 60 cm depth (Fukai and Inthapan, 1988). However, below that depth, water extraction by rice is very small and this is the main reason for the susceptibility of rice to water strees, compared with sorghum (Inthapan and Fukai, 1988). The develoment of the rice root system is also sensitive to soil water deficit (Boonjung *et al.,* 1994a).

O, Toole (1982) suggested three root-related adaptive mechanisms for rice. (1) For relatively large soil water reservoir, increase in rooting depth, root density, root-shoot ratio and possibly also root conductance. For relatively small soil water reservoir, (2) possibly increased root penetration of any physical-chemical impediment and (3) possibly osmotic adjustment of root system. High osmotic adjustment of roots would allow more thorough extraction of soil water and also enhanced dehydration tolerance which would enhance root system survival and plant recovery upon rewatering. However, experimental results to date are not available to show the effects to osmotic adjustment in roots. Most work on the root system of rice in relation to drought resistance has been conducted under upland conditions where there is a large soil water reservoir. This relates to O'Toole's first point of the adaptive mechanisms, and emphasises the importance of rooting depth, mot density, and mot thickness.

The development and function of the rice root system, and their relation to drought resistance were reviwed by Yoshida and Hasegawa (1982). Their review was mostly based on upland work conducted at IRRI in the 1970s, and their major findings are summarised here. Rice has a well developed mot system near the soil surface (0-30 cm), but generally not below 30 cm, compared with other major crops. There is, however, a lagre variation in root length density below 30 cm among rice genotypes. Generally genotypes with high root length density below 30 cm have a deeper root system. Yoshida and Hasegawa used the ratio of deep root weight and shoot weight as an index for drought resistance (avoidance) as the large deep mot system would be able to extract more water and the small shoot would require less water. They found the ratio to be positively related to field evaluation of drought resistance. Using 1081 entries, they also found that the entries with large deep root-to-shoot ratios tended to be taller and have less tillers. These characters match the description of traditional upland rice varieties, since the rice root system is composed basically of nodal roots, genotypes with large tillers tend to have more roots, particularly on secondary and tertiary tillers which appear late and have short mots. Thus, it appears that genotypes with a small number of well-developed tillers have a smaller number of longer roots and this results in high root length density at depth. They would be thick (larger diameter) and hence, have high conductance with large xylem vessels.

While a direct relationship between root length at depth and the amount of water extracted from the layer is rare. Puckridge and O, Toole (1981) found a deep rooting cultivar, Kinandang Patong, that extracted a larger amount of water at 40-70 cm depth than the two cultivars IR20 and IR36 which were shallow rooted. Similar results were shown by Mambani and Lal (1983b, c). Our recent work, also under upland conditions, (Lilley and Fukai, 1994a) shows that variation in water extraction among four cultivars was directly related to the variation in root length density. Thus when the amount of water extracted from a 20 cm layer in the soil profile is plotted against the root length density in the layer, the data from the four cultivars fall on one curve for each experiment (Fig. 2). Incresed root length density promoted the rate of water extraction, though the duration of linear phase of water extraction was to some extent reduced. In their experiments, ground cover varied among cultivars, but that apparently did not affect the root length density-extracted water relationship, indicating the importance of mot length in determining the amount of water extracted.

Lines with high root length density tend to have high leaf water potential and delayed leaf death due to water stress (Mambani and Lal, 1983a; Cruz and O'Toole, 1985; Ekanayake *et al.,* 1985a). These favourable conditions may result in higher grain yield in lines with high mot length under water limiting conditions(Mambani and Lal, 1983a), although a yield advantage is not always observed (Puckridge and

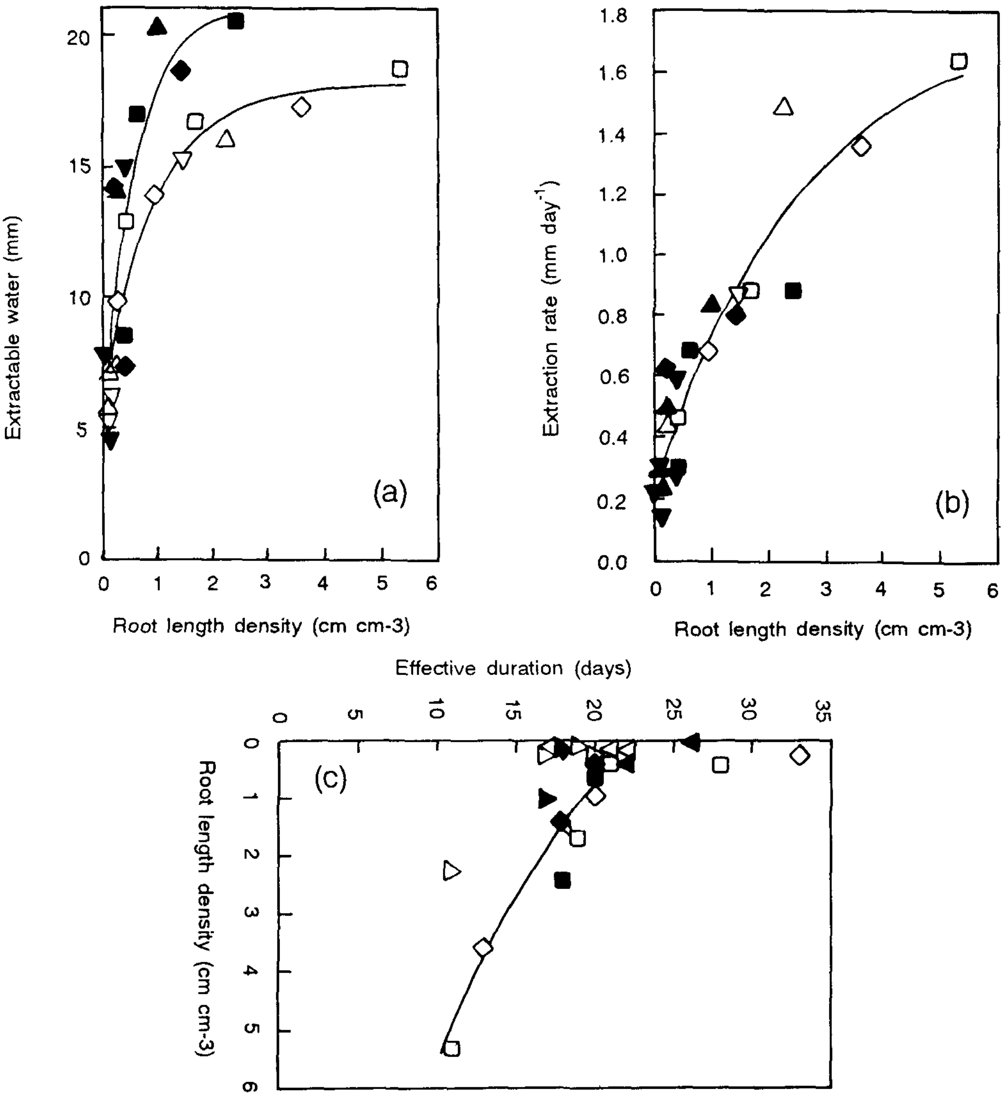


Fig. 2. Relationship between a) extractable water, b) maximum extraction rate and c) effective duration of extraction and root length density in a 0.2 m layer (0.2-0.8m depth) for four cultivars (□ CPICB,◊ Lemont,Δ Rikuto Norin 12,∇ Todoroki Wase) in the vegetative stage (solid symbols) and reproductive stage (hollow) trials. (Lilley and Fukai, 1994a).

O'Toole, 1981). In the case of Lilley and Fukai(1994b) mentioned earlier, there was an indication that the cultivar with the highest root length performed better than others under mild stress conditions, but there was no direct relationship between total root length and grain yield in the experiment where there was only one period of drought. It is likely that the advantages of varieties with larger root systems would be greater when there are several drougth periods, i.e. intermittent stress.

However, it is unlikely that the genotypes with high mot length density at 40-80 cm depth will have any advantage under most rainfed lowland conditions, as the hard pan which develops closer to the soil surface would preclude the expression of the potentially superior root system. It is rather the genotype's ability to penetrate the hard pan that may be more important in rainfed lowland conditions. In a lowland experiment where water stress developed from 45 to 75 days after transplanting, grain yield of 30 genotypes was not related to any mot characters determined in aeroponically grown plants (Ingram *et al.,* 1990). Nevertheless in some rainfed lowland fields where puddling is not practiced, for example due to sandy soil texture, high root length at depth may have direct relevance.

Root axial resistance can be important in determining the rate of water flow to the shoot. Rice plants are often not able to extract water thoroughly from deeper layers, partly because of low root length density at depth, but also increased axial resistance due to the increased distance to the shoot and also to the smaller diameter of the roots. Genotypic variation in mot thickness is associated with that in xylem size (Yambao *et al.,* 1992). However, they consider that increased xylem vessel diameter will not directly increase the drought resistance of a genotype.

Determination of root length and root depth in the field is time consuming, and quicker methods have been devised which could be used in screening for an ideal root system in a breeding programme. For example aeroponic and hydroponic culture can be used for root system determination (Loresto *et al.,* 1983; Ekanayake et al., 1985 a; Haque *et al.,* 1989). However, the value of this strategy is questionable for rainfed lowland rice given the findings of Ingram *et al.* (1990). Gomathinayagam *et al.* (1989) suggest that seminal root growth can bo used for screening deep rooted rice. In the field the root pulling resistance can be used as a measure of root systems (O, Toole and Soemenatono, 1981). Plants with high mot pulling resistance were able to maintain high leaf water potential (Ekanayake *et al.,* 1985b).

Some root system characteristics appear to have high heritability. Using F_1, F_2 and F_3 populations of the cross between IR20 (a shallow, thin root system) and MGL-2 (a deep, thick root system), Ekanayake *et al.* (1985a) found high heritability for root thickness, mot dry weight and root length density. However, heritability for root pulling resistance was rather low (Ekanayake *et al.,* 1985b).

Shoot-related mechanisms

O'Toole (1982) suggested three shoot-related adaptive mechanisms; accumulation of amino acids or growth regulators, drought avoidance mechanisms and osmotic adjustment.

Growth regulators

Little work has been conducted with rice in relation to growth regulators and drought resistance. Dingkuhn *et al.* (1991a), in the same experiment as will be reported later for osmotic adjustment and other physiological characte of seven diverse cultivars by Turner *et al.* (1986a, b), found cultivar differences in abscisic acid (ABA) accumulation, but the difference was not related to physiological behaviour of cultivars under water stress. On the other hand, they found stress-induced proline accumulation to be positively correlated with osmotic adjustment.

Avoidance mechanism

In contrast to a deep root system which can increase water uptake, avoidance mechanisms in the shoot reduce water use, thus avoiding the development of low plant water potential.

Epicuticular wax is an avoidance mechanism trait which may have a significant effect on rice growth during water stress and recovery upon rewatering. However, the contribution of this putative trait has not been examined in details. Rice is known to have much less epicuticular wax than other cereals and it has generally high cuticular (epidermal) conductance (O'Toole *et al.,* 1979). This implies that rice will lose water even when stomata are completely closed, and this may lead to rapid leaf death. There is genotypic variation in quantity of epicuticular wax (O’Toole, 1982). In our recent experiment, epidermal conductance was found to vary among rice cultivars, but there was no indication that cultivars with low epidermal conductance retain green leaves for a longer period.

Leaf diffusive conductance and leaf rolling are also avoidance mechanisms, for which genotypic variation is well documented (O'Toole and Cruz, 1980). The variation is at least partly due to differences in the ability to extract water from the soil, as a result of differences in root system. This causes differences in leaf water status (water potential), and genotypes which maintain high leaf water potential tend to maintain high leaf conductance and low leaf rolling(O’Too1e and Moya, 1978). However, the leaf rolling score and leaf water potential relationship varies among cultivars (Turner *et al.,* 1986 a; Fukai and Inthapan, 1988) possibly because of cultivar differences in osmotic adjustment. Cultivars with high osmotic adjustment can maintain turgor potential at relatively high levels under low leaf water potential. This relationship has been documented in other cereals, though strong experimental evidence is lacking in rice. Within a genotype, osmotic adjustment is known to affect leaf rolling in rice (Hsiao *et al.,* 1984).

The direct effect of these drought avoidance mechanisms on growth of rice plant under limited soil water conditions is not certain, particularly in rainfed lowland conditions where the amount of water used as transpiration would be a, rather, small proportion of total water use. The latter includes evaporation from water or soil surface, deep percolation and seepage. While Dingkuhn *et al.* (1989a) found under mild stress conditions a correlation between leaf rolling and water potential, suggesting that leaf rolling has a positive effect in maintaining high leaf water potential, our experience is that cultivars which are able to maintain high leaf water potential have a small degree of leaf rolling. This indicates that, generally leaf rolling is a result of other avoidance mechanisms, which result in high leaf water potential.

Osmotic adjustment

Osmotic adjustment is an adaptive process in which solutes accumulate in the cell and osmotic potential is decreased in response to adverse growing conditions such as drought, salinity and low temperature. As water stress develops osmotic adjustment is induced, and as such osmotic adjustment increases with decrease in leaf water potential (Steponkus *et al.,* 1982; Turner *et al.,* 1986 b). Development of osmotic adjustment however, appears to be rapid in rice, perhaps because of rapid development of water stress as measured by leaf water potential, compared to sorghum and maize (Fukai and Inthapan, 1988). Thus any benefits of high adjustment would be expected in rather early stages of a drought period in rice.

With osmotic adjustment, turgor pressure is maintained at a relatively high level in spite of reductions in leaf water potential (Cutler *et al.,* 1980). Development of leaf rolling and half death can be delayed by osmotic adjustment (Hsiao *et al.,* 1984). It should be pointed out however, that turgor is not necessarily the sole factor determining the responses of these processes to soil water deficit.

The early work by Steponkus *et al.* (1982) using four cultivars has shown rather small variation in osmotic adjustment in rice. The maximum adjustment was about 0.3-0.5 MPa. In the field studies, there was some variation in osmotic adjustment with a maximum of 0.5 MPa in lowland cultivars and less in upland cultivars among seven diverse cultivars of rice (Turner *el al.,* 1986b). However, the differences were related to the development patterns of water stressed cultivars, and the greater degree of apparent adjustment in the lowland cultivars was due to the greater degree of cumulative stress. Yang et al. (1983) found some difference in the osmotic potential water potential relationship between two constrating cultivars, Taichung Native 1 and OS4.

There is no evidance to indicate that genotypic variation in osmotic adjustment has a positive effect on growth and grain yield in rice, though probably there has been no serious attempt to test the usefulness of this character in the field. Our recent work however, does indicate some positive effect of osmotic adjustment in counteracting low leaf water potential to provide better green leaf area retention (Henderson *et al.,* 1993). Because osmotic adjustment in rice reaches its maximum value quickly and the maximum value is maintained for a while, it may be effective in buffering against the deleterious effect of water stress under situations of rather a small soil water deficit as may occur under intermittent stress.

The mechanisms of the effect of genotypic variation on yield are well documented in sorghum, and are briefly reviewed here. Several field experiments using 2-6 commercial hybrids with a contrast in osmotic adjustment have shown clear yield advantages of hybrids with high osmotic adjustment when water stress develops before anthesis or during grain filling (Wright *et al.,* 1983, Ludlow *et al.,* 1990, Santamaria et nl., 1990). Grain yield under stress conditions relative to that under well-watered conditions increased linearly with the extent of maximum osmotic adjustment of the line. Compared to genotypes with low osmotic adjustment, those with high osmotic adjustment were able to extract water more thoroughly, maintain higher grain number and translocate a greater amount of pre-anthesis assimilates to fill grains. Using lines from a sorghum population that had differences in osmotic adjustment, Tangpremsri (1989) showed a yield advantage of about 0.5 t ha^1 in the high osmotic adjustment group. These groups had similar yield under well watered conditions. Under water-limiting conditions, the high osmotic adjustment group produced larger maximum leaf area, better leaf retention during grain filling and more grains per plant. Thus, there are a number of experimental results to suggest the advantge of high osmotic adjustment when sorghum experiences a prolonged period of water stress.

The current work by J.M. Lilley and M.M. Ludlow at CSIRO, Brisbane, Australia, shows a larger genotypic variation in osmotic adjustment than previously observed in rice. Measurements on rice plants grown in pots in a controlled environment and subjected to slow (25 day) drying cycle showed that there is a large range in maximum osmotic adjustment (0.4 - 1.7 MPa) among a set of 59 lines of diverse adaptation/background. Average osmotic adjustment of lines from upland environments was lower (0.73 MPa) than that of rainfed lowland, irrigated lowland and deep water ecotypes (0.96-1.03 MPa). However, there was a large range in osmotic adjustment within each ecotype.

They also examined variation for osmotic adjustment among a sample of recombinant inbred lines from a biparental cross. The parents, Morobereken and CO39, had low (0.7 MPa) and moderate (1.4 MPa) osmotic adjustment, respectively. Osmotic adjustment of the 52 recombinant inbred lines (RIL-F7), which had been mapped with RFLP markers, ranged from 0.7-2.7 MPa (Fig. 3). The frequency distribution of level of asmotic adjustment in the RILs was continuous and there was no evidence for osmotic adjustment being simply inherited. Transgressive segregation was observed with 6 lines having significantly higher osmotic adjustment than the high parent CO39. Morgan (1991) reported that a single recessive gene accounted for the variation in osmoregulation observed in wheat. Our work in sorghum (Basnayake *et al.,* 1994a, b) suggests that the inheritance of osmotic adjustment is at least oligogenic. However, two major genes for high osmotic adjustment were identified. Current work is investigating the contribution of these genes to yield under water stress conditions.

The large genotype variation for osmotic adjustment in rice offers considerable scope for improving these traits in current cultivars. Screening for osmotic adjustment currently requires intensive measurement procedures and is time consuming and expensive. Molecular markers such as RFLPs and RAPDs could be identified for osmotic adjustment genes. The variation in the populations offers a good possibility of obtaining suitable RFLP markers for these traits so that these traits could be readily incorporatd in rice breeding programmes.

Water use efficiency

Water use efficiency (WUE) is commonly defined as dry matter production per unit of water used, and is closly related to transpiration efficiency, dry matter growth per unit of water transpired. Instantaneous measurements of leaf photosynthesis and transpiration used to approximate WUE or transpiration

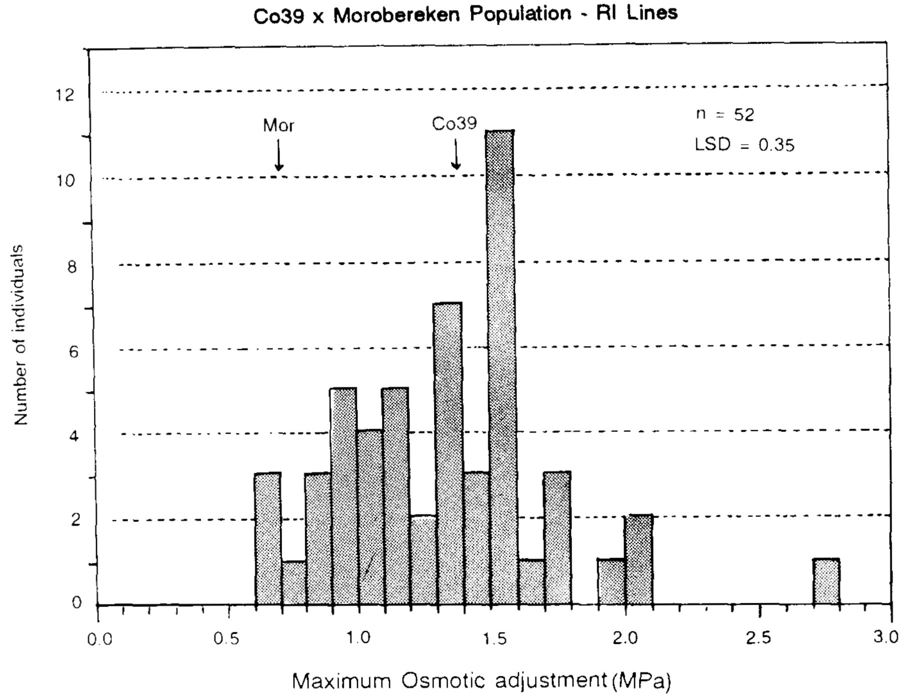


Fig. 3. Frequency distribution of maximum osmotic adjustment of lines from a Co 39 x Moroberekan cross. (J.M.Lilley and M.M. Ludlow unpublished).

efficiency. Using this technique Dingkuhn *et al.* (1989b) found WUE to be high in tropical *japonica* types, intermediate in *indica* types and low in *aus* types, and also considerable variation in WUE within the types. On the other hand Fukai *et al.* (1985) found no significant variation in WUE among four temperate *japonica* cultivars. They however, found WUE to decline rapidly with leaf ageing. One of the difficulties of estimating WUE from instantaneous gas exchanges is the fluctuation of WUE, due to leaf age or growing conditions such as vapour pressure deficit. This problem can be overcome by use of stable carbon isotope analysis. Dingkuhn *et al.,* (1991b) found a good relationship between WUE determined by the gas exchange method and carbon isotope discrimination. In contrast to drought avoidance mechanisms expressed in the shoot which decrease the rate of assimilate production, there is no cost for high WUE, and hence cultivars with high WUE would be advantageous in dry conditions, unless WUE is associated with characters which are undesirable for high yield.

Green leaf retention

Since leaf death occurs as a result of severe drought and is an easily recognisable character in the field, green leaf retention is often used as a selection criterion for drought resistance in rice (De Datta *et al.,* 1988), assuming that cultivars with good leaf retention produce a higher yield than others in dry environments. In rice, 30 days old seedlings are subjected to drought and they are visually scored using a standard (drought score) developed by IRRI. Lines which have better green leaf retention also recover better after water stress is relieved (Malabuyoc *et al.,* 1985).

Drought at the seedling stage is commonly related to leaf water potential (Chang *et al.,* 1979). Lines which can maintain high leaf water potential tend to retain green leaves and hence, have a low drought score. Thus, low drought score generally indicates that the lines possess mechanisms of drought avoidance, although some lines appear to be able to maintain green leaves better than others at low leaf water potential and hence, they are dehydration tolerant (Henderson *et al.,* 1993). Our recent experiments indicate that genotypic variation in drought score is strongly associated with variation in light interception prior to the commencement of a stress period. Thus, lines with large plant size, and hence, with high light interception were stressed more quickly and had high drought scores. Variation in drought score of a line is also associated with variation in plant size obtained under various water stress environments, i.e for some reasons a line may establish more quickly than others in one site but not in others and this causes inconsistency in relative drought score among lines. When full ground cover is achieved before drought development, the genotypic variation in plant size becomes less important in determining leaf death and this may be a reason for change of genotypic ranking on drought score between young seedlings and plants with a well developed canopy (Henderson *et al.,* 1993). In a rainfed lowland experiment where drought was developed in a crop at a high plant density from 45 to 75 days after transplanting, genotypic variation in drought score of 30 lines was found to be correlated with yield (r=-0.66) (Ingram *et al.,* 1990).

While leaf death occurs as a result of drought, it does not occur until plants are severely stressed. Under upland conditions, Boonjung *et al.* (1994c) have shown that leaf death is least sensitive to soil water deficit and leaf elongation and leaf diffusive conductance are much more sensitive. This implies that in rather mild and intermittent stress where available soil water does not decrease below 50% of the total available water, plant growth will be affected because of reduced leaf expansion growth and photosynthesis. Genotypic variation in these characters, rather than drought score, would determine crop growth. In one of our upland rice experiments we found no association between leaf conductance and drought score among 20 lines examined, indicating that selection for low drought score may not necessarily select for high leaf conductance under stress conditions.

Lines with low drought scores do not necessarily perform well in dry conditions (Puckridge and O' Toole, 1981). This again shows the importance of identifying the target environment and developing an adequate screening method suitable for the environment. The use of drought score at the seedling stage may be appropriate for drought that develops early in the season in rainfed lowland; for example in July in Thailand, particularly for direct seeded rice.

One advantage of lines with good green leaf retention is that they tend to recover quickly when the stress period terminates. This may be particularly important when stress develops around panicle initiation, as the lines with good leaf retention can supply more assimilates to the developing panicle. This in turn will result in production of a large number of spikelets (Lilley and Fukai, 1994b).

Production and retention of fertile spikelets

When a rice variety is grown under different environments, grain yield is mostly related to grain number as single grain weight is stable across environments. Grain yield is mostly limited by grain sink capacity to accept assimilates to fill grains (Fukai *et al.,* 1991). Grain number is determined by the number of spikelets at anthesis and proportion of spikelets which produce filled grains (filled grain percentage). The number of spikelets is directly related to the rate of assimilate production between panicle initiation and anthesis, regardless of whether the assimilate production is altered by water stress or shading (Boonjung, 1993). Filled grain percentage on the other hand is related to assimilates produced around anthesis, and is particularly susceptible to water stress (Cruz and O' Toole, 1984, Boonjung, 1993). Maurya and O'Toole, (1986) found large genotypic variation in filled grain percentage during the dry season. Reduction in leaf water potential at anthesis may cause poor exertion of the panicle (Cruz and O'Toole, 1984; Ekanayake *et al.,* 1989) and increase the percentage of sterile spikelets because of pollination abnormalities (Ekanayake *et al.,* 1989, 1990). Ekanayake *et al.* (1989, 1990) showed some differences in flowering response to water stress between the two cultivars they studied, and their work suggests that drought resistant varieties should be able to maintain high leaf water potential at anthesis and do not show pollination abnormalities as water potential declines, compared to susceptible varieties.

DEFINITION OF TARGET ENVIRONMENTS

We have argued that it is essential to define the types of drought environment which are encountered in the target population of environments. It is simply not sufficient in most cases to say that the breeding programme is designed to improve drought resistance in rice. The question is, how can this be achieved in a way which improves the conduct of physiological experiments and selection strategies in plant breeding programmes? The level of stress encountered in plant breeding experiments is commonly quantified in terms of the mean yield reduction relative to higher yielding trials or a high -input control experiment. However, the majority of the experiments are conducted without knowledge of what type of stress occurred. Given that different traits confer adaptation to different types of stress, there is a need to improve on this unenlightened situation to enable assessment of the relevance of individual experiments to the target environments.

Rice growing environments can be grouped into two major categories, upland and rainfed lowland conditions. The latter may be further grouped on whether a hard pan is strongly developed or not. Opportunities exist to characterise the environment by taking measurements on critical variables such as the depth of free water in the rainfed paddy. Such physical characterisation is time consuming and would need to be focussed on critical aspects of the target environments. The objective is not to develop a wish-list of measurable environmental variables but to streamline the list to allow characterisation of the environment as to its relationship to the target environments. Another strategy is to use probe genotypes to act as a bioassay of specific types of stress environments (Eisemann *et al.,* 1990). For example, near isogenic lines for osmotic adjustment could be used to assay the incidence of water stress as perceived by the plant.

In characterising an environment where a water deficit develops, it is important to identify the timing and severity of stress in relation to crop phenology. Rainfed lowland rice is commonly planted in the monsoon season in Asian countries where bimodal rainfall is common. There appears to be three types of stress development in these regions (Chang *et al.,* 1979).

Early stress

Farmers seed in a nursery early in the first rain period and prepare paddies. In some years however, there is a prolonged dry period between the first rain and second rain periods. This causes delay in transplanting and reduction in yield because of the use of old seedlings at transplanting. In some cases the dry period may occur after transplanting or if direct seeding is practiced, young seedlings may suffer from water stress. Early maturing cultivars may be affected severely by early season drought, whereas late maturing cultivars may have sufficient time to recover from the drought (Maurya and O'Toole, 1989).

Mild intermittent stress

While the periods of tillering to flowering generally coincide with the highest rainfall in the monsoon season, short intermittent stress can develop any time during this period, or any other time. It is known that even in fully flooded paddies, there can be mid day closure of stomata, probably due to the inability of roots to take up sufficient water to meet the high water demand. In some crops (e.g. sweet potato, Bouwkamp, 1989) midday wilting which develops in well-watered soil, is related to yield reduction among different cultivars. If the water supply is only slightly less than the demand, there may be no wilting or leaf rolling symptom and hence stress would be unnoticed by casual observation, but dry matter growth may be affected and yield reduced by reduced leaf area growth and stomata closure, the plant responses which are most sensitive to water deficit (Boonjung *et al.,* 1994c).

Late stress

This is a common problem when a late maturing cultivar is used, and growth during the flowering - grain filling period is affected by drought at the beginning of the dry season. Early maturing cultivars, or cultivars with appropriate photoperiod requirement may minimise the end - of - the - season stress. Late stress, however, is sometimes the result of late planting caused by a dry spell early in the season.

Identification of the timing and severity of water stress and the magnitude of the problem are likely to require experimentation for several years. The frequency of occurrence of these three types of water stress environments in the rainfed lowland regions needs to be determined. Alternatively, if the components of water balance, particularly seepage and deep percolation, are known for the paddy, a water balance model may be used to estimate the level of perched water table during crop growth and this could be used as an indicator of likely plant water stress. Comparison of grain yield under rainfed conditions and irrigated conditions will provide information on the magnitude of the drought problem.

It is likely that appropriate traits can be selected once the target environment is accurately defined. Soil factors are also important in selecting traits, as mentioned earlier for the root growth, acidity and nutritional problems. Lowered perched water table in a dry period could interact with these factors, and affect growth indirectly. Identification of these interactions should help in determining which traits are to be considered in a plant improvement programme.

The following is a list of suggested putative traits for enhancing the drought resistance of rice under different water stress conditions. It is emphasized that the usefulness of each trait for conferring high yield under drought conditions is unknown in most cases, therefore the traits listed, particularly for lowland conditions, should be considered as those on which concentrated research effort may be made by physiologists and plant breeders.

For different cultural conditions

Upland conditions:

Appropriate phenology, deep root system, shoot drought avoidance mechanisms.

Lowland conditions with hard pan:

Appropriate phenology, green leaf retention, tolerance for adverse soil conditions, high root conductance, root penetration ability.

Lowland conditions without hard pan:

Appropriate phenology, tolerance for adverse soil conditions, deep mot system.

For different types of stress

Early season stress:

Transplanting tolerance, green leaf retention, recovery growth.

Mid season, intermittent stress:

Avoidance mechanisms, appropriate phenology, spikelet retention.

Late season stress:

Appropriate phenology, green leaf retention, tolerance for adverse soil conditions.

Recently crop models have been considered as possible tools to assist investigation of the physiological and genetic basis of genotype adaptation (Shorter *et al.,* 1991) and selection decisions in plant breeding (Muchow *et al.,* 1991). Currently models are not at the level of development where they can be applied to the large number of unknown genotypes evaluated in breeding programmes. However, they may be useful in characterising the frequency of the early, mid-intermittent and late stress environment types in the target population of environments. Our current studies will evaluate the use of a rice model in this role in the rainfed lowland system in Thailand.

CONCLUSION

Crop physiology can make a strong contribution to a plant breeding programme designed for improving drought resistance. At present any improvements in drought resistance are largely a fortuitous outcome of the empirical multi-environment testing strategies used in the breeding programmes. While this traditional approach has been effective, its efficiency is widely considered to be low. We have identified the incidence of strong genotype by water stress (GxW) interactions for putative drought resistance traits and grain yield as a major constraint to the genetic improvement of drought resistance. Therefore, plant breeding strategies and physiological research focussing on drought resistance in rice must be conducted in a way which allows assessment of the effects of GxW interactions. We consider that this can be achieved by more effective characterisation of the type of stress encountered in individual experiments and relating this to relevant target environments in the rainfed lowland production system. If this approach is adopted, putative drought resistance traits can be evaluated in context with the components of indirect response to selection in a way which accommodates the effects of GxW interactions.

A number of putative drought resistance traits have been identified. The most important for all drought environments is the correct phenology which matches crop development to the water availability. Nevertheless, intermittent stress may develop at flowering time, or the rainy season may finish earlier in some years and the crop is subjected to stress at flowering. Genotypic variation in sensitivity of flowering to stress is worth further investigation.

The importance of a deep root system is established as a requirement for rice cultivars suitable for upland conditions as it ensures greater extraction of water held in deeper soil profile and therefore, maintenance of a high leaf water potential during a drought period. However, this is unlikely to be the case for rainfed lowland conditions, where the existence of hard pan inhibits root penetration to deeper layers. Water conservation strategies may also have limited success in rainfed lowland conditions, because of the small quantity of water that can be stored in the soil compared to the amount of water loss due to deep percolation, seepage and evaporation from the lowland field. For both upland and rainfed lowland conditions, cultivars with thick roots are advantageous in maintaining high water flow and hence, favourable plant water status.

It has been shown that some rice lines have better dehydration tolerance than others, judging by good green leaf retention even at rather low leaf water potential. This appears particularly useful for rainfed lowland conditions where probably a water- stress avoidance strategy has limited value. Dehydration tolerance may be achieved by increased osmotic adjustment, but this needs further testing. Osmotic adjustment has been found to vary greatly among rice genotypes.

It is essential to demonstrate the value of a trait for dry matter production during a stress period or a recovery period, or for a direct effect on yield components such as filled grain percentage or on yield itself, under a drought condition which is relevant to the target environments. A diagram for this is shown in Figure 4. Once a positive effect is established in yield determining processes, a screening method can be devised. Ultimately the success of any such screen will depend on the relative efficiency of indirect selection for yield via the putative drought resistance trait in comparison to direct selection for grain yield in the target environments. Therefore, it is essential that the merit of putative drought resistance traits is evaluated in terms of the principles of indirect selection.

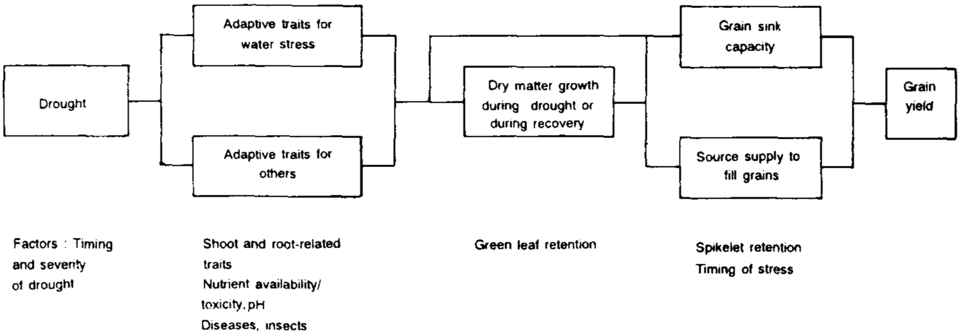


Fig. 4. A flow diagram showing processes of the effect of drought on grain yield, and important factors associated with each process.

It appears also that soil water deficit in rainfed lowlands induces changes in the environment which are not directly associated with plant water stress but may affect growth greatly. Soil conditions change from anaerobic to aerobic during cycles of flooding and drying, and there would be associated changes in nutrient availability or toxicity. Genotypic variation in response to these changes appears worth further investigation. Compared with the research effort for drought resistance in upland rice environments, the research input to the rainfed lowland conditions has been minimal.

A high priority research area is an accurate definition of the target population of environments, particularly patterns of drought development. This would assist definition of optimal multi-envimnment testing strategies for a breeding programme, ensure determination of the best phenology group for the target environment, and also focus areas of physiological research which can be directly related to the objectives of a plant breeding programme.

REFERENCES

Aastveit A H, Aastveit, K (1993) Effects of genotype-environment interactions on genetic correlations. *Theoretical and Applied Genetics* **86:** 1007-1013.

Baker R J (1988a) Differential response to environmental stress. Pages 492-504 In: Proceedings of the second international conference on quantitative genetics, B S Weir, E J Eisen, M M Goodman and G Namkkoong, eds. Sunderland, Massachusetts: Sinauer Associates, Inc.

Baker R J (1988b)Analysis of genotype-environmental interactions in crops. ISI Atlas of Science: *Animal andPlant Science* **1:** 1-4.

Basnayake J, Cooper M, Ludlow M M, Henzell R G (1994a) Inheritance of osmotic adjustment in three grain sorghum (*Sorghum bicolor,* L. Moench) crosses. *Theoretical and Applied Genetics* (submitted).

Basnayake J, Cooper M, Ludlow M M, Henzell R G (1994b) An investigation of genetic variation for combining ability of osmotic adjustment among a selected range of grain sorghum lines (*Sorghum bicolor,* L. Moench). *Field Crops Res.* (submitted).

Bidinger F R, Mahalakshmi V, Rao G D P (1987a) Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leake]. I. Factors affecting yields under stress. *Aust. J. Agric. Res.* **38:** 37-48.

Bidinger F R, Mahalakshmi V, Rao G D P (1987b) Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leake]. II. Estimation of genotype response to stress. *Aust. J. Agric. Res.* **38:** 49-59.

Boonjung H (1993) Modelling growth and yield of upland rice under water limiting conditions. Ph D thesis, The University of Queensland, Australia.

Boonjung H, Fukai S, Henderson S A (1994a) Effects of soil water deficit at different growth stages on rice growth and yield under upland conditions.I. Radiation interception, water extraction and dry matter growth under drought. *Field Crops Res.* (submitted).

Boonjung H, Fukai S, Henderson S A (1994b) Effects of soil water deficit at different growth stages on rice growth and yield under upland conditions. 2. Phenology, biomass production and yield. *Field Crops Res.* (submitted).

Boonjung H, Fukai S, Henderson S A (1994c) Responses of various stress indices to soil water deficit at different growth stages in rice under upland conditions. *Field Crops Res.* (submitted).

Bouwkamp J C (1989) Differences in mid-day wilting and yield among sweet potato genotypes. *J. Amer Soc. Hort. Sci.* **114:** 383-386.

Chang T T, Somrith B, O'Toole J C (1979) Potential for improving drought resistance in rainfed lowland rice. Pages 149-164 In: Rainfed Lowland Rice: Selected papers from the 1978 International Rice Research Conference, International Rice Research Institute, Los Banos, Philippines.

Comstock RE, Moll R H (1963) Genotype-environment interactions. Pages 164-196 In: Statistical genetics and plant breeding. W D Hansen and H F Robinson, eds. N.A.S.- N.R.C., Publication 982: Washington D.C.

Cooper M, Delacy I H, Eisemann R L (1993) Recent advances in the study of genotype x environment interaction and their application to plant breeding. Pages 116-131. In: B C Imrie, and J B Hacker, eds. Focused Plant Improvenent: Towards responsible and sustainable agriculture. Proceedings Tenth Australian Plant Breeding Conference, April 1993. Australian Convention and Travel Service, Canberra, Australia.

Cooper M, DeLacy I H (1994) Relationships among analytical methods used to study genotypic variation and genotype by environment interaction in plant breeding multi environment experiments. *Theoretical and Applied Genetics* (in press).

Cruz R T, OToole J C (1984) Dryland rice response to an irrigation gradient at flowering stage. *Agron. j.* **76:** 178- 182.

Cruz R T, O'Toole J C (1985) Water stress at reproductive stage and grain yield of dryland rice. Philip *Agriculturalist* **68:** 551-561.

Cutler J M, Shahan K W, Steponkus P L (1980) Alteration of the internal water relations of rice in response to drought hardening. *Crop Sci.* **20:** 307-310.

De Datta S K, Malabuyoc J A, Aragon E L (1988) A field screening technique for evaluating rice germplasm for drought tolerance during the vegetative stage. *Field Crop Res.* **19:** 123-134.

De Lacy I H, Eisemann R L, Cooper M (1990) The importance of genotype-by-environment interaction in regional variety trails. Pages 287-300 In: Genotype-by-environment interaction and plant breeding. M S Kang ed. Louisiana State University, Baton Rogue, Louisiana.

Dingkuhn M, Cruz R T, O'Toole J C, Doerffling K (1989a) Net photosynthesis, water use efficiency, leaf water potential, and leaf rolling as affected by water deficit in tropical upland rice. *Aust. J. Agric. Res.* **40:** 1171-1181.

Dingkuhn M, De Datta S K, Dorffing K, Javellana C (1989b) Varietal differences in leaf water potential, leaf net CO_2 assimilattion, conductivity and water use efficiency in upland rice. *Aust. J. Agric. Res.* **40:** 1183-1192.

Dingkuhn M, Cruz R T, O'Toole J C, Turner N C, Doerffling K (1991a) Responses of seven diverse rice cultivars to water deficits. 3. Accumulation of abscisic acid and proline in relation to leaf water-potential and osmotic adjustement. *Field Crops Res.* **27:** 103-117.

Dingkuhn M, Farquhar G H, De Datta S K, O Toole I C (1991b) Discrimination of 13c among upland rices having different water use efficiencies. *Aust. J. Agric. Res.* **43:** 1123-1131.

Eisemann R L, Cooper M, Woodruff D R (1990) Beyond the analytical methodology- better interpretation of genotype-by environment interaction. Pages 108-717 In: Genotype-by- environment interaction and plant breeding. MS. Kang, ed. Louisiana State University, Baton Rouge, Louisiana.

Ekanayake I J, De Datta S K, Steponkus P L (1989) Spikelet sterility and flowering response of rice to water stress at anthesis. *Ann. Bot.* **63:** 257-264.

Ekanayake I J, O'Toole J C, Garrity D P, Masajo, T M (1985a) Inheritance of root characters and their relations to drought resistance in rice. *Crop Sci.* **25:** 927-933.

Ekanayake I J, Garrity D P, Masajo T M, O'Toole I C (1985b) Root pulling resistance in rice: Inheritance and association with drought tolerance. *Euphytica* **34:** 905-913.

Ekanayake I J, Steponkus P L, De Datta S K (1990) Sensitivity of pollination to water deficits at anthesis in upland rice. *Crop Sci.* **30:** 310-315.

Falconer D S (1989) Introduction to Quantitative Genetics, Third edition. Longman Scientific and Technical : New York.

Fukai S, Inthapan P (1988) Growth and yield of rice cultivars under sprinkler irrigation in south-eastern Queensland. 3 Water extraction and plant water relations-comparison with maize and grain sorghum. *Aust. J. Exp. Agr.* **28:** 249-252.

Fukai S, Kuroda E, Yamagishii T (1985) Leaf gas exchange of upland and lowland rice cultivars. *Photosynthesis Res.* **7:** 127-135.

Fukai S, Li L, Vilmonte P T, Fischer K S (1991) Control of grain yield by sink capacity and assimilate supply in various rice cultivars. *Expt. Agri.* **27:** 127-135.

Gallais A (1984) Use of indirect selection in plant breeding. Pages 45-60. In : Lange, W.; Zeven, A.C. and Hogenboom, N.G. eds. Efficiency in plant breeding. Proceedings of the 10th Congress of EUCARPIA.

Gomathinayagam P, Natarajan S, Subramanian M, Nagarajan M (1989) A simple procedure to screen deep rooted rice entries. *Oryza* **26:** 408-410.

Haldane J B S (1946) The interaction of nature and nurture. *Ann. Eugenics* **13:** 197-205.

Hanson A D, Peacock W J, Evans L T, Arntzen C J, Khush G S (1990) Drought resistance in rice. *Nature* **234:** 2.

Haque M D, Loresto G C, Chang T T, Tepora N (1989) A comparative study of rice root characters related to the mechanisms of drought resistance under aeroponic and hydroponic cultures. *SABRAO Journal* **21:** 111-122.

Henderson S A, Fukai S, Lilley J M, George D L, Cooper M, Wamala M H, Watiki J M, Villavicincio J N, Chinyamakobvu, E, Uaiene R, Ludlow M M (1993) Influence of water stress on leaf death among rice lines: comparison between glasshouse and field. Pages 220- 223 In: Proceedings of 7th Australian Agronomy Conference, Adelaide., ETU Publications.

Hsiao T C, O'Toole J C, Yambao E B, Turner N C (1984) Influence of osmotic adjustment on leaf rolling and tissue death in rice. *Plant Physiology.* **75:** 338-341.

Ingram K T, Real J G, Maguling M A, Obien M A, Loresto G C (1990) Comparison of selection indices to screen lowland rice for drought resistance. *Euphytica* **48:** 253-260.

Inthapan P, Fukai S (1988) Growth and yield of rice cultivars under sprinkler irrigation in south-eastern Queensland. 2. Comperison with maize and grain sorghum under wet and dry conditions. *Aust. J. Exp. Agr.* **28:** 243-248.

Lilley J M, Fukai S (1994a) Effect of timing and severity of water deficit on four diverse rice cultivars. I. Rooting patterns and soil water extraction. *Field Grops Res.* (submitted).

Lilley J M, Fukai S (1994b) Effect of timing and severity of water deficit on four diverse rice cultivars. 3. Phenological development, crop growth and grain yield. *Field Crop Res.* (submitted).

Loresto G C, Chaudhary W, Chang T T (1983) Acroponic technique for screening the drought avoidance mechanism of rice genotypes by the root characters. *Garcia de Orta Serie, de Estudos Agonomicos* **10:** 77-82.

Ludlow M M, Muchow R C (1990) A critical evaluation of the traits for improving crop yields in water limited environments. *Adv. Agr.* **43:** 107-153.

Ludlow M M, Santamaria F J, Fukai S (1990) Contribution of osmotic adjustment to grain yield of *Sorghum bicolor* (L. Moench) under water-limited conditions. II. Water stress after anthesis. *Aust. J.Agric.* Res. **41:** 67-78.

Malabuyoc J A, Aragon E L, De Datta S K (1985) Recovery from drought-induced desiccation at the vegetative growth stage in direct-seeded rainfed rice. *Field Crops Res.* **10:** 105-112.

Mambani B, Lal R (1983a) Response of upland rice varieties to drought stress. 1. Relation between root system development and leaf water potential. *Plant and Soil* **73:** 59-72

Mambani B, Lal R (1983b) Response of upland rice varieties to drought stress. 2. Screening rice varieties by means of variable moisture regimes along a toposequence. *Plant and Soil* **73:** 73-94.

Mambani R, Lal R. (1983c) Responsee of upland rice varieties to drought stress. 3. Estimating root system configuration from soil moisture data. *Plant and Soil* **73:** 95-104.

Maurya D M, O'Toole J C (1986) Screening upland rice for drought tolerance. Pages 245-261 In: Progress in upland rice research. Proceedings of the 1985 Jakarta Conference. IRRI, Los Baños, Laguna, Philippines.

Morgan J M (1991) A gene controlling diiferences in osmoregulation in wheat. *Aust. J. Plant Phys.* **18:** 249-257.

Muchow R D, Hanner G L. Carberry, P S (1991) Optimising crop and cultivar selection in response to climatic risk. Pages 275-262 In: Climatic risk in crop production: Models and management for the semiarid tropics and subtropics. R C Muchow and J A Bellamy Eds. C.A.B. International: Wallingford.

Nyquist W E (1991) Estimation of heritability and prediction of selection response in plant populations. *Crit. Rev. Plant Sci.* **10:** 235-322.

O'Toole J C (1982) Adaptation of rice to drought-prone environments. Pages 195-213 In: Drought resistance in crops with emphasis on rice. IRRI, Los Banos, Laguna, Philippines.

O'Toole J C (1989) Breeding for drought resistance in cereals: Emerging new technologies. Pages 81-94 In : Drought resistance in cereals. F W G Baker Editor, CAB International, Wall-ingford, Oxon, UK.

O'Toole J C, Cruz R T, (1980) Response of leaf water potential, stomatal resistance, and leaf rolling to water stress. *Plant Physiology*. **65:**428-435.

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

O'Toole J C, Moya TB (1978) Genotypic variation in maintenace of leaf potential in rice. *Crop Sci.* **8**:873-876.

OToole J C, Soemaratono (1981) Evaluation of a simple technique for characterizing rice root systems in relation to drought resistance. *Euphytica* **30:**283-290.

Patrick W H Jr, Wyatt R (1964) Soil nitrogen loss as a result of alternate submergenceand drying. *Soil Sci. Soc. Am.Proc.* **28**:647- 653.

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

Santamaria F J, Ludlow M M, Fukai S (1990) Contribution of osmotic adjustment to grain yield in *Sorghum bicolor* (L. Moench) under water-limited conditions. I. Water stress before anthesis. *Aust. J. Agric. Res.* **41**:51-65.

Shorter R, Lawn R J, Hanner G L (1991) Improving genotypic adaptation in crops-a role for breeders, physiologists and modellers. *Expt. Agri.* **27**:155-175.

Steponkus P L, Shahan K W, Cutler J M (1982) Osmotic adjustment in rice. Pages 181-194 In: Drought resistance in crops with emphasis on rice. IRRI, Los Banos, Laguna, Philippines

Tangpremsri T (1989) Physiological studies of the performance of sorghum genotypes under moisture limiting conditions. Ph D Thesis, The University of Queensland, Australia.

Turner N C, OToole J C, Cruz R T, Namuco O S, Ahmad S (1986a) Responses of seven diverse rice cultivars to water deficits. 1. Stress development, canopy temperature, leaf rolling and growth. *Field Crops Res.* **13**:257-271.

Turner N C, O'Toole J C, Cruz R T, Yambao E B, Ahmad S, Namuco, O S, Dingkuhn, M (1986b) Responses of seven diverse rice cultivars to water deficits. 2. Osmotic adjustment, leaf elasticity, leaf extension, leaf death, stomatal conductance and photosynthesis. *Fields Crops. Res.* **13**:273-286.

Yambao E G, lngram K T, Real J G (1992) Root xylem influence on the water relations and drought resistance of rice. *J. Expt. Bot.* **43**:925-932.

Yang C M, Chen C L, Sung F J M (1983) Water relations in rice: 1.Leaf diffusive resistance and osmotic adjustment of field-grown rice genotypes. Proceedings of the National Science Council, Part B, **7**:288-292.

Yoshida S, Hasegawa S (1982) The rice root system: its development and function. Pages 97-114 In: Drought resistance in crops with emphasis on rice. IRRI, Los Banos, Laguna, Philippines.

Wright G C, Smith R C G, McWilliam J R (1983) Differences between two grain sorghum genotypes in adaptation to drought stress. l. Crop growth and yield responses.. *Aust. J. Agric. Res.* **34**:615-666

VARIETAL CHARACTERISTICS AND SOIL MANAGEMENT TO REDUCE DROUGHT STRESS

☐ *H.U. Ahmed, M.L. Ali, S.K. Zaman,*
M.A. Kabir and N.M. Miah[1]

SUMMARY

The Rainfed Lowland Rice Research Consortium site in Bangladesh is located at northwest part, known as Barind Tract, which is characterized by low annual rainfall. Rice crop in this region often faces drought stress at reproductive phase. Soil is poor in organic matter with hard and thick (8.0 cm) ploughpan. Two hundred and fortyeight advanced breeding lines and varieties were screened and evaluated with respect to different plant characters under field condition to find out suitable varieties which can tolerate drought at later growth stages. Fortytwo advanced breeding lines were identified as drought tolerant, out of which two lines-BR4974-45-9-2 and BR4974-42-1-3 have deep rooting ability and can even penetrate such hard ploughpan and also produce higher grain yield than the local varieties under rainfed condition. Another line, IR41054-81-2-3-22 identified as early maturing was found to escape drought and produce about 30% more grain yield than the local popular early maturing variety. Soil management manipulation treatment for reducing the ploughpan thickness through deep tillage and ploughpan perforation through *dhaincha* (*Sesbania aculeata*) roots significantly increased grain yield and root mass of rice genotypes.

INTRODUCTION

About 36% of South and Southeast Asian rice growing areas come under rainfed lowland rice ecosystem (BRRI, 1992). Uncertainty characterizes rice farming in this ecosystem where it often suffers from drought, floods, pests, weeds and soil constraints, sometimes all in the same field and in the same season. Rainfall is erratic and other conditions for growing rice crop are diverse and unpredictable.

In Bangladesh, about 44% of total rice area is occupied by rainfed lowland rice (transplant aman), out of which about 50% is covered by high yielding varieties (HYV) developed by Bangladesh Rice Research Institute (BBS, 1992). Rest of the areas are still being covered with traditional varieties, characterized by low yield and photoperiod sensitivity enabling for late planting due to late recession of flood water and late harvesting of preceding aus and jute crops.

The existing HYV are not suitable for cultivation under unfavourable rainfed lowland situation and may suffer from drought, low temperature and soil stress at

---

[1] Bangladesh Rice Research Institute, Gazipur, Bangladesh

reproductive and ripening phases particularly when the crop is late planted. Therefore, steps are to be taken to develop varieties and associated technologies to overcome drought, low temperature and soil stresses.

Drought in rice is a real concern and a serious yield limiting factor on much of the world's 70 million hectares of non- irrigated rice (O'Toole and Chang, 1978). Lack of rainfall and the resultant soil moisture deficit form the basis of drought. To overcome drought stresses, plants develop some defensive mechanism such as stomatal closure, thick cuticle, leaf rolling, profuse, or deep and thick root system (O'Toole and Chang, 1978). Early maturity is also a way to escape drought stresses.

Extensive study is difficult to test all the above characters for a large number of varieties/lines. Field screening by visual scoring would appear to be an indirect means of screening for root system development (O'Toole and Chang, 1978). The percentage of filled grain on the panicle is a useful criteria in ascertaining reactions to reproductive phase drought. Proportional reduction in yield in a genotype due to stress acts as a indicator of drought resistance or susceptibilitiy (O'Toole and Chang, 1978). Plant height and panicle exertion is also an indication to resistance or susceptibility to drought. Root system plays an important role under water deficit conditions and the nature and extent of root development are major factors governing plants response to moisture condition (Russell, 1959). Haque *et al.,* (1988) also stated that selection based on root characters for drought resistance could be done in the early stage of growth. A thick and dense ploughpan layer restricts the rootzone volume of soil and hence reduces its moisture storage capacity.

The rainfed lowland rice research consortium site located in the 'Barind Tract' has a ploughpan at shallow depth (about 10 cm) which creates adverse conditions for root development of rice crop. The Barind tract receives less annual rainfall than most of the parts of Bangladesh (Fig. 1).

The distribution of rainfall is concentrated in a few months, from June to September (Fig.2).

Transplant aman often faces terminal drought stress. The soil in this area is also low in organic matter content, which adversely affects other soil properties (Table 1). Rainfall is the only source of water for crop growth because large scale irrigation is not possible due to undulating land scape and poor aquifers. To address some of these problems a number of experiments were conducted at the site from 1991 to 1993.

Experiment 1. Screening of advanced breeding lines for drought tolerance at reproductive phase under rainfed condition.

Materials and methods

Eighty seven advanced breeding lines/varieties in 1991, 62 in 1992 and 99 in 1993 were grown for screening reproductive phase drought tolerance. In 1991, twenty eight-day old seedlings were transplanted in two different sites- high and lowland situation at Alimganj and in irrigated plot at BRRI, Rajshahi station. Each entry had

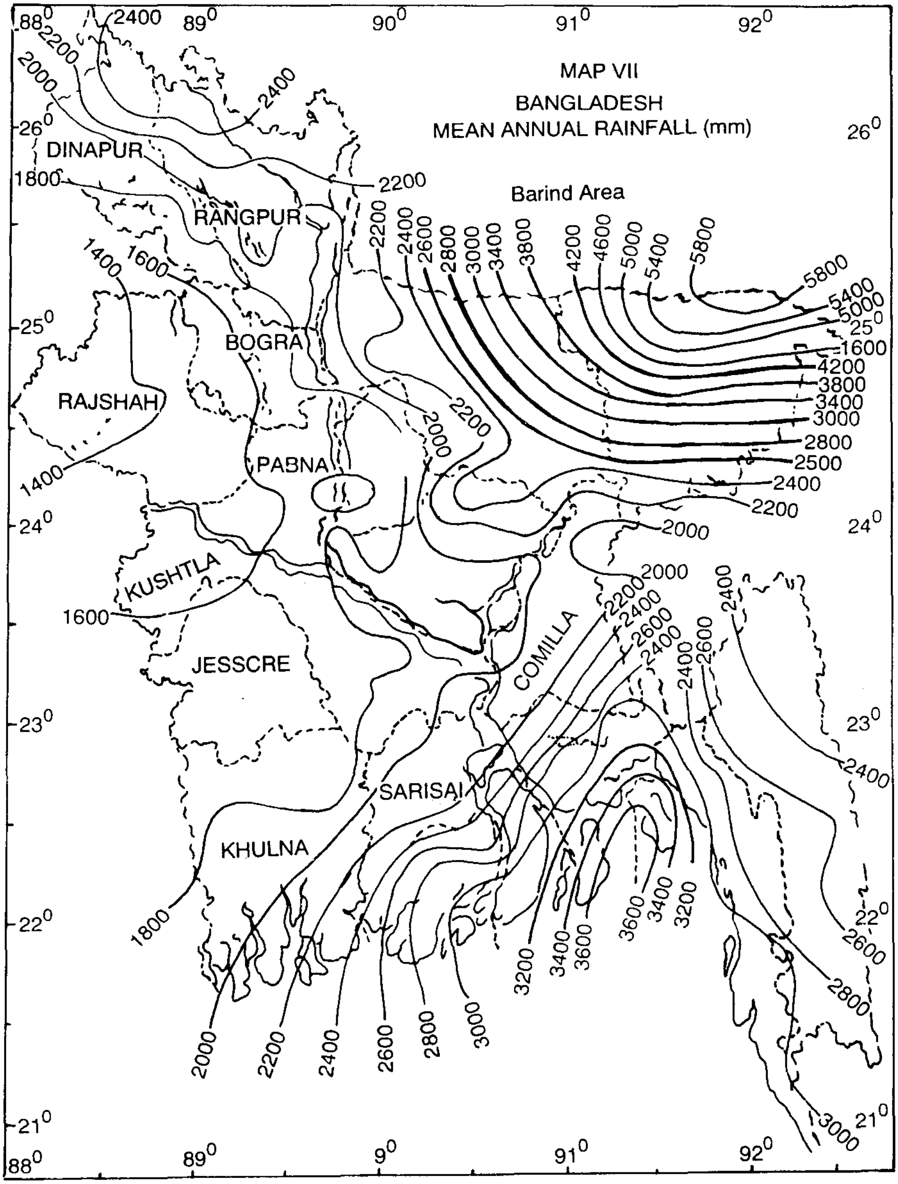


Fig. 1. Map of Bangladesh Showing Barind area and mean annual rainfall.

5m x 2 rows plot with three replications in RCB design having normal and late planting in all the three situations. In 1992, thirty-day old seedlings were transplanted in irrigated field and forty three-day old seedlings were transplanted in rainfed field each with 5m x 2 rows plot in three replications in RCB design only at BRRI, Rajshahi

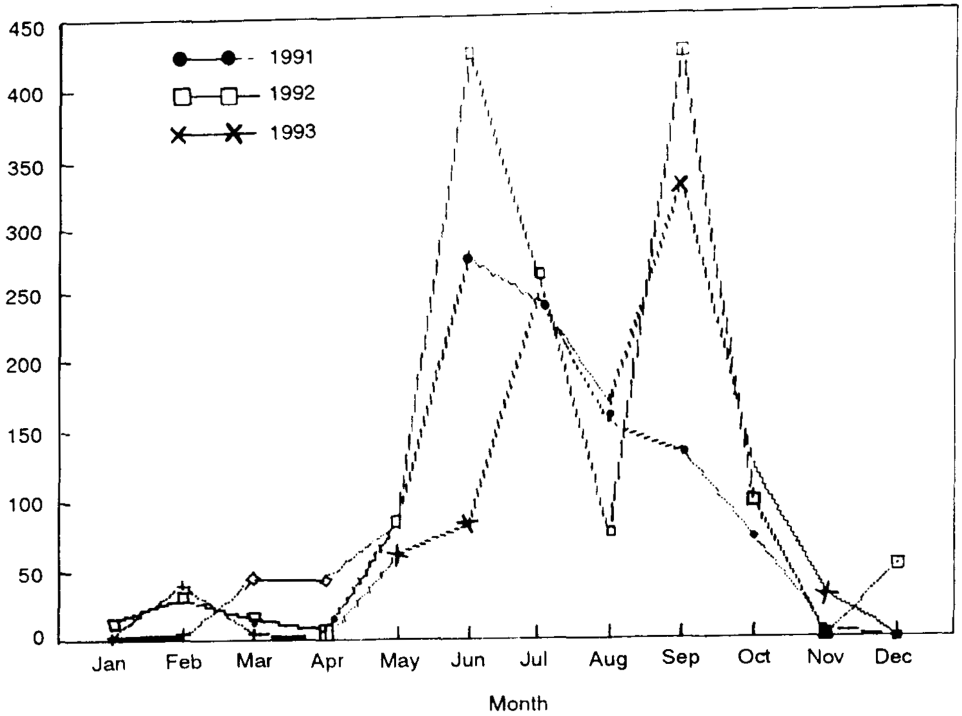


Fig. 2. Monthly rainfall, Alimganj, 1991-93

station. In 1993, thirty-day old seedlings were transplanted under rainfed condition in 4m x 2 rows plot at Alimganj with three replications following RCB design. The seeds were sown in late July to face the drought stress. Two-three seedlings were planted per hill at a spacing of 25 x 15 cm with a fertilizer dose of 80:60:40 kg NPK/ha for all three years. Total quantity of phosphorus and potassium were applied as basal. Nitrogen was applied in two equal splits- one at tillering stage and another at panicle initiation stage. Insect pests were controlled as and when necessary. Soil moisture content from 7th October to harvesting stage was also recorded (Fig. 3).

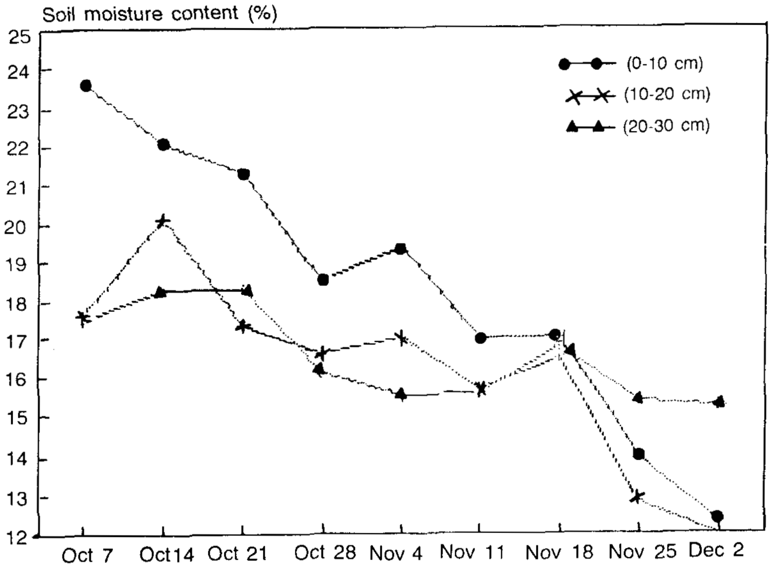


Fig. 3. Soil moisture content, Alimganj, 1993

Table 1 Physical and chemical properties of the experimental field at Alimganj. T.Aman, 1993.

Textural Class	**Silty Clay**
Sand (5%)	5.00
Silt (%)	51.00
Clay (%)	44.00
Water holding capacity (%)	57.00
Bulk density (g/cm^3)	1.58
Soil pH	5.8
Organic matter (%)	1.48
Total N (%)	0.056
Available P (ppm)	15.00
Exchangeable K (meq/100g)	0.23
Available S (ppm)	15.00
Available Zn (ppm) (01NHC1)	2.3
Cation exchange capacity (meq / 100 g)	15.00

Results and discussion

In 1991, twelve lines were selected on the basis of panicle exertion ratio and spikelet sterility percentage (Table 2a).

Table 2a. List of the advanced breeding lines selected for drought tolerance at reproductive phase. T. Aman, 1991.

Advanced lines	Pancile exertion ratio						Sterility percentage					
	Highland		Lowland		Irrigated		Highland		Lowland		Irrigated	
	1st set	2nd set	1st set	2nd set	1st set	2nd set	1st set	2nd set	1st set	2nd set	1st set	2nd set
BR4548-2B-70	0.955	0.869	1.005	0.885	1.010	0.946	20.24	34.17	19.24	31.72	20.17	28.39
BR2575-2B-62-1-1	1.022	0.928	1.088	0.868	1.155	0.937	38.49	69.95	23.37	42.30	28.34	71.00
BR4970-37-1-2	0.991	0.882	0.935	0.898	1.127	0.990	35.17	56.52	24.43	49.02	28.48	63.52
BR4970-107-2-6	1.036	0.960	1.094	1.033	1.058	1.138	35.42	55.12	36.34	45.40	34.79	39.37
BR4974-23-1-1	1.066	0.874	1.194	0.932	1.176	0.895	31.11	39.39	27.17	47.33	22.10	66.66
BR4974-45-9-2	1.079	0.874	1.188	0.999	1.261	1.051	39.52	40.20	44.45	41.20	3211	32.56
BR4548-2B-222	0.825	0.913	1.058	1.023	1.168	1.004	45.17	58.04	34.30	43.67	16.93	38.66
BR5437-2B-13-2	1.034	0.947	1.038	0.946	0.984	0.921	10.49	21.23	15.08	22.10	13.13	42.80
BR4974-13-2-9	0.884	0.862	0.941	0.896	1.104	0.805	34.92	72.48	44.42	54.61	21.19	97.28
BR5204-B-24	0.994	0.983	0.974	0.730	0.999	0.846	19.26	41.65	14.43	56.34	17.72	46.70
BR5323-B-52	1.055	0.843	1.075	0.944	1.104	0.930	27.32	41.82	20.62	31.18	16.24	25.22
BR1870-88-1-1	0.947	1.015	0.943	0.996	0.977	0.854	34.86	41.97	37.91	28.62	16.40	28.69
BR11	0.975		0.950		0.938		44.49		24.84		26.86	
BR22	0.894		0.833		0.873		48.19		54.58		22.06	
Nizersail	0.959		1.066		0.974		43.62		34.68		16.47	

	Normal planting	**Late planting**
Date of Seeding:	17.7.91	6.8.91
Date of Transplanting :	14.8.91	17.9.91

Month	**Temperature** **Minimum (range)°c**	**Maximum (range)°c**
October	19.0-25.5	25.0-35.0
November	10.0-19.0	26.0-30.5
December	7.5-13.5	17.2-28.0

All the twelve entries showed good panicle exertion both in the normal (1st set) and late planting (2nd set) in case of high land and low land situation compared to irrigated plot. The spikelet sterility of all the twelve entries of the normal planting (1st set) under high land, lowland and irrigated situations was lower compared to check entries. BR2575-2B-62-1-1, BR4974-23-1-1, BR5437-2B-13-2 and BR4974-13-2-9 showed exceptionally high spikelet sterility in the irrigated situation.

In 1992, twelve lines were selected on the basis of visual panicle exertion and visual fertility score under field condition (Table 2b).

Table 2b. List of the advanced breeding lines selected for drought tolerance at reproductive phase, T.Aman, 1992.

Advanced lines/ varieties	Plant height (cm)		Date of flowering		Panicle exertion score		Fertility score	
	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed
BR4761-3B-7-2	104	62	14/11	16/11	2	5	1	5
BR4761-3B-108-2	112	61	14/11	12/11	3	5	1	5
BR4764-3B-3-2	126	72	12/11	14/11	1	3	1	3
BR4972-92-1-3-1	100	56	12/11	14/11	1	5	1	5
BR4972-92-1-3-1	100	52	12/11	14/11	1	5	1	5
BR4761-3B-208-1	100	61	12/11	14/11	3	3	1	3
BR4761-3B-18-4	106	62	13/11	14/11	3	3	1	3
BR4961-3B-70	113	85	8/11	15/11	3	3	3	3
BR1192-2B-10-1-1	86	58	14/11	16/11	1	3	1	5
BR1867-26-3-1-1	92	63	13/11	16/11	3	3	1	3
BR850-22-1-4	88	68	10/11	11/11	3	5	1	3
BR4974-48-2-3	103	82	17/11	18/11	2	3	2	5
Nizersail (ck.)	94	78	12/11	14/11	1	3	1	3
BR22 (ck.)	85	63	12/11	14/31	3	3	1	3
BR23 (ck.)	83	51	14/11	16/11	5	5	5	5

Date of seeding 23-07-92 Date of transplanting Irrigated = 26-8-92; Rainfed = 08-9-92

Plant height and date of flowering were also considered. All the selected entries showed fertility score of 1, except BR4961-3B-70 and BR974-48-2-3 which showed score of 3 and 2, respectively, under irrigated conditions. However, fertility score under rainfed condition varied between 3 and 5 for all entries including checks.

Table 2c. List of the advanced breeding lines and varieties selected for drought tolerance at reproductive phase. T. Aman, 1993.

Advanced lines/ varieties	Plant height (cm)	Date of flowering	Panicle exertion score	Fertility score
BR4872-72-1-4-3-1	128.2	11/11	2	1
BR4872-72-1-4-3-3	141.6	11/11	1	1
BR5226-21-2–3-2	126.6	6/11	1	1
BR5296-29-1-7-2	119.2	16/10	1	1
BR5439-39-8-1	119.7	23/10	3	1
BR5800-9-1	124.2	31/10	1	1
BR1725-13-7-1-6	105.4	21/10	3	3
BR4974-2-6-1-3-1	143.2	30/10	1	3
BR5204-213-2-9	128.4	27/10	1	1
BR5226-21-6-3-3	122.2	30/10	1	1
BR5225-2-3-1-4	120.1	20/10	1	3
BR5323-B-73-2-2	141.8	25/10	1	1
BR5452-6-2-2	123.4	10/10	2	1
BR5455-16-1-1	130.4	22/10	2	1
BR5479-11-6-1	119.1	26/10	1	2
BR554-156-1-2-1-1-519	103.1	2/11	2	1
BR5226-5-4	125.0	3/11	2	1
BR830-22-1-4	106.4	2/11	2	1
BR11(ck.)	106.3	23/10	3	3
BR22(ck.)	114.3	7/11	3	3
Batraj (ck.)	130.4	3/11	2	1

Date of sowing : 3.7.93 Date of Transplanting : 25.7.93

In 1993, 18 lines were selected on the basis of visual panicle exertion and visual fertility score. List of the selected entries is presented in Table 2c. Most of the entries flowered earlier than BR22 (photoperiod sensitive modern variety). However, only three entries BR4872-72-1-4-3-1, BR4872- 72-1-4-3-3 and BR-5226-21-2-3-1 flowered at more or less same time with BR22. These three lines had better panicle exertion and fertility score than BR22 and assumed to have some degree of tolerance to drought stress at reproductive phase.

Experiment 2. Evaluation of selected advanced breeding lines for reproductive phase drought tolerance.

Materials and methods

Eighteen advanced breeding lines selected from the field screening for reproductive phase drought tolerance under rainfed condition in 1991 and 1992 wet season and three popular transplant aman varieties were included in this trial. Twenty five-day old seedlings were transplanted in a plot of 5m x 6 rows with a spacing of 25 x 15 cm using 2-3 seedlings per hill. Fertilizers were applied @ 80:60:40 kg NPK/ha. Total quantity of phosphorus and potassium was applied as basal and nitrogen was applied in two equal splits, one at tillering stage and another at panicle initiation stage as top dress. Insect-pests were controlled as and when necessary. The seeds were sown on 3rd July and transplanted on 28th July under both rainfed and irrigated conditions at Alimganj.

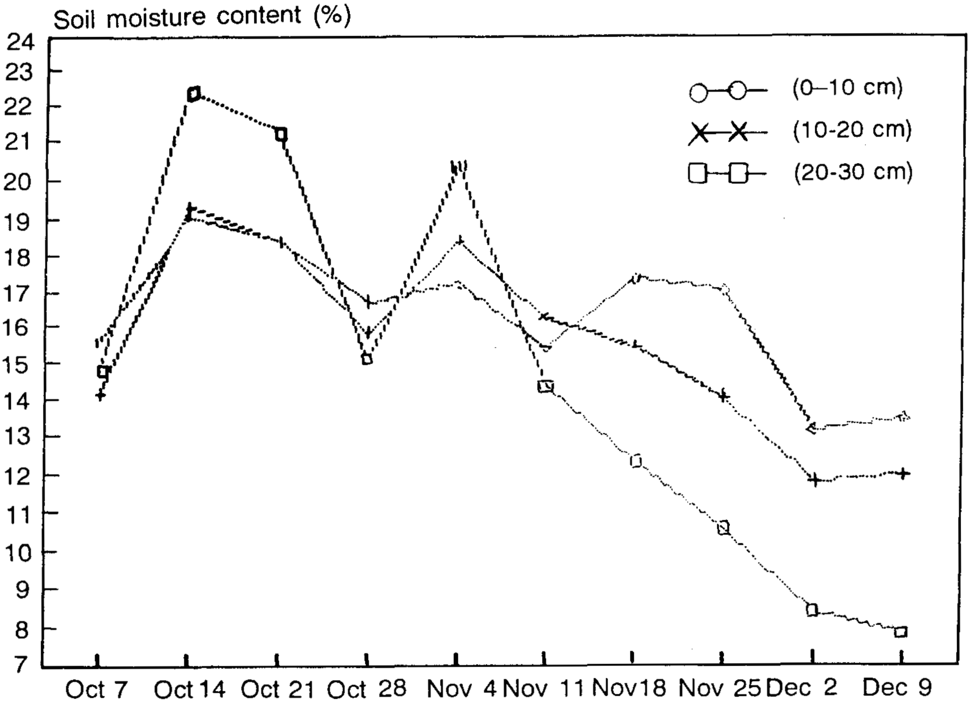


Fig. 4. Soil moisture content, Alimganj, 1993

Observations were recorded on plant height, phenotypic acceptability, date of flowering, panicle exertion, spikelet sterility, plot yield and root mass density upto 30 cm with an increment of 10 cm. Soil moisture content from 7th October to harvesting stage was also recorded (Fig. 4).

Results and discussion

Out of eighteen advanced lines, two lines viz. BR4974-42-1-3 and BR4974-45-9-2 were identified as promising with respect to tolerance to drought stress. These two lines showed better panicle exertion and lower spikelet sterility and had comparable yield with checks under irrigated condition and better yield under rainfed condition (Table 3). In respect of root mass density distribution, BR4947-42-1-3 had 3.78 % root within 10-20 cm depth and 0.81% below 20 cm keeping 95.41% root within 0-10 cm and BR4997-45-9-2 had 92.37% root at 0-10 cm depth, 6.22% at 10-20 cm and 1.41% at 20-30 cm soil depth (Table 4).

BR4764-3B-3-2, BR4761-3B-7, BR2575-2B-62-1-1, BR4970-47-1-6 and BR4974-23-1-1 have also good distribution of toot below 10 cm depth (Table 4) and presumed to have some degree of drought tolerance. Though the root distribution of BR4761-3B-7 was not so good but it gave good yield (3.35t/ha) under rainfed condition presumably due to physiological characters such as stomatal closure, thick cuticle, leaf rolling etc (O'Toole and Chang, 1978).

Experiment 3. Evaluation of photoperiod insensitive advanced breeding lines for early maturity.

Materials and methods

In 1992, eleven advanced breeding lines and one check (BR14) were grown in lowland situation at Alimganj. The experiment was conducted in RCB design with 3 replications. The plot size was 5m x 8 rows with spacing of 25 x 15 cm. In 1993, three advanced breeding lines were tested for early maturity. The experiment was conducted in RCB design with 3 replications under strictly rainfed condition at Alimganj in three different toposequences viz. high, medium and low. The plot size was 5m x12 rows in each toposequence with a spacing of 25 x 15 cm. Fertilizer dose was 80:60:40 kg NPK/ha for both the years. All phosphorus and potassium were applied as basal and nitrogen in two equal splits as top dress, one at tillering stage and another at panicle initiation stage.

Results and discussion

In 1992, out of 11 advanced lines, three lines namely, BR5363-10-2-1, BR5363-10-2-3 and IR41054-81-2-3-2 were selected on the basis of higher grain yield and early maturity (Table 5). These lines also matured earlier than the check variety, BR14.

The growth duration of all the three advanced lines ranged from 117 to 125 days in 1993 (Table 6). Varieties with such growth durations can easily escape drought and can be harvested in early November. Though yield differences between the toposequences were low, yet on the basis of yield, and phenotypic acceptability at maturity and growth duration compared to the checks (BR14 and Biharibatraj), IR54104-81-2-3-2 with an average yield of 3.83 t/ha having long slender grain was selected which can substitute BR14 in this region.

Table 3. Grain yield and some ancillary characters of advanced breeding lines selected for reproductive phase drought tolerance grown in T. Aman, 1993 at Alimganj.

Advanced lines	Plant height (cm)		Date of flowering		Pancile exertion ratio		Spikelet sterility		Yield (t/ha)		Phenotype acceptability at maturity	
	Irrig-ated	Rain-fed	Irrig-ated	Rain-fed	Irrig-ated	Rain-fed	Irrig-ated	Rain-fed	Irrig-ated	Rain-fed	Irrig-ated	Rain-fed
BR4761-3B-7	145	138	8/11	8/11	1.02	1.01	21	38	4.06	3.35	3	5
BR4761-3B-7	145	138	8/11	8/11	1.02	1.01	21	38	4.06	3.35	3	5
BR4761-3B-108-2	112	110	30/10	30/10	1.01	1.01	17	20	2.93	2.75	4	4
BR4761-3B-208-1	121	99	8/11	9/11	1.14	1.11	21	31	3.46	2.70	5	5
BR4761-3B-18-4	127	104	7/11	8/11	1.06	1.04	30	45	3.33	2.30	5	5
BR4764-3B-3-2	140	118	9/11	10/11	1.08	1.03	23	29	2.74	2.18	4	5
BR4972-92-1-3-1	124	113	6/11	5/11	1.10	1.07	24	31	3.25	2.63	5	5
BR4761-92-1-3-1	132	115	6/11	5/11	1.10	1.08	34	33	2.93	2.50	3	5
BR4761-38-70	149	124	7/11	6/11	1.06	1.05	36	25	2.27	2.12	3	4
BR1192-2B-101-1	148	122	9/11	6/11	1.03	1.01	29	37	2.88	2.43	3	4
BR1867-26-3-1-1	135	118	4/11	2/11	1.02	0.97	30	46	3.20	2.12	3	4
BR850-22-1-4	151	121	4/11	31/10	0.97	0.94	26	33	3.17	1.95	5	5
BR4974-48-2-3	131	110	7/11	4/11	1.02	0.99	22	26	3.55	3.50	3	5
BR2575-2B-62-1	117	105	7/11	4/11	1.07	1.06	24	27	3.66	2.13	5	5
BR4970-47-1-6	118	104	6/11	5/11	1.02	1.02	28	37	3.60	3.25	3	5
BR4974-23-1-1	140	115	3/11	4/11	1.06	1.03	34	28	3.55	2.95	3	5
BR4974-34-6-6	149	117	5/11	5/11	1.03	0.98	31	36	3.71	3.00	3	4
BR4974-42-1-3	154	117	4/11	4/11	1.03	1.01	27	32	4.26	3.48	3	5
BR4974-45-9-2	148	114	4/11	5/11	1.11	1.05	31	27	3.87	3.46	3	5
BR11 (ck.)	111	95	24/10	20/10	0.96	0.97	28	28	4.34	3.25	5	5
BR22 (ck.)	122	101	10/11	7/11	0.93	0.94	28	29	4.19	2.95	4	4
Niwrsail (L.ck.)	144	125	8/11	4/11	1.01	1.09	17	29	3.17	2.86	4	5

Date of sowing: 3.7.93 Date of Transplanting : 28.7.93

Table 4. Root weight and distribution pattern of some advanced lines selected for reproductive drought tolerance grown under rainfed condition, T. Aman, 1993 at Alimganj.

	Rootmass weight (mg/cm^3)			Distribution (%)		
	Soil layer (cm)			Soil layer (cm)		
Advanced lines	0-10	10-20	20-30	0-10	10-20	20-30
BR4761-3B-7	2.364	.033	.012	98.13	1.37	0.50
BR4761-3B-20-2	2.418	.041	.014	97.66	1.65	0.69
BR4761-3B-208-1	2.447	.059	.034	96.34	2.32	1.34
BR4761-3B-18-4	3.086	.049	.019	97.85	1.55	0.60
BR4764-3B-3-2	2.810	.087	.038	95.74	2.96	1.30
BR4972-92-1-3-1	2.345	.059	.024	96.58	2.43	0.99
BR4772-92-1-3-2	2.466	.044	.019	97.51	1.74	0.75
BR4761-3B-70	2.412	.095	.022	95.37	3.76	0.87
BR1192-2B-10-1-1	2.823	.067	.028	96.74	2.30	0.96
BRl867-26-3-1-1	2.973	.077	.022	96.78	2.51	0.71
BR850-22-1-4	3.115	.059	.016	97.65	1.85	0.50
BR4974-48-2-3	2.842	.051	.027	97.33	1.75	0.92
BR2575-2B-62-1-1	2.728	.075	.038	96.02	2.64	1.34
BR4970-47-1-6	2.435	.085	.019	95.90	3.35	0.75
BR4974-23-1-1	2.356	.063	.039	95.85	2.56	1.59
BR4974-34-6-6	2.772	.059	.038	96.62	2.06	1.32
BR4974-42-1-3	1.994	.079	.017	95.41	3.78	0.81
BR4974-45-9-2	1.961	.132	.030	92.37	6.22	1.41
BRll (ck.)	2.002	.063	.020	96.02	3.02	0.96
BR22(ck.)	3.133	.072	.012	97.39	2.24	0.37
Nizersail (ck.)	2.607	.057	.050	96.06	2.10	1.84

Experiment 4. Ploughing layer, ploughpan thickness, soil moisture and root distribution.

Materials and methods

A survey was done during 1st and 2nd week of November in 1991 when the rice crop was in milk to dough stage in Alimganj area to investigate the ploughpan depth and thickness in relation to root distribution at high and low toposequences.

Due to undulating landscape, sampling was done from high and low toposequences dividing each into 3 sites and from each site 10 sampling spots were chosen.

Table 5. Grain yield and some ancillary characters of the early maturing photoperiod insensitive breeding lines tested in Alimganj during T.Aman, 1992.

Advanced lines	Plant height (cm)	Panicle m/^{2}	Phenotypic acceptability at Veg.	Phenotypic acceptability at Mat.	Days to flow.	Days to mat.	Grain yield (t/ha)
BR5000-2B-6-1	143	188	5	6	100	127	2.0
BR5344-38-2-2	121	178	5	5	112	139	2.3
BR5363-10-2-1	105	244	4	5	92	119	3.6
BR5363-10-2-3	112	256	5	5	92	119	3.7
IR28941-1-3-5-1-2	82	224	4	6	106	132	2.9
IR38499-60-368-3-21-1	95	177	5	5	95	121	2.7
IR40931-26-3-3-5	106	194	4	5	107	133	3.2
IR41054-81-2-3-2	97	260	4	5	93	119	3.7
IR48776-10-2-1	104	246	4	5	93	120	2.3
B3894-40D-PN-5-1	109	204	5	3	97	124	2.9
B5986-MR-B-1-10	99	234	5	5	94	121	3.1
BR14(ck.)	102	234	4	4	96	124	3.8

Date of sowing : 10-7-92; Date of transplanting : 9-8-92

Results and discussion

The study revealed that the ploughpan depth ranged from 12.5 to 17.5 cm. The ploughpan thickness was 7.5 cm and 10.0 cm for low and high toposequences, respectively. On an average, maximum root weight ranged from 5.9-9.5 mg/cm^3 and major root distributions were found within 0-10 cm soil depth for both the toposequences (Table 7). The probable cause may be the shallow plough layer beneath which the hard ploughpan existed. More than 99% roots were confined to 0-10 cm soil layer. BR11 yielded the highest (4.5 t/ha), followed by Biharibatraj, Magursail, and Jhingasail. The yield of local varieties ranged from 2.5-3.0 t/ha.

Table 6 : Grain yield and ancillary characters of the early maturing breeding lines/varieites grown under rainfed conditions at alimganj, T. aman. 1993.

Designation	Plant height (cm)			Days of flowing			Growth duration days			Panicle			Accepta-bility		Yield (t/ha)			Ave. Yield (t/ha)
	H.	M.	L.	H.	M.	L.	H.	M.	L.	H.	M.	L.	Veg	Mat	H.	M.	L.	
BR5363-10-2-1	125	130	141	87	90	90	117	120	120	234	288	247	3	5	3.32	3.55	3.25	3.37
BR5363-10-2-3	127	128	131	90	93	94	120	123	124	221	275	241	3	5	2.89	3.28	3.88	3.35
BR41054-81-2-3-2	108	112	116	92	93	95	122	123	125	257	223	221	3	4	3.69	3.85	3.95	3.85
BR14 (Chek)	107	108	112	95	95	97	125	125	127	237	213	205	3	4	3.69	2.97	3.47	3.38
Bihari batraj (L. Check)	138	138	140	103	103	105	133	133	135	364	312	288	4	5	2.98	2.97	2.82	2.92

Date of sowing : 4.7.93; Date of transplanting : High land (H) : 27.07.93; Medium land (M) : 29.07.93; Low land (L) : 31.07.93

Experiment 5. Effect of Ploughpan management on the performance of rice under rainfed lowland situation.

Materials and methods

The experiment was conducted at Alimganj during T. aman, 1993. Four ploughpan manipulations were: i) control (undisturbed ploughpan or normal tillage, i.e. farmers practice of 6-8cm depth), ii) reduced ploughpan through deep tillage (12-15cm), iii) reduced ploughpan through deep tillage (18-20cm)and iv) ploughpan perforation through *dhaincha (Sesbania aculeata)* rooting with normal tillage. Three varieties, BR11, BR25 and Biharibatraj and two breeding lines-BR4974-45-9-2 and BR1870-88-1-11 were tested. The experiment was laid out in split plot design with 3 replications having ploughpan manipulation in the main plot and varieties/lines in the sub-plot. The unit plot size was 4 x 4m.

In the ploughpan perforation treatment, *dhaincha* seeds were sown on 23rd April, 1993 at the rate of 60 kg/ha and 90 days old *dhaincha* plants were harvested at ground level and removed from the experimental plot. Phosphorus, potassium and sulphur were applied at 25:35:20 kg/ha as basal. Nitrogen was applied at the rate of 80 kg/ha in 3 equal splits as top dress.

Table 7. Root weight and distribution pattern at different soil profile depths at Alimganj, Rajshahi, 1991 (mean of 10 spots for each site).

Site	Root weight (mg/cm^3)			% Distribution of root		
	Soil depth (cm)			Soil depth (cm)		
	0-10	10-20	20-30	0-10	10-20	20-30
			Low toposequence			
Site 1	5.94	0.031	0.004	99.41	0.52	0.52
Site 2	6.85	0.037	0.002	99.43	0.54	0.03
Site 3	9.48	0.063	0.002	99.32	0.66	0.02
			High toposequence			
Site 1	6.20	0.030	0.002	99.49	0.48	0.03
Site 2	6.51	0.042	0.001	99.34	0.64	0.02
Site 3	8.70	0.046	0.003	99.44	0.53	0.03

Twenty-five-day old seedlings were transplanted with a spacing of 20 x 20 cm, on July 30,1993. Cultural practices were done as and when necessary. Observations were taken on plant height, tiller number, grain yield, and root mass density upto 30 cm soil depth with 10 cm interval. Soil analysis was done by following the standard procedures.

Results and discussion

Ploughpan existed at 9 cm soil depth and continued upto 17 cm. The hard pan gradually developed due to excessive clay (50%) in the soil, terraced land type, puddling, for growing mono rice crop and shallow ploughing by country plough. Reduced ploughpan through deep tillage and ploughpan perforation through *dhaincha* root increased root mass over farmers practice in all the varieties and breeding lines (Table 8). Reduced ploughpan through *dhaincha* rooting treatment gave higher root mass at 10-20 cm soil depth in all the varieties/lines. More than 95% of root mass was confined to 0-10 cm soil layer.

Reduced ploughpan through deep tillage and ploughpan perforation through *dhaincha* roots significantly increased the grain and straw yield over farmers practices. The promising lines, BR4974-45-9-2 and BR1870-88-1-1 and BR11 produced identical yields (Table 9). Soil penetration resistance, measured after harvesting at different soil depths, was higher(2.0-2.25 kg/cm) in normal tillage plot than in the ploughpan manipulated plots at 10-15 cm soil depths. Its values reduced (0.75-1.0 kg/cm) in ploughpan manipulated plots through *dhaincha* rooting at 10-15 cm soil depth. (Table 10).

Table 8. Effect of plouhgpan management on the root mass density* (mg/cm^3) at flowering stage. Alimganj T. Aman, 1993.

Ploughpan management	Varieties**				
	V_1	V_2	V_3	V_4	V_5
	Soil depth 0-10 cm				
Farmer practice (6-8 cm) deep tillage	4.04	4.20	3.28	3.94	3.18
	(97)	(98)	(98)	(98)	(98)
Reduced ploughpan through (1215 cm) deep tillage	4.09	4.25	3.32	3.88	3.19
	(96)	(96)	(97)	(96)	(96)
Reduced ploughpan through (18-20 cm) deep tillage	3.38	4.16	3.32	3.95	3.03
	(95)	(95)	(97)	(95)	(95)
Ploughpan perforation through *dhaincha* rooting with farmer practice	4.10	4.32	3.45	4.05	3.26
	(95)	(96)	(96)	(96)	(96)
	Soil depth 10-20 cm				
Farmer pratice (6-8 cm) deep tillage	0.08	0.09	0.05	0.08	0.07
	(3)	(2)	(2)	(2)	(2)
Reduced ploughpan through (1225 cm) deep tillage	0.16	0.18	0.10	0.15	0.14
	(4)	(4)	(3)	(4)	(4)
Reduced ploughpan through (18-20 cm) deep tillage	0.21	0.23	0.12	0.21	0.16
	(5)	(5)	(3)	(5)	(5)
Ploughpan perforation through *dhaincha* rooting with farmer practice	0.23	0.22	0.14	0.14	0.15
	(50)	(5)	(4)	(4)	(4)

* Figures in parenthesis represents percent distribution.

** V_1 = BR 497445-9-2 ; V_2 = BR 1870-88-1-1; V_3 = BR 11; V_4 = Biharibatraj; V_5 = BR 25

Table 9. Effect of Ploughpan management on the yield (t/ha) of two promising lines and three rice varieties under drought prone environment. Alimganj, T. aman, 1993.

Ploughman management	V_1	V_2	V_3	V_4	V_5	Mean
			Grain Yield (t/ha)			
Farmer practice (6-8 cm) deep tillage	4.6	4.7	5.1	2.4	2.9	3.9
Reduced ploughpan through (12-15 cm) deep tillage	4.9	5.0	5.3	3.0	3.3	4.3
Reduced ploughpan through (18-20 cm) deep tillage	5.2	5.2	5.3	3.1	3.5	4.5
Ploughpan perforation through *dhaincha* rooting with farmer practice	5.3	5.2	5.6	2.7	3.5	4.5
Mean	5.0	5.0	5.3	2.8	3.3	
LSD (0.05)	0.63					
			Straw Yield (t/ha)			
Farmer practice (6-8 cm) deep tillage	5.9	5.4	5.8	5.1	4.5	5.3
Reduced ploughpan through (12-20 cm) deep tillage	6.1	5.8	5.7	5.2	3.9	5.5
Reduced ploughpan through (18-20 cm) deep tillage	6.1	5.9	6.0	5.9	4.8	5.7
Ploughpan perforation through *dhaincha* rooting with farmer practice	6.1	5.8	5.7	5.5	5.0	5.6
Mean	6.1	5.7	5.8	5.4	4.8	
LSD (0.05)	0.25					

* V_1 = BR 4974-45-9-2 ; V_2 = BR 1870-88-1-1; V_3 = BR 11; V_4 = Biharibatraj; V_5 = BR 25

Table 10. Soil penetration resistance (Kg/cm^2) as affected by ploughpan management at different depths. Alimganj, 1993

Ploughpan Management	Soil depth (cm)					
	5	10	15	20	25	30
Farmer practice (6-8) deep tillage	0.5	2.0	2.2	2.2	1.5	1.0
Reduced ploughpan through (12-15 cm) deep tillage	0.5	1.5	1.5	1.0	0.1	0.1
Reduced ploughpan through (18-20) cm deep tillage	0.5	1.0	1.5	1.0	0.5	0.7
Ploughpan perforation through *dhaincha* rooting.	0.5	0.7	1.0	1.2	0.5	0.5

REFERENCES

BBS (1992) Bangladesh Bureau of Statistics, Dhaka, Bangladesh.

BRRI (Bangladesh Rice Research Institute) (1992) regional station, Rajshahi research report for 1991 wet season, Rainfed lowland rice research consortium site at Rajshahi, Bangladesh.

Haque M E, Chang T T, Tepora N M, G C Loresto (1988) Root and shoot characters of rice (*Oryza sativa* L.) in relation to drought resistance aeroponic and hydroponic culture. *Bangladesh J. Plant Breeding and Genetics* 1 (l&2): 18- 25.

IRRI (International Rice Research Institute (1992) Challenges and opportunities in less favourable ecosystem: Rainfed lowland rice. IRRI information series no. 1, IRRI, Los Banos, Philippines.

O'Toole J C, Chang T T (1978) Drought and rice improvement in perspective. *IRRI Research Paper Series No.* 14.:IRRI, Los Banos, Philippines.

Manalo E B (1975) Agro-climatic survey of Bangladesh. The Bangladesh Rice Research Institute and the International Rice Research Institute.

Russell M B (1959) Water and its relation to soils and crop. *Advances in Agron.* **11** :1-122.

MODELLING THE SOIL-PLANT-WATER BALANCE OF RAINFED LOWLAND RICE

☐ *M.C.S. Wopereis[1], M.J. Kropff[2] and T.P. Tuong[2]*

SUMMARY

A soil-water balance module (PADDY) and a module predicting the response of rice to drought (DSTRESS) were developed and linked with a crop growth simulation model (ORYZA1) to simulate rice growth and production in rainfed lowland rice ecosystems. The combined PADDY-DSTRESS-ORYZA1 model (ORYZA-W) was validated using two field experiments in the Philippines. Measured and simulated changes in ponded water depth under flooded soil conditions were in good agreement. In one of the field experiments, temporary drought was induced at different stages. The model satisfactorily predicted change in root zone water content, leaf area index, total aboveground dry matter, and panicle dry weight across drought treatments over time. The model was subsequently used to predict rainfed rice yield as a function of soil hydraulic properties and long-term weather data (25 yr) in Tarlac Province of Philippines. Risk involved in growing rainfed rice was quantified by calculating yield probability distribution for seven major soil types under rice cropping. Coupling ORYZA-W to a GIS allowed a spatial analysis of risk in Tarlac Province.

INTRODUCTION

Process-based simulation models can be used as a tool to unravel some of the complexity and variability of rainfed lowland rice ecosystems. Such models allow detail analysis of experimental data, or extrapolation of research findings to other environments.

Quantifying the responses of rice to drought stress is essential for predicting the impact of soil and weather conditions on rice production. For lowland rice, grown in puddled soils, there is little information on the link between soil-water status and crop response, although drought is generally seen as a major cause of yield loss in rainfed rice production system. Existing rice growth simulation models use standard drought stress responses often derived for other crops.

The man-made puddled layer in lowland rice soils is often effective reducing water loss through percolation to deeper soil layers. The effect of puddling on the

---

[1] Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, The Netherlands

[2] International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines.

hydraulic conductivity of the various layers is, however, not well understood. Drying of previously submerged rice soils creates cracks that may extend through the plow sole at the bottom of the puddled layer. This can cause a drastic and often irreversible increase in water losses due to increased percolation rates. Existing soil-water balance modules do not consider such changes and are not directly applicable to puddled rainfed lowland rice soils.

A new soil-water balance module, PADDY, and a 'drought stress' module, DSTRESS, were developed and coupled to the model ORYZAI, (Kropff *et al.,* 1993; IRRI, 1993) for use in rainfed ecosystems. The combined ORYZAI-DSTRESS-PADDY simulation model (ORYZA-W) was validated using two experiments conducted at IRRI in 1991 and 1992, and used to predict rainfed rice yield on a regional scale for a province in the Philippines.

MATERIALS AND METHODS

The crop simulation model ORYZA1 is documented elsewhere (Kropff *et al.,* 1993). Input requirements for ORYZA1 are :

- Geographical latitude ;
- Daily data on solar radiation and minimum and maximum temperature ;
- Plant density ;
- Date of crop emergence or transplanting ; and
- Parameters describing the morphological and physiological characteristics of the rice variety.

In water-limited environments, water availability, light, and temperature determine the crop growth rate (provided no nutrient limitations occur). Wopereis (1993) derived functions that describe a number of physiological and morphological responses of the rice crop to soil-water content of the root zone. These functions were incorporated in the module DSTRESS. The module PADDY was developed to predict the soil-water status of a puddled root zone. Both modules are described in detail below. The linkage between ORYZAI, PADDY, and DSTRESS is illustrated in Figure 1. PADDY and DSTRESS are written in FORTRAN and make use of the Fortran Simulation Environment (van Kraalingen, 1991). A detailed user's manual for ORYZA-W is in preparation.

Description of *PADDY*

An irrigated puddled soil profile consists of a muddy layer with little resistance to water flow, a less permeable plow sole and, the non puddled subsoil. The muddy layer gradually increases in bulk density with depth but is treated here as a uniform layer. In PADDY, it is assumed that the first two layers of the soil profile comprise the muddy layer and the plow sole, respectively. Time step of integration in PADDY is 1.

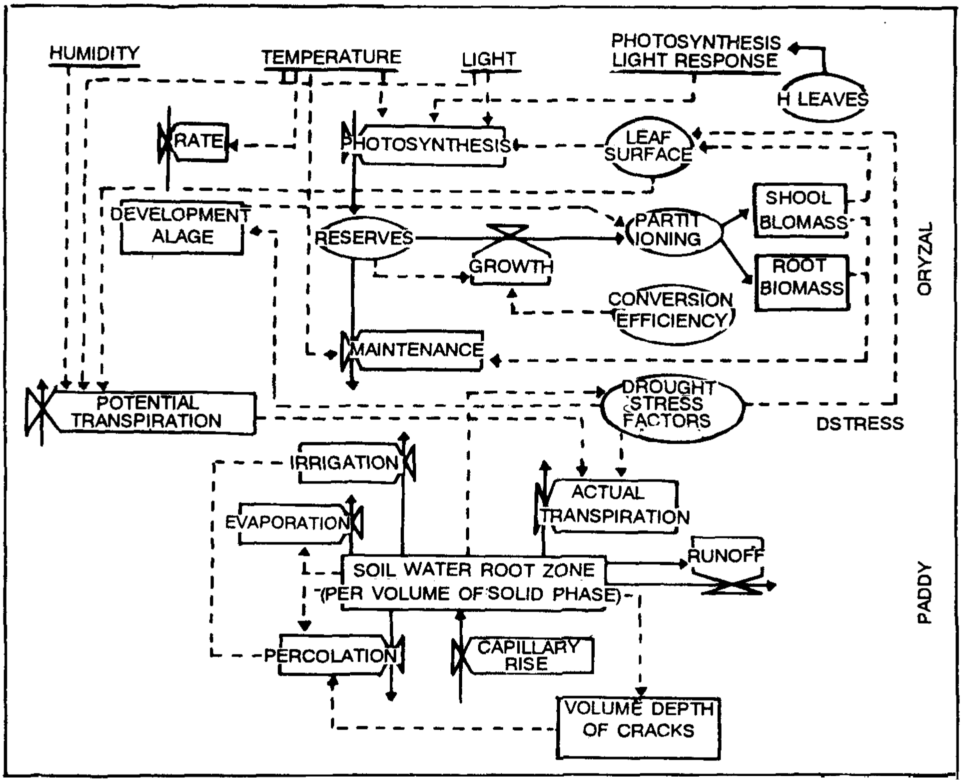


Fig. 1 : Linkage between the modules ORYZA1, PADDY, and DSTRESS

In PADDY, precolation rate can either be an input or can be calculated using an iterative Newton-Raphson Procedure (Wolfram, 1991) comparing fluxes through the plow sole and nonpuddled subsoil. Capillary rise is calculated based on integration of the Darcy equation for steady, upward, vertical flow (Gardner, 1958). Capillary rise can be ignored if the groundwater table is sufficiently deep, or if roots have not reached the nonpuddled subsoil (see for details Tuong *et al.,* 1993). The potential rates of evaporation from soil and water and crop transpiration with soil background (dry field) or water background (wet field) are derived from the Penman reference evapotranspiration calculated from daily weather data (vapor pressure, temperature, wind speed) using a Penman type equation (Penman, 1948). Actual transpiration rate is estimated from the potential transpiration ratg and a drought stress factor calculated by DSTRESS, described below. Actual evaporation rate from soil is calculated by assuming that cumulative evaporation is proportional to the square root of time (Stroosnijder, 1982). The rate on the first day is assumed to be 60% of potential soil evaporation. In reality, puddled clay qoil will probably dry out faster because of the rapid appearance of shrinkage cracks, which may increase the evaporation surface to more than double in a puddled clay soil (Fujioka and Sato ,1986). This aspect has not been taken into account in PADDY.

The continuous drying of a puddled clay soil results in shrinkage cracks and subsidence of the soil surface. To simulate cracking of the puddled root zone, knowledge of the soil's shrinkage characteristic is needed (Fig. 2), where moisture ratio v is defined as the volume of water V_w over the volume of the solid phase Vs, and void ratio e is defined as the volume of pores Vp over the volume of solid phase. The shrinkage characteristic is used to calculate the volume of pores per volume of soil (e, m^3/m^3), the volume of water per volume of soil (q, m^3/m^3), the subsidence of the puddled soil surface, and the change in crack volume (Bronswijk, 1988). It is assumed in PADDY that shrinkage is irreversible and that the puddled muddy topsoil gradually regains structure, a process that usually is referred to as 'soil ripening'. Total porosity e therefore, declines upon drying and will not increase if the water content of the root zone increases. In PADDY, cracks are assumed to have penetrated through the plow sole if its simulated moisture ratio drops below 1.2, which for IRRI soil is equivalent to a soil pressure potential *h* of - 100 kPa (IRRI, 1992).

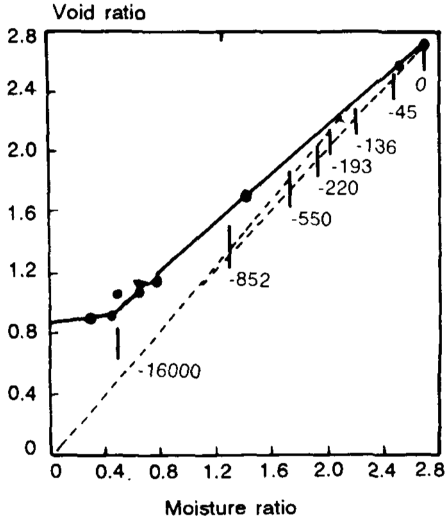


Fig. 2. Soil shrinkage characteristic of a puddled clay soil. Values in diagram indicate soil pressure heads (cm).

If soil cracks have not yet reached the plow sole, it is assumed that all incoming water is used to replenish the first soil compartment but that cracks will not close. During this phase the percolation rate is zero. As soon as the water content of the top compartment has reached saturation, water starts ponding again and the percolation rate will be governed by the hydraulic conductivity of the plow sole. The amount of water that can be stored in the top compartment is calculated taking into account the changes in volume and porosity of the top compartment due to cracking. If cracks are deep enough to reach the plow sole (i.e.h<–100 kPa), all water in excess of field capacity will be drained from the top compartment. Because of the soil ripening process, the conventional field capacity concept (i.e. volumetric water content at h=-10 kPa) is hard to use for puddled soil conditions. The field capacity water content of the topsoil was, therefore, defined as 95% of total porosity. For the nonpuddled subsoil, the conventional definition for field capacity was used. In PADDY, water that drains from the cracked root zone will fill up soil layers below the root zone up to field capacity. Any excess water will be drained at a maximum rate equal to the saturated hydraulic conductivity of the subsoil horizon. The water content of soil compartments below the groundwater table depth is reset to saturation.

The required data for PADDY are :

* Saturated soil-water content of puddled topsoil;
* Saturated soil-water content of ripened topsoil and nonpuddled subsoil;
* Soil-water content at wilting point of the nonpuddled subsoil (h= -1.5 MPa);
* Soil-water content at field capacity of the nonpuddled subsoil (h=-10 kPa);
* Saturated hydraulic conductivity of the plow sole, or infiltration rate;
* Hydraulic conductivity characteristics of the subsoil (if groundwater table is relatively deep, or if roots cannot reach the subsoil because of a plow pan, capillary rise can be ignored and only the saturated hydraulic conductivity of the subsoil is needed);
* Groundwater table depth throughout the growing season (usually average groundwater table depths will be used);
* Soil shrinkage characteristics of puddled topsoil and nonpuddled subsoil (optional; if not available, default values will be used).

Description of ***DSTRESS***

DSTRESS is largely based on data from a greenhouse experiment conducted at IRRI in the dry season (December - May) of 1992. In this experiment, the response of lowland rice cultivars IR20 and IR72 grown in puddled clay soil to temporary drought at different growth stages (transplanting, 2 wk after transplanting, mid-tillering, panicle initiation, and flowering) was studied. Morphological responses (inhibition of leaf production, leaf rolling, appearance of dead leaves) and physiological responses of the crop (reduction in transpiration rate and decrease in development rate) were expressed as a function of soil moisture ratio of the root zone. A similar approach was taken by Sinclair (1986) and McCree and Fernandez (1989). During the experiment, the degree of leaf rolling was visually examined daily at midday using a leaf rolling scale (1-5). A leaf score of 1 indicates the fipst sign of leaf rolling, whereas a score of 5 means that the leaf has completely rolled up (after O, Toole and Cruz, 1980). The experiment was repeated in the 1992 wet season. For reasons of brevity, only results from the drought at mid-tillering treatment conducted in the dry season are reported here (Fig. 3).

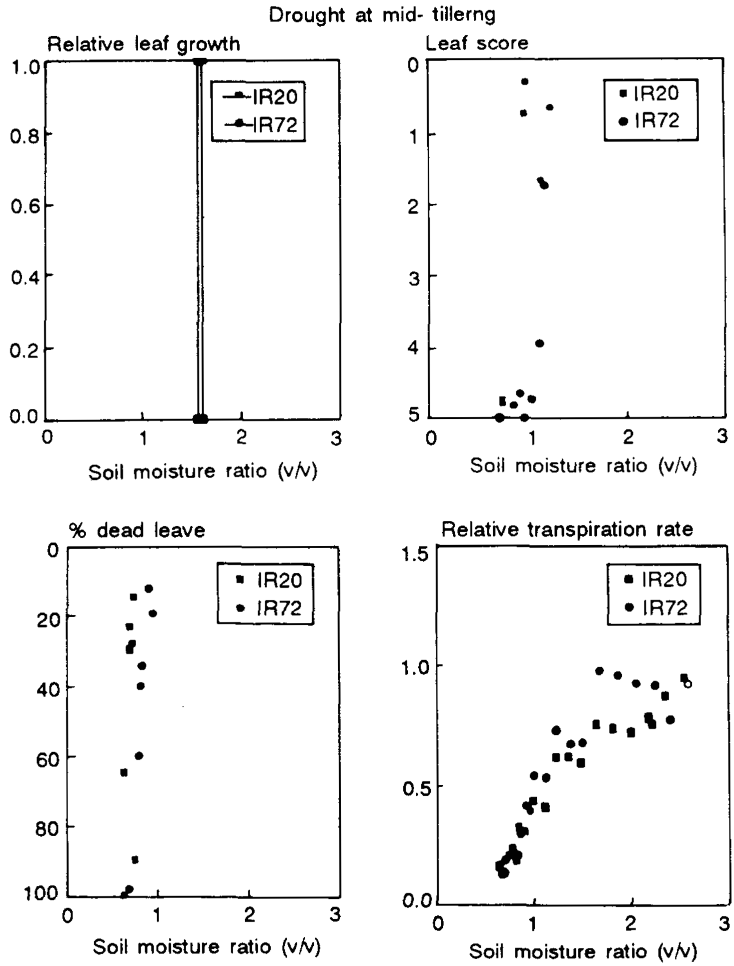


Fig. 3 . Relationships between soil moisture ratio (cm^3/cm^{-3}) and (a) relative leaf growth, (b) leaf score, (c) % dead leaves, and (d) relative transpiration rate in a greenhouse experiment conducted at IRRI in the dry season of 1992 (from Wopereis, 1993).

Relative leaf growth (defined as the ratio between the leaf growth of stressed plants and that of well-watered plants) decreased rapidly from 1 to 0 if soil moisture ratios dropped below 1.7, i.e. leaf expansion of plants subjected to drought stopped (Fig. 3a). Leaf rolling started at lower moisture contents, and leaf rolling score increased from 1 to 5 within a relatively narrow range of soil moisture ratios (Fig. 3b). As drought progressed, the percentage of dead leaves increased rapidly as well (Fig. 3c). Both leaf rolling score and percentage of dead leaves were linearly related to soil moisture ratio. Transpiration rate per unit of area of plants subjected to drought (T_d) remained equal to that of well-watered plants (T_w), even if soil-water status dropped nearly 50%. As soil-water content declined further, a decrease in relative transpiration rate (defined as T_d/T_w) was observed (Fig. 3d). Well-watered plants and plants that were temporarily stressed in the vegetative phase did not differ significantly in yield for either cultivar. However, flowering and maturity were strongly delayed. Severe drought in the reproductive phase greatly reduced yields. The following morphological and physiological plant responses to drought were quantified for the different growth stages : a) inhibition of new leaf production, b) leaf rolling, c) leaf senescence, d) decrease in relative transpiration, and e) decrease in development rate in the vegetative stage. Responses a, b, and c followed each other more or less sequentially, whereas response d) started at roughly the same soil-water content as response a) and declined to zero when leaves were dead (end of c) (Fig.3).

The effect of drought stress on development rate in the vegetative phase (e) could not be directly measured and is therefore not shown in Figure 3. In DSTRESS, the development rate in the vegetative phase used in ORYZA1 (Kropff *et al.,* 1993) is multiplied by a factor that increases from 0 to 1 between transplanting and flowering. This means that the closer the development stage is to flowering, the smaller the postponement effect. No delay in growth is simulated if drought occurs in the reproductive phase.

In the greenhouse study, production of new leaves was strongly inhibited than dative transpiration per unit leaf area during drought periods in the vegetative phase. This means that CO_2 assimilation continues, but the C produced cannot be used for leaf production. In DSTRESS, excess C is stored in a pool and released for leaf production as soon as drought stress is released. The 1992 dry season experiment was repeated in the 1992 wet season.

Model validation

The ORYZA-W model was tested for flooded soil conditions using data from a field experiment conducted at IRRI in the 1991 dry season (cv IR72) and described in detail by Wopereis *et al.* (1994) and Bouman *et al.* (1994). Input variables were rainfall, irrigation, evapotranspiration rate from daily weighing of pots installed in the field, and groundwater table depths measured using piezometers. Average and upper and lower extreme values for measured hydraulic conductivity of the plow sole and the non puddled subsoil were used. Simulated and observed changes in ponded water depth were compared.

For nonflooded soil conditions, the ORYZA-W model was tested using data from a second experiment (field experiment 2) conducted in the 1992 dry season on a 2,000 m^2 field (cv IR72). Four drought treatments in four replications were tested in a randomized complete block design in 10 x 5 m subplots. These subplots were separated by bunds and hydraulically isolated by plastic sheets placed 0.6 m into the soil. Prior to the start of the experiment, all plots were submerged for 10 d, then plowed three times and harrowed three times using a water buffalo.

Drought was initiated at transplanting (T1), at mid-tillering (T2), at panicle initiation (T3), or during the grain filling stage (T4) by simply draining the ponded water from the plots. For comparision, a well-watered treatment was included (T0). Two drought durations (D) were imposed based on the 1-5 leaf rolling scale of O'Toole and Cruz (1980). For Dl, plots were rewatered to allow plant recovery from drought when leaves showed initial leaf rolling (leaf score = 1). For D2, plots were rewatered when leaves showed clear sign of leaf rolling (leaf score = 3).

All simulations were conducted using parameters obtained from the 1992 dry season experiment with IR72 reported in Kropff *et al.* (1993), except for the development rates of the vegetative and reproductive phase and leaf N concentration as a function of time, which were derived from the well-watered TO plots.

Model application

The ORYZA-W model was used to predict rainfed rice yield for the wet season (June-November) in the Province of Tarlac which is located in the northern part of the Philippines on the island of Luzon (Fig. 4). It covers an area of approximately 300, 000 ha and comprises 17 municipalities with a total population of about 740, 000 (BSWM, 1992).

A soil map of Tarlac Province (1:50, 000), which was provided by the Bureau of Soils and Water Management, Quezon City, Philippines, was digitized using the geographic information system (GIS). The total number of mapping units was reduced from 67 to 14 through generalization taking into account similarity in soil properties and importance of the unit in terms of surface area. A similar approach was taken by Bregt *et al.* (1989).

As a first qualitative step, soil unsuitable for rice growth, which included the mountainous area and light-textured soils, were eliminated from the analysis. However, light textured soils classified on the soil map as ‘severely flooded’ because of their proximity to a river were not excluded; it was assumed that rice grown on such soils does not suffer from drought stress. Simulations were conducted for potentially suitable soils only. Potential (irrigated) rice yield was simulated using the model ORYZA1 for 25 yr of weather data derived from a meteorological station in the center of the province.

Water-limited (rainfed) rice yield for the same set of 25 yr was simulated using the ORYZA-W model. Guided by the detailed soil map representative profiles for major soil type under rice cropping were located. The soil hydraulic properties needed in ORYZA-W were determined for all soil horizons in each representative profile. Procedures and results of these measurements are presented elsewhere (Wopereis *et al.,* 1993). Crop parameters for rice cultivar IR72 were derived from a wet-season experiment conducted at IRRI in 1991 (Kropff *et al.,* 1993). Simulations started at transplanting, assuming that seedlings were 30 days old. Initial leaf area index (LAI), temperature sum (sum of thermal units over a base temperature), and development stage of the seedlings were taken from field experiment 2. Initial rooting depth was assumed to be 0.05 m. After discussion with an expert from the Bureau of Soils and Water Management, Quezon City, Philippines (W. Sanidad, pers. commun.), transplanting of rice was assumed to start when cumulative rainfall exceeded 75 mm during seven consecutive days after 1 June. Thickness of the puddled topsoil was set to 0.15 m with the plow sole occurring between 0.15 and 0.20 m depth. At transplanting, the puddled topsoil was assumed to be saturated with an initial ponded water depth of 0.05 m. Subsoil horizons were assumed to be at field capacity (h= -10kPa).

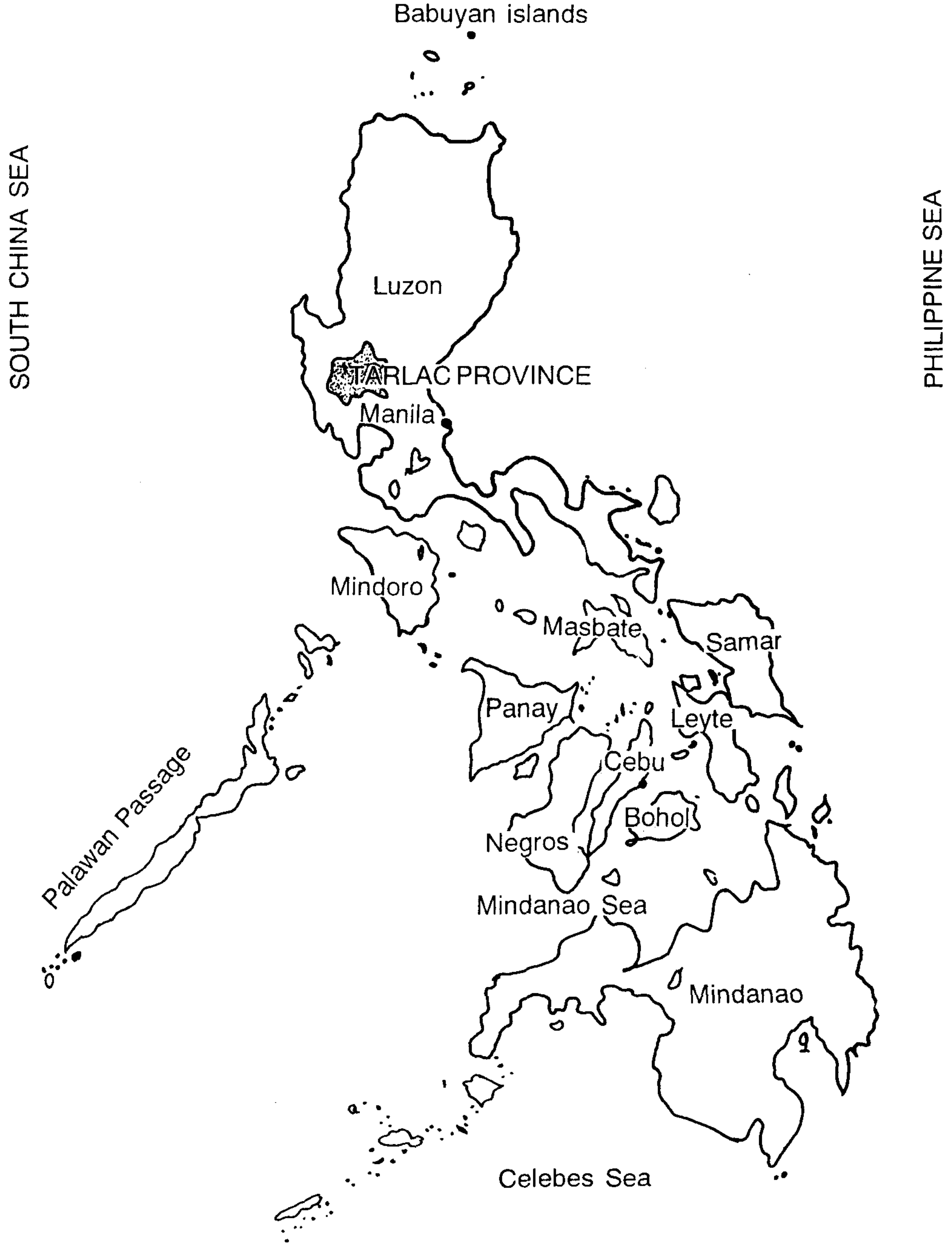


Fig. 4. Location of the Province of Tarlac in the Philippines.

The impact of groundwater table depth and thoroughness of puddling on rainfed rice yield was investigated for each of the major soil types under rice cropping. Groundwater table depth was varied between 0.5 and 1.0m. Wopereis *et al.* (1992) determined the saturated hydraulic conductivity of the least permeable layer (i.e. plow sole) in the top 0.2 m of a puddled clay soil at the experimental farm of the International Rice Research Institute. Average value was 0.036 cm/d, with 95% confidence limits at 0.027 and 0.045 cm/d. In this study, two classes of puddling (poorly puddled and well puddled) were considered and expressed in terms of the hydraulic conductivity k_s of the plow sole: well puddled, K_s (plow sole) = 0.01 cm/d and poorly puddled K_s (plow sole) = 0.10 cm/d. Combined with the two water table depths, four simulation series were created:

1 : K_s plow sole=0.01 cm/d; water table depth = 0.5m

2 : K_s plow sole=0.01 cm/d; water table depth = 1.0m

3 : K_s plow sole=0.10 cm/d; water table depth = 0.5m

4 : K_s plow sole=0.10 cm/d; water table depth = 1.0m

Probability distributions of rainfed rice yield for all soil types under rice cropping were estimated. Maps of simulated rainfed rice yield at different levels of cumulative probability were produced using the GIS software.

RESULTS AND DISCUSSION

ORYZA-W validation

The water balance module PADDY accurately predicted the changes in ponded water depth for field experiment 1 (Fig. 5). Wopereis *et al.* (1993) tested the more

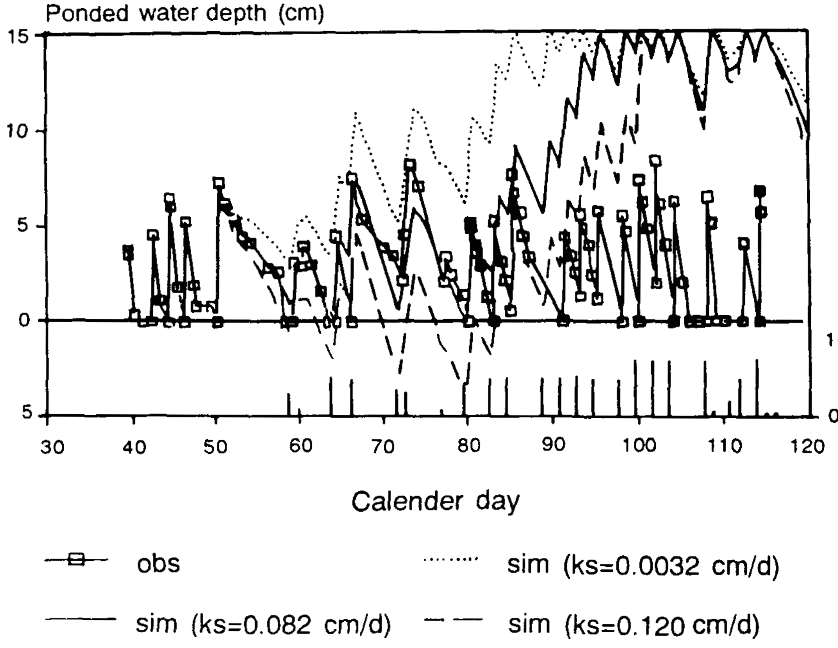


Fig. 5. Simulated and observed changes in ponded water depth in field experiment 1 using soil-water balance module PADDY.

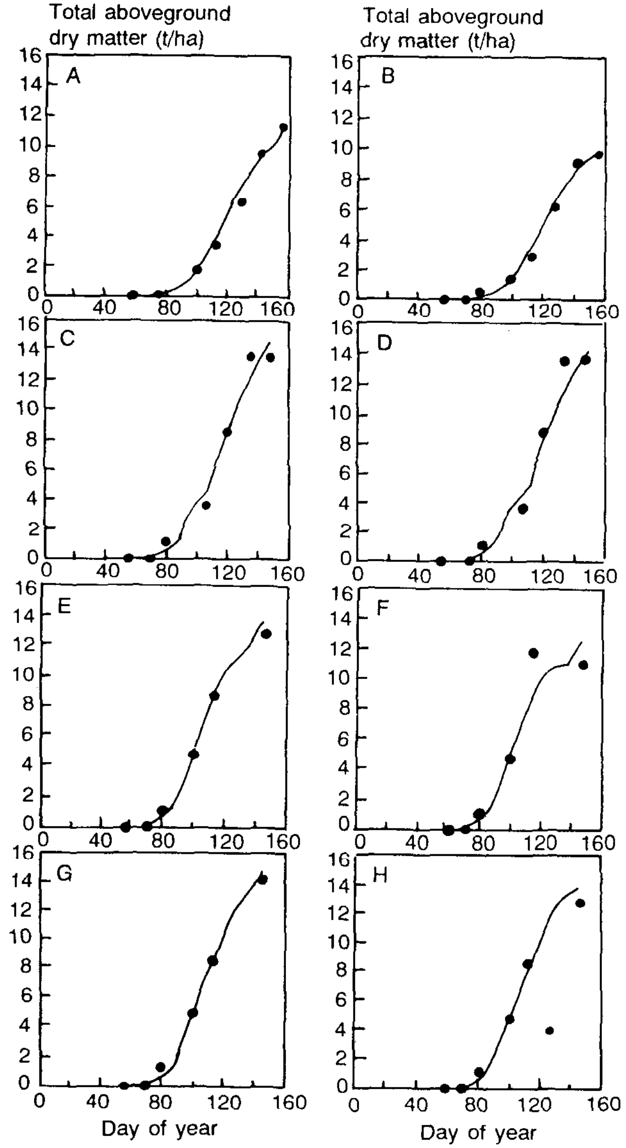


Fig. 6. Simulated (lines) and observed (symbols) total dry matter weights (t ha^{-1}) for cv. IR72 in field experiment 2 for all drought treatments : A is drought at transplanting, early recovery; B at transplanting, late recovery; C at mid-tillering, early recovery, D at mid-tiliering, late recovery; E at panicle initiation, early recovery; F at panicle initiation, late recovery; G at flowering, early recovery; H at flowering, late recovery.

complicated differential SAWAH soil-water balance module (ten Berge *et al.,* 1992) using the same field data. Results from this study showed that the iteration procedure used in PADDY to calculate the flux through the soil profile under flooded soil conditions was as effective as the small time step calculations used in SAWAH. The observed and simulated total above ground matter (Fig. 5), LAI, panicle dry weight, and root zone water content (Fig. 6) were compared. The results indicated that ORYZA-W could satisfactorily explain the differences in biomass production and soil water content across drought treatments, although for root zone, water content predictions were less good at severe stress and for drought at flowering.

Tarlac simulations

Potential yields in Tarlac Province varied from 5.4 to 6.7 t/ha (Fig.7), which are considerably higher than the irrigated rice yields (2.5-3.5 t/ha) reported by BSWM (1992). This discrepancy may be due to a number of factors, e.g. lack of fertilizer, incidence of pest and diseases, etc. that wen' taken into account by the ORYZA-W model.

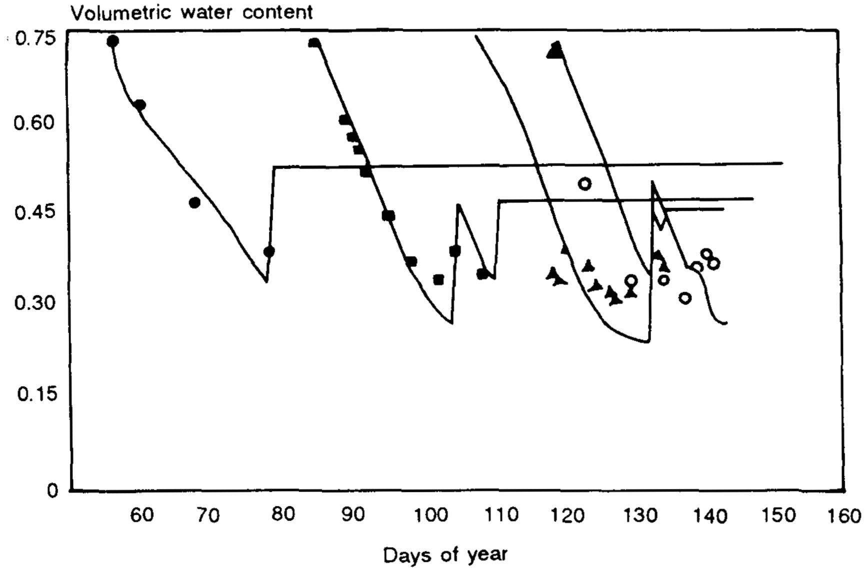


Fig. 7. Simulated (lines) and observed (symbols) soil water content m^3/m^{-3} for cv. IR72 in field experiment 2 for drought at transplanting (0-5 cm, late recovery, closed circles), drought at mid-tillering (0-10 cm, late recovery, squares), drought at panicle initiation (0-10 cm, late recovery, triangles), and drought at flowering (0-1 0 cm, no recovery, open circles).

Rainfed rice yields ranged from 0 to 6.7 t/ha. For reasons of brevity, the variability of rainfed rice yield over 25 years for the four simulation series is shown in Fig. 8 for two distinct soil types only : Zaragoza clay loam (light texture) and Padapada clay soil series (heavy texture). Potential yields are also shown for comparison.

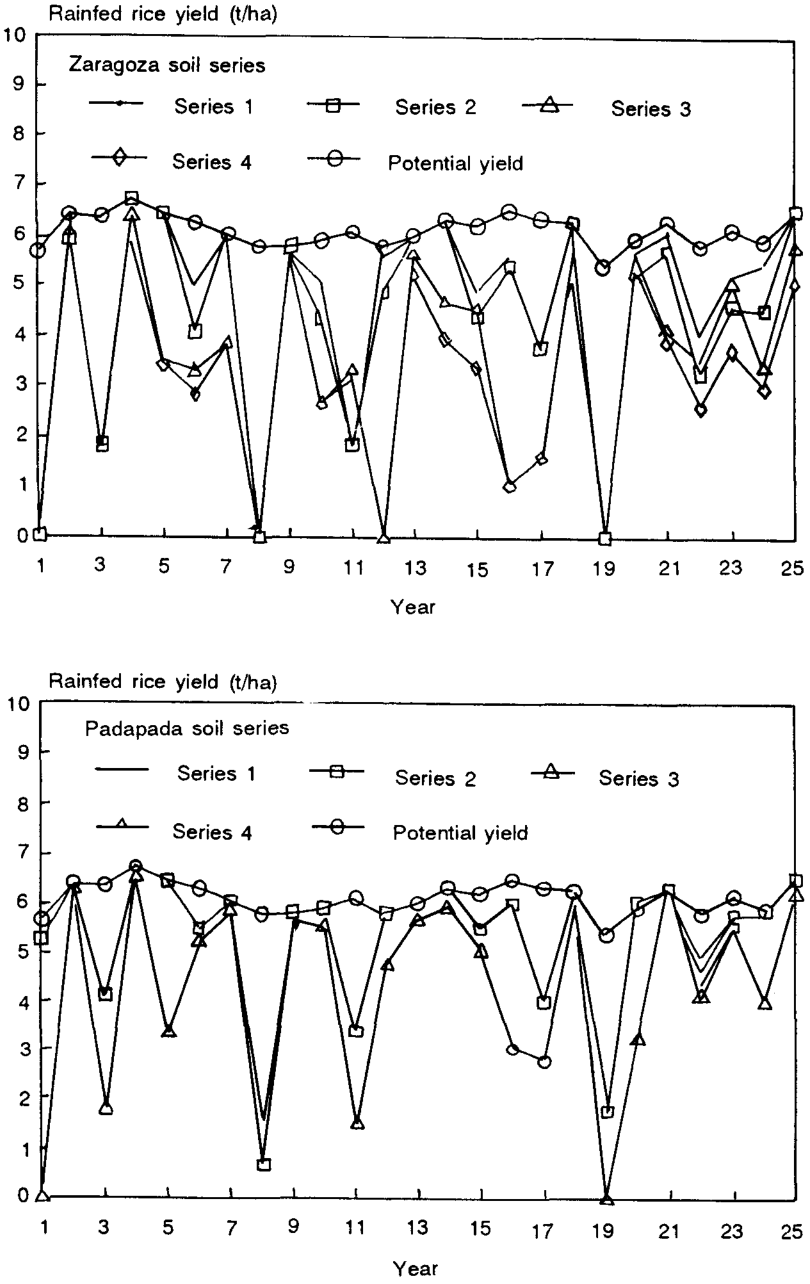
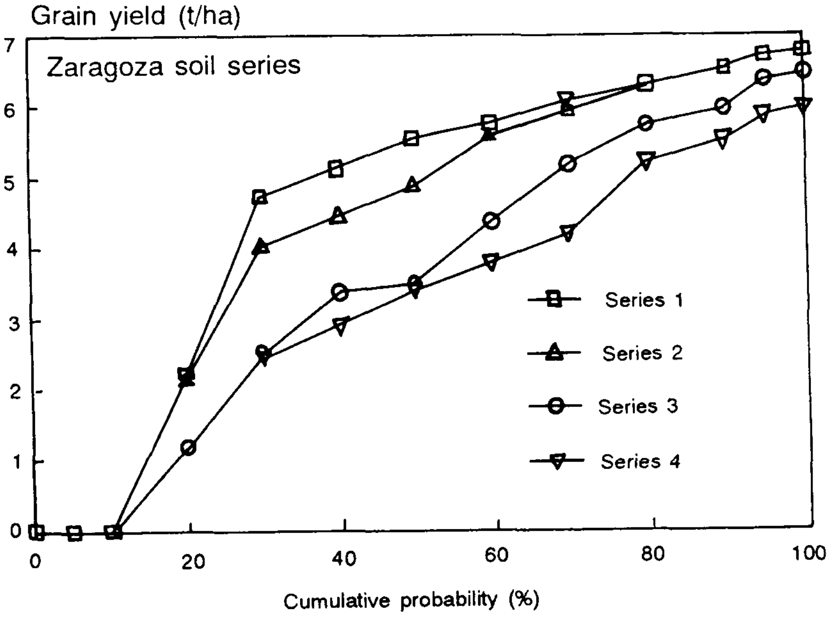


Fig. 8. Potential and rainfed rice yield calculated for 25 consecutive wet seasons and four simulation scenarios on Zaragoza and Padapada soil.



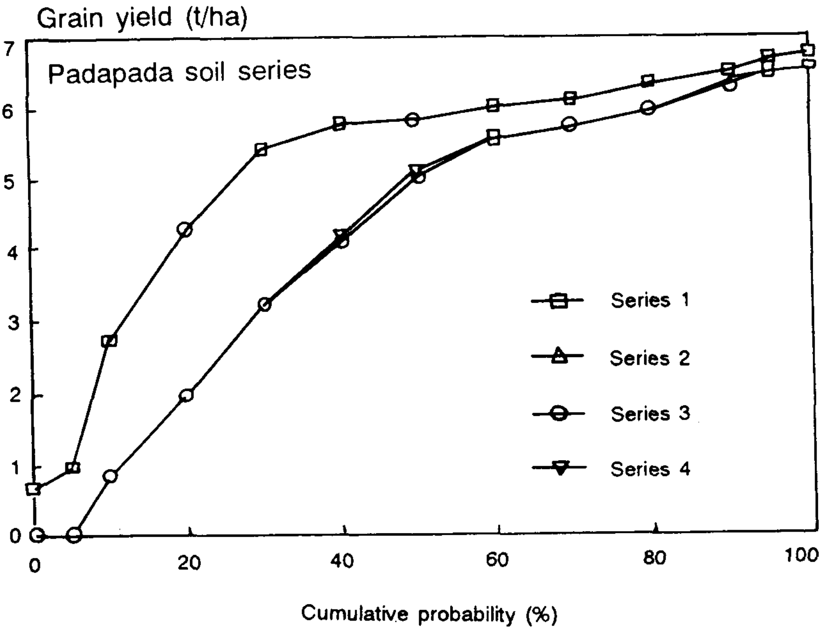


Fig. 9. Cumulative distribution functions for rainfed rice yield on Zaragoza and Padapada soil.

Comparison of rainfed rice yield with potential yields quantifies the yield gap between fully irrigated and rainfed production. This information indicates the yield loss farmers will experience due to lack of irrigation water, under otherwise optimal growing conditions. Production risk was quantified by calculating cumulative probability functions for rainfed rice yield for each soil type (Fig. 9). For Zaragoza, a shallow groundwater table had a positive effect on grain yield due to increased capillary rise to the root zone. For Padapada, this effect was almost non- existent. Poor puddling resulted in yield losses for both soils, especially for Zaragoza.

The hydraulic conductivity of the plow sole was an important determinant of rainfed rice yield for light-textured soils with a relatively permeable subsoil, like the Zaragoza soil series. If no information on this soil parameter is available, a constant percolation rate determined for the various soil types may be used as an input for the PADDY soil-water balance module (Wopereis et al., 1994; Bouman et al., 1994). Tuong et al. (1994) showed that percolation losses toward and into bunds, and the effect of poorly puddled sites may be important in areas with a relatively permeable subsoil. More complex numerical models that allow for lateral flow into the bunds (eg. Walker and Rushton, 1984) are needed under these circumstances. On a regional scale, one-dimensional models, such as the PADDY soil-water balance module can still be used, provided a constant percolation rate is assumed, incorporating both vertical and lateral percolation losses.

Simulated rainfed rice yield was mapped at the 10 and 90% cumulative probability levels using the GIS software. Simulations were conducted assuming average ks values of the plow sole determined in the laboratory and a water table depth of 1.0 m. The Zaragoza soil series occupies a large part of the potential rice-growing area in Tarlac Province (Wopereis, 1993). Growing rice under rainfed conditions in that province is, therefore, risky.

The approach outlined above can only result in a broad overview of yield losses due to drought in Tarlac. Soil types were characterized using measurements conducted at one representative site only. Spatial variability of soil hydraulic properties or thickness of soil horizons was not taken into account.

CONCLUSION

The GIS and crop simulation modelling can be used to quantify rice yield losses due to drought at a regional level. Rainfall variability has a strong impact on yield variability in Tarlac Province. Field experiments conducted for 1 or 2 yr in such environments may give misleding results. Long-term weather data are needed to determine probability distributions of crop yield to perform an economic evaluation (Anderson, 1991). Unfortunately, there is a lack of long-term weather data in many rice-growing countries in Asia as was also the case for the study presented here (detailed weather data were only available for one station in the entire province).

Supplementary irrigation increased wet-season rainfed rice yields and reduced yield variability. Irrigation may also increase the potential for a dry-season crop (eg. mungbean), which would boost total production and income per year relative to rainfed conditions. The scope for a dry-season crop after rice could be investigated using the PADDY soil-water balance and good explanatory model for the dry-season crop.

FUTURE RESEARCH NEEDS

One of the major problems in the application of crop-soil models is the lack of data on soil hydraulic functions. Data bases, that relate these functions to soil characteristics derived from soil survey data, are needed. Maintenance and installation of weather stations should be promoted partly through research consortia. It is important to have a few well-selected and well-maintained sites that can be carefully monitored. Only if good data sets are available can simulation models be used to extrapolate new technologies or to identify constraints or opportunities in rice production. More research is needed on how to deal with limited data in crop modelling studies.

The rainfed rice model ORYZA-W can be used to investigate yield losses due to drought in rainfed, puddled environments and may also be used to quantify the benefits of improved irrigation facilities. ORYZA-W is also a starting point for simulation studies on rice upland crop rotations. The model, however, needs further validation for a broader range of environmental conditions and for different rice varieties. PADDY needs to be expanded to include simulation of water table depth. Sensitivity analyses to investigate the importance of variability in model-input parameters must be conducted.

The increased water-use efficiency of rice-based cropping systems is becoming increasingly important. This can be done by improving irrigation facilities, introducing water-saving techniques, and adjusting the planting time and/or cropping system to maximize rainfall utilization. For any of these approaches, a thorough systems analysis to evaluate the different solutions for different environments is needed. One of the most promising water-saving techniques is dry seeding of rice. The drought stress functions used in this study were all derived for puddled soil conditions. More research is therefore needed on drought stress responses of dry seeded rice and their relation to root zone water content. Special attention should be paid to root development and the effect of drought on root growth.

REFERENCES

Anderson J R (1991) A framework for examining the impacts of climatic variability. Pages 3-17, In : Climatic risk in crop production: Models and management for the semiarid tropics and subtropics. R.C. Muchow and J.A. Bellamy, eds. CAR International, Wallinglord, UK.

ten Berge H F M, Jansen D M, Rappoldt K, Stol W (1992) The soil water balance module SAWAH : User's guide and outline. CABO-TPE Simulation Report Series, no. 22 CABO Wageningen, The Netherlands, 78 pp. + appendices.

Bouman B A M, Wopereis M C S, Kropff M J, ten Berge H F M, Tuong T P (1994) Understanding the water efficiency of flooded rice fields. II. Percolation and seepage losses. *Agricultural water management* (in press).

Bregt A K, Wosten J H M, Denneboom J (1989) GIS: belangrijk hulpmiddel bij bodemfysische interpretatie van bodemkaarten. *Landinrichting* **29** (3): 9-14 (in Duch).

Bronswijk J J B (1988) Modelling of water balance, cracking and subsidence of clay soils. *J. Hydrol.* **97** : 199-212.

BSWM (1992) Soils/land resources evaluation project Tarlac Province. Physical environment, agro-socio-economic and land evaluation. Department of Agriculture, Bureau of soils and Water Management, Quezon City, Philippines.

Fujioka Y, Sato K (1986). On the drying of clayey paddy field (11). Tarns. *JSIDRE, **26:***1-7. (in Japanese with english abstract).

Gardner W R (1958) Some steady state solution of the unsaturated moisture flow equation with application to evaporation from a water-table. *Soil Sci.* **85:** 228-232.

IRRI (1992) Programme report for 1991. International Rice Research Institute, P.O. Box 933, 1099 Manila, Philipppines.

IRRI (1993) Programme report for 1991. International Rice Research Institute, P.O. Box 933, 1099 Manila, Philipppines.

Kraalingen D W g van (1991) The FSE system for crop simulation. Simulation Report CABO-IT no. 23, Centre for Agrobiological Research, P.O. Box 14, Wageningen The Netherlands, 77 pp.

Kropff M J, van Laar H H, ten Berge H F F (1993) ORYZA1, a basic model for irrigated rice production. International Rice Research Institute, P.O. Box 933,1099 Manila, Philippines, 78 pp.

McCree K J, Fernandez C J (1989) Simulation model for studying physiological water stress responses of whole plants. *Crop Sci.* **29:** 353-360.

O'Toole J C, Cruz R T (1980) Response of leaf water potential, stomata1 resistance and leaf rolling to water stress. *Plant Physiology.* 65:428-432

Penman H L (1948) Natural evaporation from open water, bare soil and grass. *Proceeding of the Royal Sciety of London Series A* **193:** 120-146.

Sinclair T R (1986) Water and nitrogen limitations in soybean grain production. I. Model development. *Field Crops Res.* **15:** 125-141.

Stroosnijder L (1982) Simulation of the water balance. Pages 175-193. In: Penning de Vries, F.W.T. and van Laar, H.H (Eds). Simulation of plant growth and crop production. Simualtion Monograps. Pudoc, Wageningen.

Tuong T P, Wopereis M C S, Singh A K, Kropff M J, ten Berge, H F M (1993). Modeling lowland rice agrohydrology. Presented at the Dec. 14-17 1993 ASAE International Winter Meeting. Paper No. 932528.

Tuong T P, Wopereis M C S, Marquez J, Kropff M J (1994) Mechanisms and control of percolation losses in puddled rice fields. *Soils Science Society of American Journal.* (In press).

Walker S H, Rushton K R (1984) Verification of lateral percolation from irrigated rice fields by a numerical model. *J. Hydrol.* **71:** 335-351.

Wolfram S (1991) Mathematica. A system for doing mathematics by computer Second edition. Addison-Wesley Publishing Company Inc., Redwood City, California, 961 pp.

Wopereis M C S, Wosten J H M, Bouma J, Woodhead T (1992) Hydraulic resistenace in puddled rice soils measurement and effects on water movements *Soil & Tillage Research* **24:** 199-209.

Wopereis M C S (1993) Quantifying the impact of soil and climate variability on rainfed rice production. Ph.D. Thesis, Wageningen Agricultural University, The Netherlands. ISBN 90- 5485-147-3.

Wopereis M C S, Kropff M J, Hunt E D, Sanidad W, Rouma J (1993) Case study on regional application of crop growth simulation models: Tarlac Province, Philippines. Pages 27-46. In : Bouman, B.A.M., van Laar, H.H. and Zhaoqian, W. (Eds). Agro- ecology of rice-based cropping systems. ISBN 90- 73384-18-4.

Wopereis M C S, Bouman B A M, Kropff M J, ten Berge H F M, Maligaya A R (1994) Understanding the water use efficiency of flooded rice field,s I. Validation of the soil-water balance model SAWAH. *Agricultural Water Management* (in press).

DROUGHT RESPONSE OF DRY SEEDED RICE AND ITS MODELLING

□ *A.K Singh*[1], *T.P. Tuong*[1], *K.T. Ingram*[2], *R Pernito*[1] *and J, Siopongco*[1]

SUMMARY

Dry seeded rice (DSR) provides an option to increase crop production and intensity by utilizing early-season rainfall, escaping late-season drought and reducing turnaround time for a post-rice crop. Experiments conducted in 1992 and 1993 at the Tarlac Rainfed Lowland Consortium Key-site evaluated and quantified the response of DSR to drought in a rainfed lowland environment. The treatments were different dates of seeding and varying water regimes, each having three levels. The seeding dates were May 18, June 11, and July 8 in 1992, and May 27, June 11, and August 4 in 1993. The three water regimes were (i) totally rainfed conditions, (ii) initially irrigated conditions to ensure complete emergence and then rainfed, and (iii) fully irrigated conditions. The ORYZA1 model was parameterized for DSR through vegetative and reproductive development rates and tested to simulate DSR growth under fully irrigated conditions. Transpiration and evaporation were determined by daily weighing of 20x20x40cm lysimeters installed in the fields. The final yield was not significantly affected by the various water regimes except for the first seeding date. Under rainfed conditions, the second seeding date resulted in the highest yield. Rice plants transpired at a potential rate as soil water content of the mot zone decreased from saturation to field capacity (-0.03 MPa matric potential). Below field capacity, the relative transpiration rate decreased linearly with decreasing soil moisture. This linear decrease appeared to be independent of the fertility level and climatic conditions. ORYZA1 satisfactorily estimated dry matter production and yield under fully irrigated conditions.

INTRODUCTION

About 27% of the total rice area in the world has been classified as rainfed lowland, which contributes less than 18% to global rice production. More than 95% of the world's total rainfed lowland area is in Asia (IRRT, 1993). Even a small increase in the productivity of these regions would add significantly to global rice production. With the availability of modern, short-duration, high yielding varieties, dry seeded rice (DSR) provides an option to increase the productivity in rainfed lowland ecosystems. DSR can be sown even before the onset of the wet season, which permits

---

[1] International Rice Research Institute. P.O. Box. 933, Manila, Philippines.

[2] Peanut CRSP Management Office, University of Georgia, Griffin, Georgia 30223-1797, U.S.A.

utilization of early-season rainfall (Tuong *et al.,* 1993). Seeds of DSR remain viable in the soil for as long as 40 days without detrimental effect on germination (Furoc *et al.,* 1978). The early harvest of DSR enables the crop to escape and/or minimize the adverse effects of drought at the end of the wet season, and leaves enough time, as well as available soil moisture and late-season rainfall, for a second crop (Saleh *et al.,* 1993). Since DSR is done in nonpuddled conditions, it saves on turnaround time for post-rice crops.

The uncertainty of rainfall may expose the crop to drought of varying intensity and duration during the growing season. This is one of the key factors limiting yields of rainfed rice. Advancing the seeding date in DSR aggravates this problem because the crop is established before the steady monsoon season rain. DSR, because of its very nature of cultivation, is associated with many problems starting with crop establishment, high weed competition and periodic dry spells. Since the soil is not puddled, DSR represents a totally different environment for rice root development as well as for water and nutrient uptake compared with transplanted rice (TPR). There is a dearth of precise and systematic information on the soil-water-plant-atmospheric interactions in relation to DSR. It is, therefore, essential to quantify the effects of drought on soil-water extraction and plant performance in DSR grown under rainfed lowland ecosystems. It will enable development and/or modification of a model linking environmental conditions to dynamics of soil water and plant growth which could be utilized for identifying conditions and locations suited for DSR, the risks associated with it and the year to year yield variations.

The main objectives of this paper are :

1) to quantify the effect of drought on the transpiration rate of dry seeded rice; and
2) to test the ORYZA1 model, a validated crop growth model for potential production of TPR (Kropff *et al.,* 1993), for DSR under fully irrigated conditions, as a first step toward a full scale modelling of DSR under rainfed conditions.

MATERIALS AND METHODS

Experimental site

The experiments were conducted at the Tarlac Rainfed Lowland Consortium Key site located at Village Masalasa, Victoria, Central Luzon, Philippines. The annual rainfall of Victoria is 1610 mm, with 1310 mm being recorded from June to October (16 year average). The wet season is characterized by frequent typhoons. The general texture of the soil profile is clay loam averaging 38% clay, 42% silt, and 20% sand. The surface soil layer (0-10 cm) had 0.85% organic carbon content. The soil water characteristic (pF) curve is shown in Figure. 1.

Performance of rainfed DSR

To evaluate the performanceof rainfed DSR, field experiments were conducted during the wet season (WS) of 1992 and 1993 in Tarlac. Since the amount and

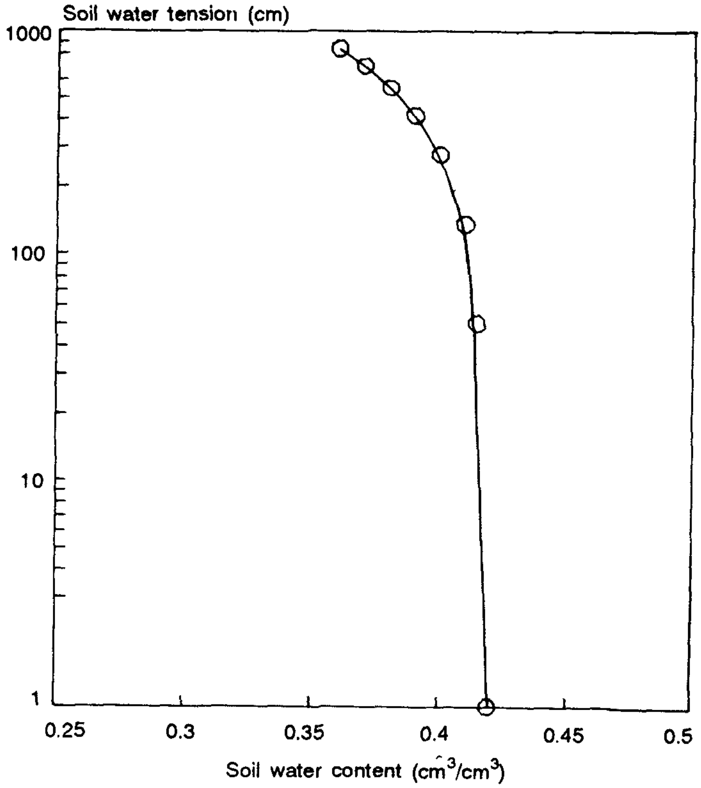


Fig. 1. Water retention characteristics of the surface soil (0-20 cm) at Tarlac.

frequency of rainfall are highly variable and uncertain, the seeding dates were varied during the same growing season in order to expose the crop to drought at various stages under field conditions. The treatments were three seeding dates and three water regimes. The dates of seeding (Dl, D2, and D3) were May 18, June 11, and July 8 in 1992 and May 27, June 11 and August 4 respectively in 1993. Water regimes were (i) totally rainfed (IO), (ii) irrigated initially to ensure complete emergence and then rainfed (11), and (iii) fully irrigated control (I2). All plots were separated from surrounding plots by plastic sheets embedded 60 cm deep around each plot. The experiment was laid out in a split plot design with water regimes as the main plot and seeding date as subplot treatment, replicated five times. The subplot was 7.5x11.5 m. Nitrogen (120 kg/ha) was applied in four toydressed equal splits, i.e. 15 days after emergence (DAE), maximum tillering, panicle initiation, and heading. Twenty five kg P/ha and 45 kg K/ha were also applied. Seeds were sown at a rate of 100 kg/ha in rows 20 cm apart and 2 cm deep. IR72 was used in both experiments. The experimental plots were kept free of weeds and pests, following recommended practices.

Emergence count of the crop under IO was monitored daily in four 1-m-long rows in each subplot from seeding until a constant number, i.e. final emergence, was attained. Plant samplings from two 0.5m-long-rows in each subplot were carried out for biomass production, leaf area index (LAI) and leaf N content. Samplings were done at 15 DAE, mid-tillering, maximum tillering, panicle initiation, between panicle initiation and flowering, and maturity.

Rainfall, wind speed, solar radiation, relative humidity, and maximum and minimum temperatures were also recorded daily at a weather station located adjacent to the experimental fields.

Measurement of transpiration

Two experiments were conducted during the 1993 dry season (DS) and 1993 wet season (WS) to investigate the effect of drought on DSR, by weighing lysimeters (20x20 cm cross-sectional area and 40 cm deep, with an undisturbed soil profile of 0-30 cm) installed in the fields. The soil surface within the lysimeter was covered with a plastic sheet to prevent evaporation, allowing for water loss through transpiration only. Transpiration was derived from changes in the daily weights of the lysimeters which were also used to calculate the average soil water content in the lysimeter.

The 1993 DS experiment consisted of two main treatments each having two levels. The main treatments were water regimes, stressed (described below) and fully irrigated, and fertilizer application rates of 60 and 120 kg N/ha, replicated four times. The 1993 WS experiment consisted of three seeding dates described earlier and two water regimes, stressed (described below) and fully irrigated, replicated three times.

Stress was imposed in the lysimeters by withholding irrigation at the panicle initiation stage (1993 DS experiment) and at the maximum tillering stage (1993 WS experiment). In the wet season, the lysimeters were also sheltered from rains during the stressed period to prevent alleviation of drought by rain. Stress was relieved by supplying water when the plants registered a leaf-rolling score of 5 (O'Toole and Cruz, 1980). The rice variety used was IR72.

The effect of water stress on the plants was expressed in terms of the relative transpiration rate, defined as the ratio of the actual transpiration (Ta) and potential transpiration (Tp) rates. Imposition of stress slowed down plant growth and leaf area development resulting in reduced leaf area in stressed plants compared with well-watered plants. The potential transpiration recorded for the well-watered plants (Tp_{ns}) would be higher than the potential transpiration of the plants having a leaf area equivalent to that of stressed plants. Tp_{ns} was therefore corrected to the potential transpiration rate (Tp) of a plant having the same leaf area as the stressed plant on a daily basis (Wopereis, 1993). The steps involved are explained below.

$$Tp = Tp_{ns} \text{ x } CF \quad (1)$$

where CF is the correction factor given by :

$$CF = [1\text{-exp.}\{-0.4\text{x}LAI_s\}]/[1\text{-exp.}\{1\text{-exp.}\{-0.4\text{x}LAI_{ns}\}] \quad (2)$$

where LAIs is the leaf area index of stressed plant and LAIns is the leaf area index of fully irrigated plants.

Since destructive sampling could not be carried out from the lysimeters until maturity, plants were sampled from an equivalent area within the plots of fully irrigated treatments to obtain LAI_{ns} at the start and at termination of stress. LAI_{ns} and LAI_s were considered equal at the initiation of stress. After the stress was relieved, the stressed plants began transpiring at a potential rate (Tp) that was less than the transpiration rate of well-watered plants (Tp_{ns}). The difference between Tp and Tp_{ns} was due to the difference in the LAI of stressed and non-stressed plants at the end of the stress period. LAI_s at the end of the stress period was derived from LAI_{ns} Tp; and Tp_{ns} using the relation.

$$LAI_s = -2.5\, ln\, [1-(T_p/T_{pns})\, (1-\exp.(-0.4 x LAI_{ns})]$$

where *'ln'* is natural logarithm.

Daily values of LAI_{ns} and LAI_s were worked out from the LAI_s values obtained at the initiation and end of stress, assuming that the change in LAI during that period was a linear function of time. Daily CF values were then derived using equation 2.

Modelling of DSR

The ORYZAI crop growth model was tested for simulation of growth and yield of fully irrigated DSR. ORYZAI was originally developed and validated to simulate growth and yield of TPR rice under potential production conditions (Kropff *et al.,* 1993). The model requires radiation, temperature, planting dates, crop development, and relative growth rates as well as time course of leaf N content as input. Measured LAI can also be input; otherwise, it is predicted by the model.

Development rate parameters and leaf N content are important for simulation of rice growth for a given environment (Kropff et al., 1993). However, the development rate of DSR will differ from that of TPR. As a first step, therefore, the development rate parameters of DSR were derived from the first sowing date of I2 in the 1993 WS experiment described earlier, based on seeding, flowering, and physiological maturity dates using the program DRATES (Kropff *et al.,* 1993). Measured leaf N content was used as input. Simulations predicted the total biomass and panicle dry weight of I2 treatments for all sowing dates in 1992 and 1993. LAI was also simulated, but the results are not presented in this paper.

RESULTS AND DISCUSSION

Rainfall pattern

Figure 2 presents the cumulative rainfall from seeding to harvest at different seeding dates. It varied from slightly above 1000 mm in D3-92 WS to more than 1700 mm recorded in D2-93 WS, thereby providing a wide range of water availability during those two years. Varying the seeding dates, therefore, generated different water availability conditions during the same growing season.

Emergence of rainfed DSR

In the rainfed treatment (I0), emergence of DSR was influenced by the rainfall after sowing and the soil water content at the time of seeding. At the first seeding, the soil water content in the top layer was around 10-11% (Table 1), which is much

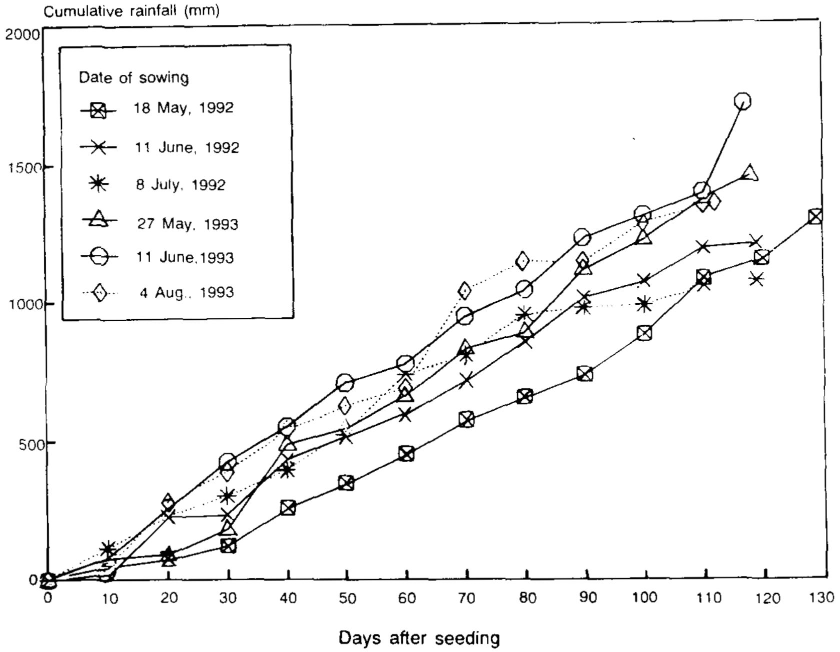


Fig. 2. Cumulative rainfall during 1992 and 1993 in dry seeded rice (DRS) as a function of days after sowing.

below the water held by the soil at wilting point (-1.50 MPa matric potential). In this treatment, emergence was delayed by almost a week and the emergence percentage in 1993 was 64% (Fig. 3). The emergence in 10 of the first seeding of the 1993 WS was triggered by 69 mm of rain (8 days after seeding) and the emergence count stabilized at a cumulative rainfall of less than 100 mm. Germination in the subsequent seeding dates was 80% or more because of higher initial soil-water content and greater amount of rainfall.

Table 1. Soil water content in 0-10 cm layer at sowing time in 1992 and 1993.

Sowing date	Soil water content (cm^3/cm^3)
1992	
18 May	0.11
11 June	0.16
8 July	0.20
1993	
27 May	0.10
11 June	0.21
4 Aug.	0.23

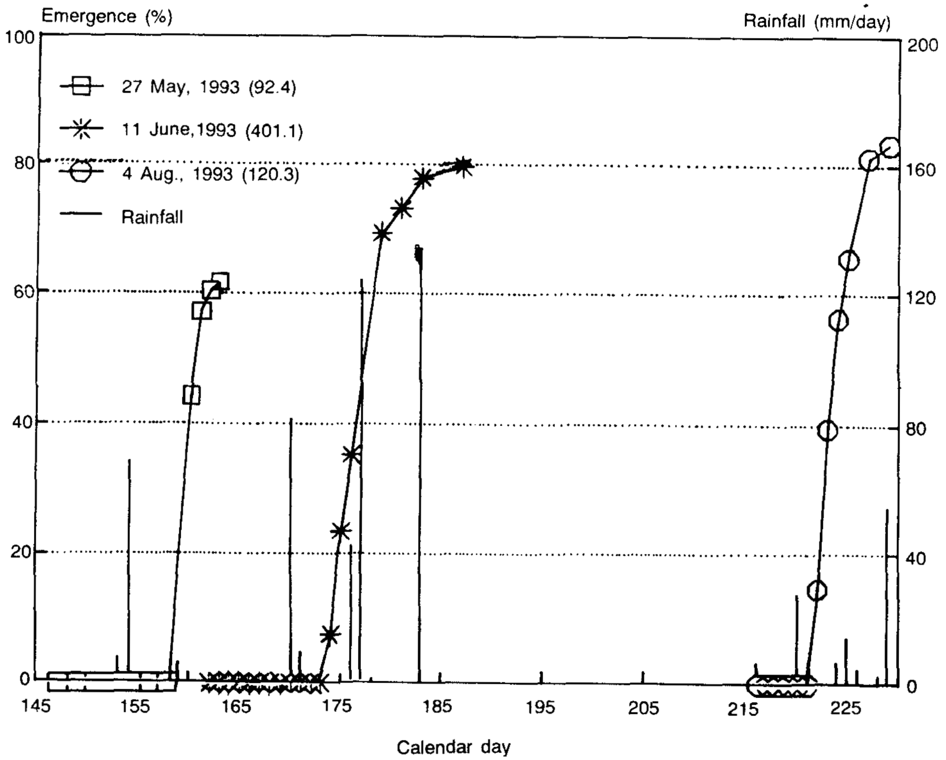


Fig. 3. Effect of sowing date on emergence of rainfed (I0) DSR IR72. Numbers in parentheses are cumulative rainfall totals (mm) at which emergence count became constant.

Grain yield

The final yield was not significantly affected by the various water regimes except on the first date of seeding (Table 2). Under rainfed conditions the second date of seeding gave maximum yields because of better water availability throughout the growing season. Heavy rainfall, coinciding with flowering of the crop slightly reduced yield in I2 for the second sowing date in 1992 compared with other treatments. Tuong *et al.* (1993) reported similar observations of yields remaining unaffected even though drought spells delayed emergence and other plant phenological stages under rainfed conditions.

Transpiration ratio

For Ta/Tp, the results of the experiments conducted during 1993 DS and WS were pooled and are shown in Figure 4 as a function of soil water content. Ta/Tp during the DS were for 60 and 120 kg N/ha, whereas that for WS was at 120 kg N/ha. In well-watered plants during DS, transpiration rates were 10 mm/day and reduced to 2 mm/day in the stressed plants at the time of drought termination (at leaf rolling score of 5). During WS, transpiration rate of well- watered plants was

5-6 mm/day and was reduced to 1.5 mm/day or less at the later stages of stress. For all seasons and N levels, the rice plant was able to transpire at a potential rate until the soil moisture was around field capacity, i.e. at a soil pressure potential of -0.03 MPa. Beyond this soil water content, Ta/Tp decreased linearly with decrease in soil water content, (R^2=0.9254). In a study of transplanted rice under non nitrogen-limiting conditions, Maligaya *et al.* (1993) and Wopereis (1993) obtained similar trends in the relative transpiration rate as a functiol of soil moisture ratio, which could be translated into soil water content. In their study, Ta/Tp began declining at a soil moisture ratio of 1.7, representing soil water content below field capacity when water stress was initiated at mid- tillering stage for both IR20 and IR72. The critical soil moisture at which Ta/Tp starts to decline needs to be investigated further as it may be both crop and stage-specific as well as being influenced by the crop establishment method.

Table 2. Effect of seeding date and water regimes on the yield of dry seeded rice IR72.

Seeding date*	Water regime	Yield** (t/ ha)	
		1992	1993
Dl	I0	2.9b	3.7ab
	I1	2.5b	3.4b
	I2	4.0a	4.la
D2	I0	3.8a	4.3a
	I1	4.0a	3.8b
	I2	3.3b	3.9ab
D3	I0	3.8a	3.8a
	I1	3.8a	3.7a
	I2	4.0a	3.8a

* Dl refers to 18 May in 1992 and 27 May in 1993; D2 refers to 11 June in both 1992 and 1993; D3 refers to 8 July in 1992 and 4 Aug. in 1993.

** Means having a common letter in the same column are not significantly different at the 5% level by DMRT.

Plants respond to the imposition of stress through stomatal closure and leaf rolling. Stomatal closure reduces water loss through transpiration whereas leaf rolling directly reduces the leaf area exposed to the environment, which also contributes to reduced transpiration losses. Reduction in transpiration rate directly affects the rate of photosynthesis. This relationship (Fig. 4) representing reduction in relative transpiration rate as a function of soil water content can be used to link a potential production simulation model to production under water-limiting

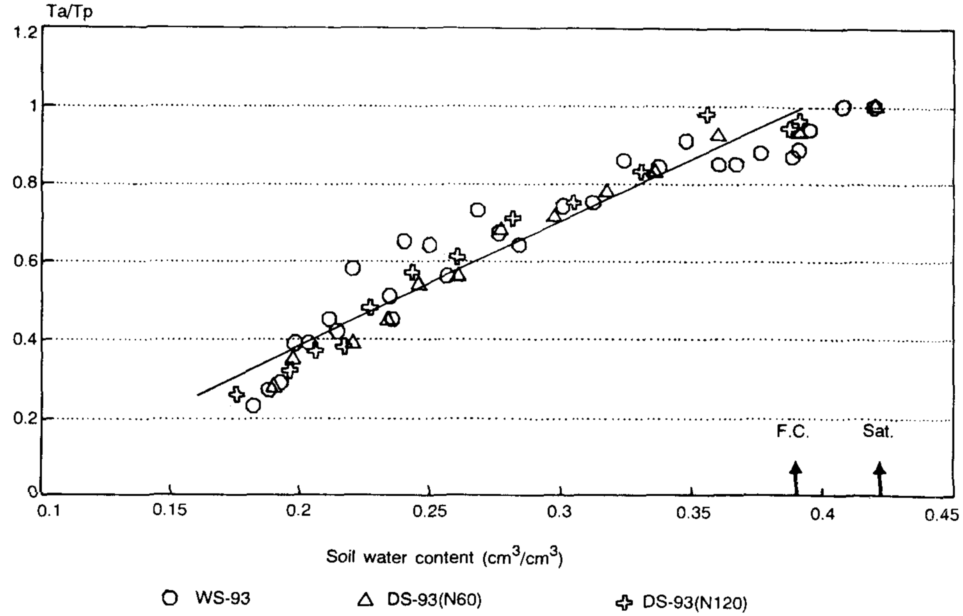


Fig. 4 . Relative transpiration rate (Ta/Tp) of DSR as a function of soil water content (WS=wet season; DS=dry season; N60=60kg Nha; N120=120 kg N/ ha).

environments through a water balance model. This could lead to a model that can be used to quantify the effects of water stress on crop growth and yield of DSR.

Modelling of dry seeded rice

The crop development rates for the vegetative and reproductive phases of DSR derived from the first sowing date of I2 in 1993 using DRATES were 0.000576 and 0.001568, respectively. The corresponding values for TPR IR72, as reported by Kropff *et al.* (1993), were 0.000751 and 0.00168. The crop development rate of DSR during the vegetative phase was markedly different from that of TPR. The simulated results for total above ground dry matter production for all sowing dates corresponding to I2 of 1992 and 1993 are shown in Figure 5. The dry matter prediction is generally within 10% of the observed values except in the case of the third seeding in 1992. As indicated by Figure 5, the biomass is overestimated for all seedings in 1992. This is also reflected in the panicle dry weight predictions (Fig. 6). One of the possible causes for this overestimation could be the existence of field conditions inadequate for potential production, caused by untimely typhoons and heavy rains, leading to yield reductions. Despite these discrepancies, the fitness of simulated and measured biomass and panicle dry weights was satisfactory (R^2= 0.8699).

The model needs to be evaluated further to simulate growth of DSR under water-stressed conditions. It also requires linking up with a module that can simulate the dynamics of soil water under rainfed lowland situations, where perched water

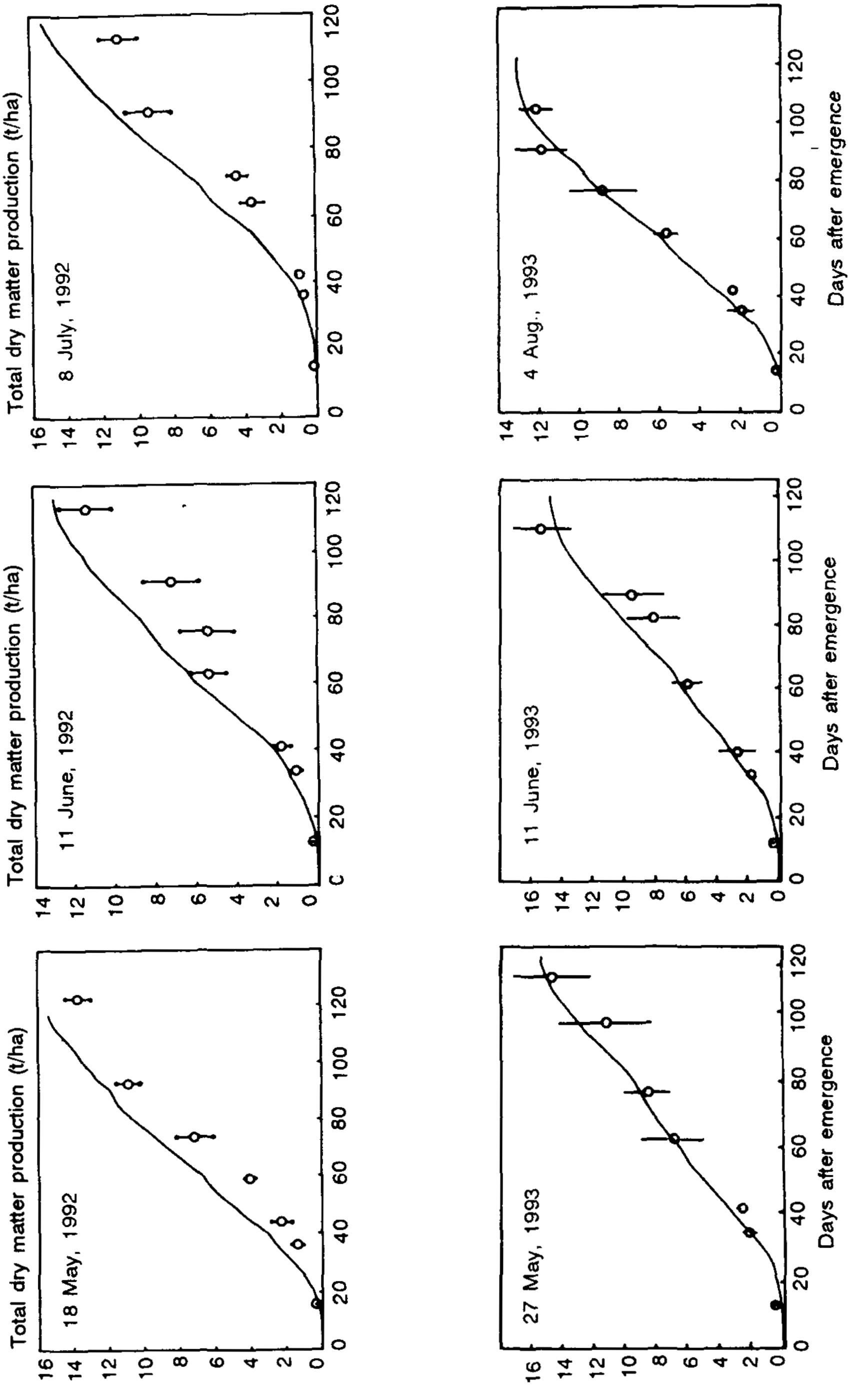


Fig. 5 . Observed (0) and simulated (—) values of dry matter production for all sowing dates of I2.

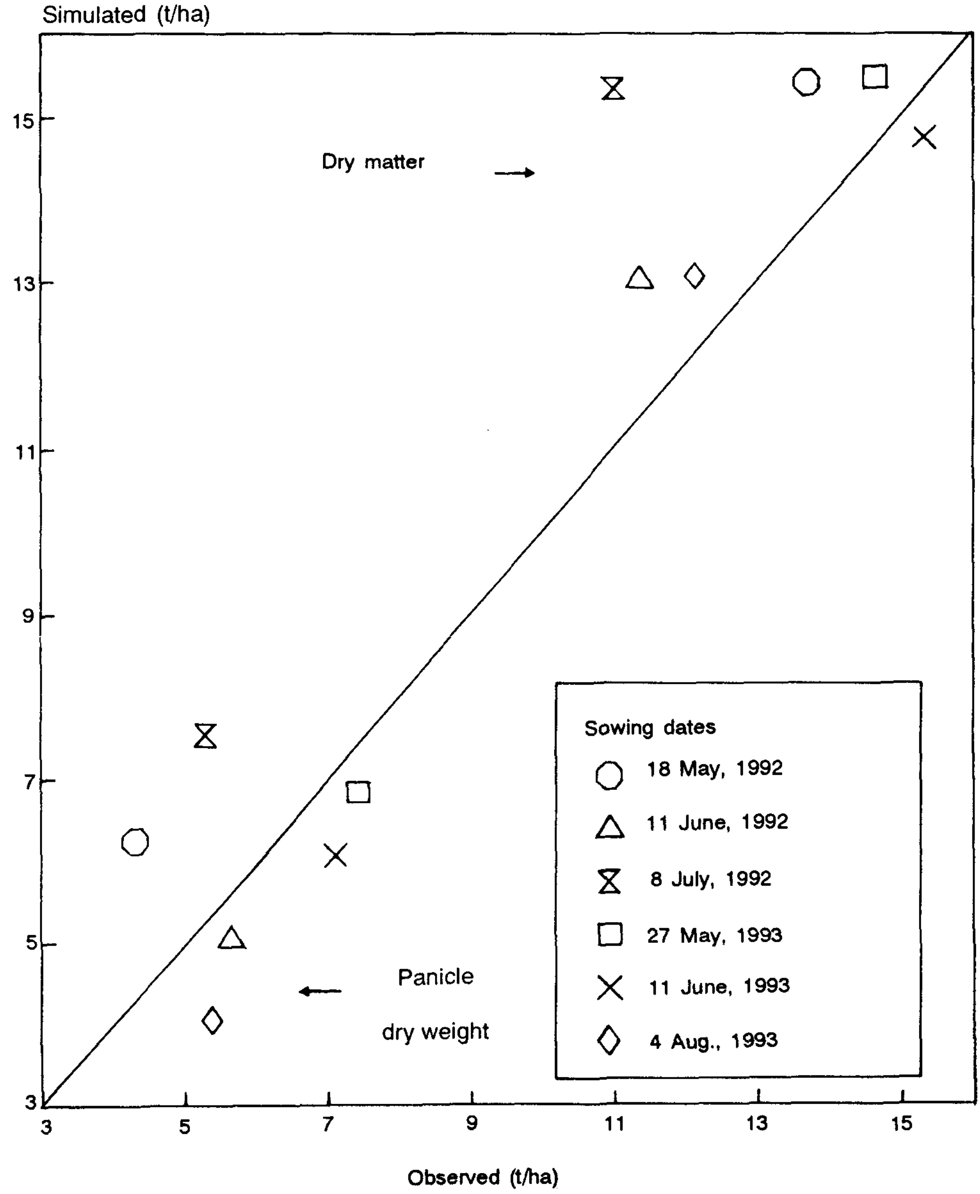


Fig. 6 . Comparison of observed and simulated dry matter production and panicle dry weight of well-watered DSR IR72.

tables occur frequently and for several weeks an unsaturated layer can be observed below a saturated one in the soil profile. Initial testing of process-based water balance model SAWAH has indicated that it can be used successfully under these situations (Tuong *et al.,* 1993).

CONCLUSION

Results of our experiments indicate that Ta/Tp was a sound parameter for characterizing stress as it appeared to be independent of N application rate and the prevalent climatic conditions. ORYZA1 satisfactorily simulated the dry matter and yield of DSR under fully irrigated conditions. Further work is required to modify the model to simulate crop growth under water- stressed situations, and coupling the crop component with a water balance model for rainfed lowland ecosystems.

REFERENCES

Furoc R E, Magbanua R D, Gines H C, Morris R A (1978) Identification of criteria for late dry-seeded rice planting. Paper presented at the 9th Annual Scientific Meeting of the Crop Science Society of the Philippines, 11-13 May, 1978, Iloilo City, Philippines.

IRRI (1993) International Rice Research Institute. IRRI rice almanac, P.O. Box. 933, Manila, Philippines.

Kropff M J, Van Laar H H, ten Berge H F M (1993) ORYZA1-A basic model tor irrigated lowland rice production : Simulation and Systems Analysis for Rice Production (SARP). International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Maligaya A R, Wopereis M C S, Kropff M J (1993) Drought stress responses of two lowland rice cultivars. Paper presented at the 9th Federation of the Crop Science Society of the Philippines Scientific Meeting, 10-14 May, 1993, Aklan, Philippines.

O'Toole J C, Cruz R T (1980) Response of leaf water potential, stomatal resistance and leaf rolling to water stress. *Plant Physiology* ***65:*** 428-432

Saleh A F M, Lantican M A, Bhuiyan S I, Agua M M (1993) Increasing productivity of droughtprone rainfed lowlands in Northern Luzon, Philippines. Paper presented at the Symposium of the rainfed Lowland Rice Research Consortium, 8-13 Feb. 1993, Semarang, Indonesia.

Tuong T P, Ingram KT, Siopongco J D, Confessor R B, Boling A A Singh U, Wopereis M C S (1993) Performance of dry seeded rainfed lowland rice in response to agrohydrology and N-fertilizer management. Paper presented at the Symposium of the Rainfed Lowland Rice Research Consortium, 8-13 Feb. 1993 Semarang, Indonesia.

Wopereis M C S (1993) Quantifying the impact of soil and climate variability on rainfed rice production. Ph D thesis, Agricultural University, Wageningen, The Netherlands.

RICE ROOT SYSTEMS DEVELOPMENT UNDER RAINFED CONDITIONS

□ *G. Pantuwan*[1], *K. T. Ingram*[2] *and P.K. Sharma*[3]

SUMMARY

Field experiments to quantify root growth of rice cultivars under rainfed conditions were conducted at the Ubon Rice Research Centre, Northeast Thailand, during the 1991 and 1992 wet seasons. Root length, root mass, and root:shoot ratio were measured at panicle initiation and anthesis. Genotype, soil hydrology, and soil type significantly affected root length density (RLD) and root mass density (RMD). The RLD and RMD of genotypes at plots subjected to alternate wetting and drying were generally higher than those at plots that were continuously flooded. Greater RLDs and RMDs were observed in loamy sand soil than in clay soil. Root:shoot ratio was higher in loamy sand than in clay soil irrespective of hydrology. Roots in clay soil exhibited less root branching than roots in loamy sand. Loamy sand soil subjected to alternate wetting and drying may be an appropriate growing condition for evaluating rice root growth.

INTRODUCTION

Optimum root growth is required for stabilizing shoot growth in plants subjected to drought stress. A deep and dense root system has been shown to be a heritable characteristic, and has been assumed to be essential for allowing plants to avoid or tolerate drought. Thus, rice breeders have attempted to incorporate favourable root characteristics into rice genotypes for drought- prone, rainfed lowland areas.

A measurable variation in root system characteristics of rice genotypes has long been recognized (Yoshida and Hasegawa, 1983; O'Toole and Bland, 1988). It has also been shown that soil physics, hydrology, and agricultural practices influence rice root growth (Maurya and Ghildyal, 1975; Sharma *et al.,* 1987; Thangaraj *et al.,* 1990; Ogunremi 1991). Rice roots, therefore, exhibit a large degree of phenotypic plasticity. Coupled with genotype x environment interactions, root phenotypic plasticity makes evaluation of root system characteristics difficult. The soundness of information on rice root traits depends on whether plants were grown in an environment where full expression of their growth potential is realized. Such growing environments need to be identified.

---

[1] Ubon Rice Research Centre, P.O. Box 65, Ubon 34000, Thailand.

[2] Peanut CRSP Management Office, University of Georgia, Griffin, Georgia, 30233-1797, U.S.A.

[3] Department of Soil Science, H.P. Krishi Vishwavidyalaya. Palampur-176062, H.P.. India

This paper summarizes information from research on the growth and development of rice root systems on various soil types and hydrological regimes in rainfed areas of Northeast Thailand.

MATERIALS AND METHODS

Experiments were conducted during the 1991 and 1992 wet seasons at the Ubon Rice Research Centre in Northeast Thailand, to quantify root system growth and development under rainfed conditions. In 1991, three rice cultivars KDML105, RD9, and IR46 were transplanted (28 d old seedlings) on puddled soils at three locations giving different combinations of hydrology and soil texture :

1) High toposequence, loamy sand, alternate wetting and drying, mostly nonflooded;
2) Low toposequencc, loamy sand, flooded most of the time during the growing season; and
3) Low toposequence, clay soil.

Six rice cultivars IR-20, KDML 105, NSG 19, RD9, Chieng Saen, and IR46 were used in the 1992 experiment. Seedlings (30 d old) were transplanted in puddled loamy sand soil, at high and low toposequence position. Experiments in both years were laid out in randomized complete block design with five replications. Fertilizer application, in both years, consisted of 25-25-25 kg/ha of N, P, and K incorporated before transplanting and 50 kg/ha of N topdressed at panicle initiation (PI).

The genotypes used in the experiment were chosen to represent contrasts in stature, photoperiod sensitivity, and drought susceptibility. KDML 105, (photoperiod sensitive) and NSG19 (photoperiod insensitive) are traditionally selected, tall cultivars, resistant to drought stress. IR20 (short stature high yielding) and Chieng Saen (tall traditional cultivar) are known to be susceptible to drought stress. Cultivars IR46 and RD9 are photoperiod insensitive, medium-statured, improved, and high yielding.

Genotypes were sampled for roots at the same physiological age at PI and anthesis. Root and shoot sampling was done on median plants at randomly selected locations within plots. Roots were collected from four hills in each replication using a 20 x 20 x 50 cm metal monolith sampler. Root sampling was centered over a hill. Each soil core was sectioned into five 10 cm layers. Roots were washed free of soil over a metal screen (1 mm mesh size). Root length was measured with a Comair root length scanner (Commonwealth Aircraft Corporation Limited, Australia). Roots were oven-dried at 70° for 48 h to determine mass. Root length density (RLD) and mot mass density (RMD) were calculated as the quotient of mot length and oven dry weight, and the volume of the soil sample. Above ground biomass was determined in a manner similar to root mass. Root : shoot ratios (root oven dry weight/shoot oven dry weight) were calculated from the data.

In the 1991 experiment, root form and proliferation were observed using the pinboard technique. Pins were driven through the sampler in one hill in each replication at anthesis. The monolith was carefully dug out, and removed from the ground. Roots in the sampler were washed free of soil, allowing observation of relative root distribution in the soil profile.

RESULTS AND DISCUSSION

Root length and root mass

Root length density was significantly affected by soil type, hydrology, and crop stages. The 1991 experiment showed that the RLD of the three rice cultivars was higher at high toposequence position than at low toposequence position. Genotypes exhibited differences in RLD at the high toposequence position only (Fig. 1). The 1992 experiment, using six rice cultivars, gave results similar to those of the 1991 experiment (Fig. 2). Differences in root length density among genotypes, particularly at anthesis, were greater at high toposequence position. Alternate wetting and drying at the high toposequence position might have led to increased mot length density of the cultivars. Kawata and Ishihara (1959) found that in aerobic soil, drying periods induced the development of root hairs and nodal roots.

Root length density was generally higher in loamy sand than in clay soil (Fig. 1). Observations of root proliferation, using pinboard technique, confirmed that there was greater root branching in loamy sand than in clay soil (Fig. 3). Greater root branching in loamy sand soil may be due to its greater porosity, being dominated by pores of relatively large radii, thus providing room for root growth (Kar *et al.,* 1979).

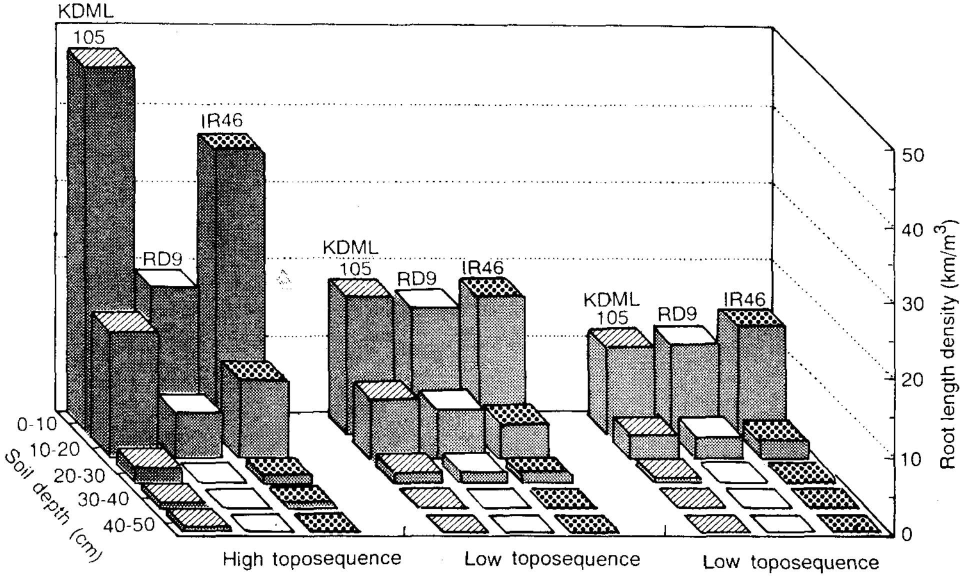


Fig. 1. Root length density at anthesis stage of 3 rice cultivars at 3 toposequence positions (Pantuwan *et al* 1992, unpubl).

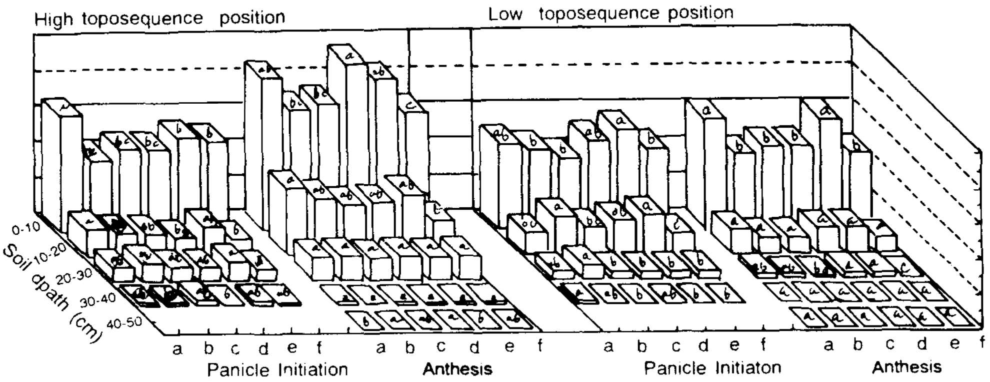


Fig. 2. Root length density of 6 rice cultivars (a) KDML 105, (b) MSG 19, (c) RD 9, (d) Cheing Saen, (e) IR 20 and (f) IR 46 growth at high and low toposequence positions (Pantuwan *et al* 1993, unpubl. data).

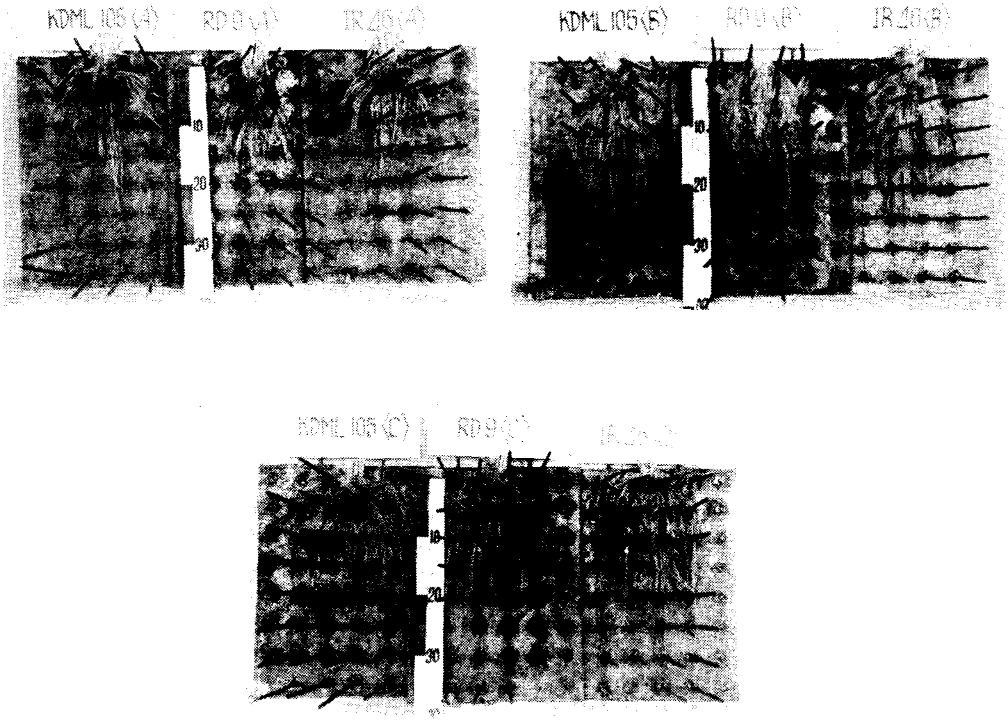


Fig. 3. Root systems of three rice cultivars grown in (a) clay loamy sand (b) low toposequence and (c) loamy sand high tosposequence position.

Root mass density (RMD) exhibited the same trend as RLD. Roots in loamy sand produced greater RMD than the roots in clay soil (Fig. 4). Root mass density was higher at high toposequence than at low toposequence positions (Fig. 5). Higher RMD in the high toposequence may be related to the higher RLD observed at this toposequence position.

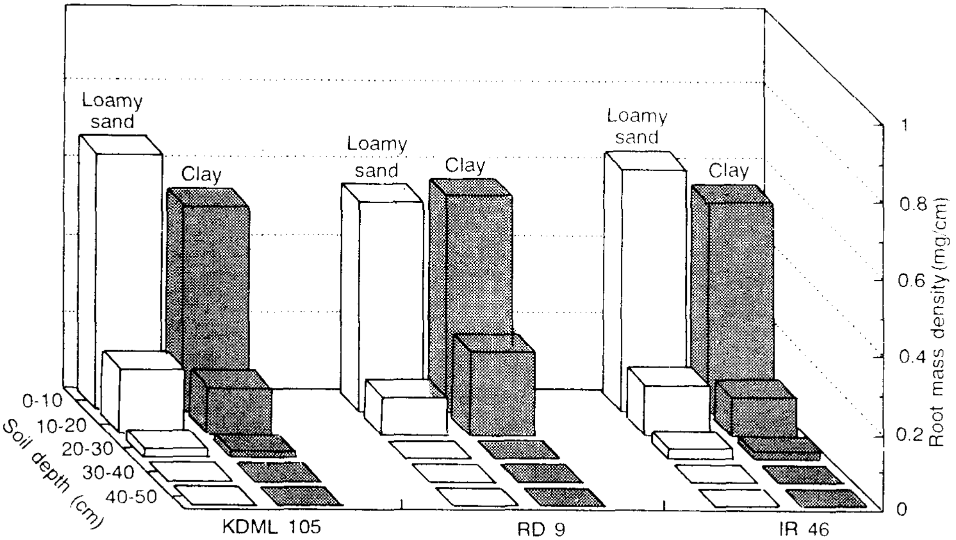


Fig. 4. Effect of soil texture on root mass density of 3 rice cultivars sown at low toposequence (Adapted from Sharma, 1994).

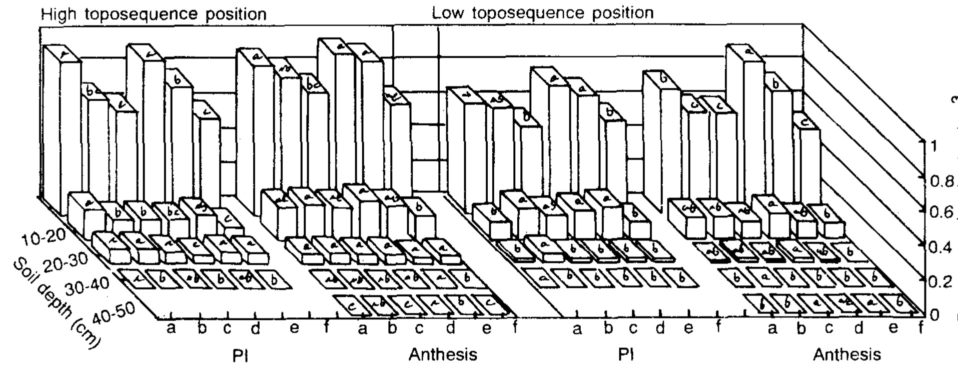


Fig. 5. Root mass density of 6 rice cultivars (a) KDML 105, (b) MSG 19, (c) RD 9. (d) Chieng Saen, (e) IR 20 and (f) IR 46 grown at high and low toposequence positions (Pantuwan *et al,* 1993 unpubl. data)

More than 80% root length and 90% root mass were obtained in the top 20 cm soil layer, irrespective of soil hydrology (Tables 1, 2). Both RLd and RMD decreased exponentially with the soil depths in all genotypes. This trend was similar to previousstudies on rice roots (Pantuwan *et al.,* 1992; Sharma *et al.,* 1987). Genotypes on the low toposequence position had higher percentage of roots in the top l0cm soil layer than genotypes on the high toposequence position. This relationship was reversed in the 10-50 cm soil layer.

Table 7. Percent root length distribution of six rice cultivars grown under two toposequence positions at Ubon Rice Research Centre, Thailand. (Pantuwan *et al.,* 1993, unpubl. data).

Cultivar	Root length distribution(%) at soil depth								
	0.10 (cm)	10-20 (cm)	20-30 (cm)	30-40 (cm)	0-10 (cm)	10-20 (cm)	20-30 (cm)	30-40 (cm)	40-50 (cm)
	Panicle initiation				Anthesis				
High toposequence									
KDML 105	71.43	17.11	8.97	2.483	61.63	27.48	9.46	1.410	0.017
	±2.01	±1.62	±0.73	±0.251	±5.01	±5.17	±0.69	±0.318	±0.008
NSG19	60.61	20.40	16.09	2.894	58.69	28.00	12.15	0.983	0.176
	±2.60	±1.60	±1.52	±0.364	±3.45	±2.65	±0.88	±0.275	±0.042
RD9	65.09	18.50	11.72	4.691	62.63	25.06	10.97	1.233	0.100
	±3.08	±3.06	±1.36	±1.306	±1.75	±2.15	±1.09	±0.260	±0.026
Chieng Saen	70.01	16.55	11.91	1.533	67.71	21.55	9.69	0.892	0.152
	±1.63	±1.48	±1.06	±0.365	±3.88	±3.96	±0.95	±0.225	±0.049
IR20	63.50	19.92	13.58	3.024	63.50	28.82	9.62	1.013	0.050
	±1.78	±0.73	±0.86	±0.670	±3.81	±3.13	11.23	±0.201	±0.011
IR46	72.60	13.88	10.33	3.195	65.00	19.47	13.80	1.636	0.094
	±2.24	±1.99	±1.98	±1.336	±3.35	±2.30	±2.29	±0.484	±0.044
Mean	67.2	17.7	12.1	2.970	63.2	24.6	10.95	1.195	0.098
	±1.97	±0.99	±1.02	±0.421	±1.25	±1.38	±0.71	±0.117	±0.024
Low toposequence									
KDML105	71.58	18.21	7.73	2.475	77.34	17.28	3.98	0.879	0.323
	±5.26	±3.31	±1.42	±1.010	±3.11	±2.38	±0.88	±0.208	±0.035
NSG19	58.79	28.27	11.57	1.376	76.85	16.99	3.87	1.854	0.430
	±1.89	±1.65	±1.11	±0.689	±2.57	±3.76	±1.00	±1.185	±0.091
RD9	66.01	25.70	7.46	0.827	79.96	15.43	2.66	1.185	0.685
	±2.34	±1.99	±1.36	±0.372	±2.12	±2.22	±0.45	±0.195	±0.191
Chieng Saen	67.79	25.71	5.59	0.896	70.17	21.67	5.82	1.856	0.477
	±3.09	±2.22	±1.36	±0.297	±1.88	±1.99	±0.88	±0.173	±0.061
IR20	66.96	26.67	5.85	0.522	76.20	17.91	4.46	1.107	0.318
	±1.94	±2.02	±1.58	±0.166	±2.97	±2.28	±0.94	±0.168	±0.049
IR46	71.70	19.04	8.42	0.836	79.84	16.69	2.13	0.750	0.586
	±1.51	±2.74	±1.66	±0.268	±2.51	±1.91	±0.59	±0.156	±0.069
Mean	67.1	23.9	7.8	1.155	7676	17.66	3.82	1.284	0.470
	±0.75	±0.48	±0.24	±0.10	±0.91	±0.84	±0.43	±0.14	±0.027

Table 2. Percent mot mass distribution of six rice cultivars grown under two toposequence positions at Ubon Rice Research Centre, Thailand. (Pantuwan *et al.,* 1993, unpubl. data).

Cultivar	Root mass distribution(%) at soil depth								
	0-10 (cm)	10-20 (cm)	20-30 (cm)	30-40 (cm)	0-10 (cm)	10-20 (cm)	20-30 (cm)	30-40 (cm)	40-50 (cm)
	Panicle initiation				Anthesis				
High toposequence									
KDML105	75.66 ±2.53	15.37 21.65	8.03 20.96	0.941 ±0.302	77.07 ±0.48	17.09 ±1.06	5.31 ±0.57	0.519 ±0.15	0.008 ±0.001
NSG19	75.75 ±3.21	13.52 21.48	10.36 ±1.85	0.371 ±0.093	73.96 ±2.24	18.94 ±1.89	6.26 ±0.49	0.804 ±0.253	0.037 ±0.003
RD9	75.24 ±1.77	15.09 ±2.27	8.73 ±1.58	0.935 ±0.358	73.27 ±1.32	19.57 ±0.89	6.29 ±1.03	0.857 ±0.230	0.013 ±0.003
Chieng Saen	83.63 ±0.90	11.06 ±0.53	5.08 ±0.67	0.233 ±0.042	75.63 ±2.56	18.79 ±2.29	5.08 ±0.60	0.478 ±0.055	0.039 ±0.002
IR20	76.91 ±1.84	14.83 ±0.89	7.74 ±1.13	0.525 ±0.099	78.09 ±1.23	17.24 ±0.71	3.66 5.68	0.983 ±0.140	0.030 ±0.004
IR46	78.36 ±1.08	11.27 ±1.56	9.90 ±1.58	0.480 ±0.055	76.86 ±2.59	16.66 ±2.23	1.85 ±1.09	0.618 ±0.104	0.009 ±0.002
Mean	77.6 ±1.29	13.5 ±0.79	8.3 ±0.77	0.581 ±0.120	75.8 ±0.77	18.0 ±0.49	5.41 ±0.40	0.710 ±0.082	0.023 ±0.006
Low toposequence									
KDML105	83.22 ±2.73	12.84 ±1.59	3.18 ±1.18	0.860 ±0.334	83.72 ±2.69	14.13 ±1.90	1.74 ±0.70	0.377 ±0.251	0.029 ±0.008
NSG19	72.25 ±1.76	20.64 ±1.56	6.71 ±0.69	0.391 ±0.175	78.63 ±1.53	16.49 ±2.03	3.20 ±0.80	1.637 ±0.458	0.047 ±0.008
RD9	75.52 ±2.27	20.07 ±1.35	4.22 ±1.17	0.181 ±0.048	82.89 ±1.74	14.20 ±2.07	2.24 ±0.39	0.580 ±0.190	0.090 ±0.013
Chieng Saen	80.20 ±1.79	16.77 ±1.49	2.79 ±0.78	0.239 ±0.084	85.25 ±1.06	13.66 ±0.68	2.54 ±10.35	0.504 ±0.101	0.047 ±0.011
IR20	76.39 ±0.94	19.90 ±1.6	3.45 ±0.85	0.258 ±0.104	85.49 ±1.86	12.15 ±1.06	1.99 ±0.86	0.297 ±0.193	0.074 ±0.011
IR46	82.03 ±1.31	14.46 ±1.62	3.27 ±0.50	0.235 ±0.069	82.98 ±2.54	14.99 ±2.20	1.73 ±0.53	0.258 ±0.054	0.040 ±0.006
Mean	78.3 ±1.73	17.4 ±1.35	3.9 ±0.59	0.361 ±0.104	82.8 ±0.93	14.3 ±0.59	2.2 ±0.23	0.609 ±0.211	0.054 ±0.009

Coefficients of variation of RLD and RMD within and between genotypes were small near the soil surface and increased with soil depth in all growing conditions. However, data at high toposequence position tended to have smaller coefficients of variation than the data at low toposequence position.

Root : shoot ratio

In comparison to soil hydrology, soil texture had a more dominant effect on root:shoot ratio (Table 3). Root : shoot ratios were higher in loamy sand than in clay soil. High nutrient content associated with a clay texture, coupled with assured water supply, apparently led to the production of more shoots than roots. This may indicate that under nonlimiting nutrient and water supply, deep or extensive root systems may not be required. Root : shoot ratio did not vary as much among genotypes as among growing environments (see SEM values in Table 3).

Table 3. Root : shoot ratios of three rice cultivars grown under rainfed conditions.

	Toposequence/soil type					
Cultivar1 Physiological age	High/ loamy sand	Low/ loamy sand	Low/ clay	High/ loamy sand	Low/ loamy sand	Mean±SEM
	1991			1992		
Panicle initiation						
KDML105	0.37	0.34	0.26	0.16	0.19	0.26±0.046
RD9	0.36	0.28	0.25	0.18	0.17	0.25±0.039
IR46	0.41	0.36	0.34	0.17	0.15	0.29±0.059
Mean	0.38	0.33	0.28	0.17	0.17	
±SEM	±0.015	±0.024	±0.0028	±0.006	±0.012	
Anthesis						
KDML105	0.14	0.13	0.09	0.09	0.10	0.11±0.012
RD9	0.15	0.14	0.11	0.12	0.13	0.13±0.008
IR46	0.14	0.13	0.08	0.09	0.12	0.13±0.016
Mean	0.14	0.13	0.09	0.10	0.12	
±SEM	±0.003	±0.003	±0.008	±0.010	±0.009	

CONCLUSION

Under rainfed conditions, rice root systems were significantly affected by genotype, soil water regime, and soil type. Differences in root systems among genotypes were large in loamy sand soil subjected to alternate wetting and drying. Differences in root systems decreased under flooded conditions on fine textured soils. Root:shoot ratios were affected more by soil type than by soil hydrology. Coarse-textured soils subjected to alternate wetting and drying may provide appropriate growing environment for the evaluation of root systems of rainfed rice.

REFERENCES

Kawata S, Ishihara S (1959) Study on the root hairs in rice plant. *Proc. Crop Sci. Soc. Jpn.* **27:**341-348.

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

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

Ogunremi LT (1991) lnfluence of bulk density and moisture regime of a permeablesoil on the performance of lowland rice, *Oryza sativa* L. *Trop. Agric.* **68:**129-134.

O'Toole J C, Bland W L (1988) Genotypic variation in crop plant root systems. *Adv. Agron.* **41:**91-145.

Sharma P K, De Datta S K, Redulla C A (1987) Root growth and yield response of rainfed lowland rice to planting method. *Exp. Agric.* **23:**305-313.

Thangaraj M J, O'Toole J C, De Datta S K (1990) Root response to water stress in rainfed lowland rice. *Exp. Agric.* **26:**287-296.

Yoshida S, Hasegawa S (1982) The rice root system : its development and function. Page 97-114. In : Drought resistance in crops with emphasis on rice. International Rice Research Institute, Philippines.

SOCIAL CONSEQUENCES OF STRESSED ENVIRONMENTS

☐ *Thelma R. Paris*[1], *Abha Singh*[2] *and Mahabub Hossain*[1]

SUMMARY

Socio-economic studies were conducted in Chandpur and Mungishpur villages of eastern U.P., interfaced with the biophysical characterization of selected rainfed environments. This paper examines the labour contributions by gender differentiation and social and economic groups and the problems of women farmers in agricultural productions in different lowland rice ecosystems. The paper provides suggestions which can improve crop and animal productivity as well as improve the welfare of the entire family, particularly the females, and children. The study revealed that the sexual division of labour is related to the social position of the household and access to non-farm income. The crop-production, livestock raising and non-farm activities are interrelated. The farmers can bear more risks in rice cultivation if they have access to income from non-farm sources and would be receptive to input-intensive technologies.

INTRODUCTION

In recent years, greater attention is being given to the complex, diverse and risk prone (CDR) rainfed regions where mostly the poor people are located. India has 40 million hectares of rice growing areas. While Northern and Southern India has benefitted from the modern rice varieties and irrigation, the vast rainfed areas in eastern India has lagged behind. Eastern India which is comprised of Assam, Bihar, West Bengal, Orissa and eastern parts of Uttar Pradesh and Madhya Pradesh has the highest incidence of rural poverty in the country. Although it is the largest rice growing area in India, accounting 60% of the country's rice area (26.8 million ha), only a third of the total rice production comes from this region. About half (480 million) of the country's population living in this region is largely dependent on rice farming. Macro level analysis of rice growing ecosystems showed that out of the 26.8 m ha rice areas, only 21.2% is irrigated, 47.7% is under rainfed lowlands and the remaining 14% is under deep and very deep water ecosystems. The rainfed lowlands ape drought prone and submergence prone (Singh, 1992).

---

[1] Social Sciences Division, IRRI, P.O. Box 933, Manila Philippines

[2] N D University of Agriculture and Technology, Kumarganj, Faizabad, India

Narendra Deva University of Agriculture and Technology (NDUAT), Kumarganj, Faizabad, Uttar Pradesh is one of the agricultural research centres under the ICAR-IRRI Collaborative Rainfed Rice Project in eastern India which is involved in conducting on-farm research to increase rice production while improving the efficiency of resources use in rice farming. The multidisciplinary team involved in the project emphasizes on specific environments and socioeconomic circumstances of the farmers of the region and focuses the attention on development of technology consistent with resource endowments and farmer's needs. However, constraints to increasing rice productivity, particularly in stressed and fragile environments can not be well understood without knowing how farming households, their female members in particular, allocate scarce resources to achieve and maintain food security. The Social Sciences Division of IRRI in collaboration with the NDUAT conducted socioeconomic studies which will be interfaced with the biophysical characterization of selected rainfed environments in Uttar Pradesh, eastern India.

This paper a) specifically examines the labour contributions of men and women by different social groups in different lowland rice ecosystems; b) identifies problems which women farmers face in agricultural production and; c) recommends strategies which can improve crop and animal productivity as well as increase the welfare of the entire family, particularly, the female members and children.

We hypothesize that due to adverse physical and socioeconomic conditions, poverty drives women to increase their time and labour allocation to rice cultivation. The proximity of rice based villages to towns and cities and higher wages from non-farm employment induce male migration either seasonally or permanently and this increases women's participation in farming. Further more, we hypothesize that social classes and gender are important variables which affect rice cultivation in eastern Uttar Pradesh.

METHODOLOGY

We selected two typical lowland rainfed sites, in eastern Uttar Pradesh, namely Chandpur and Mungishpur which are different in terms of proximity to the city and physical endowments. Chandpur is closer (3 kms) to Faizabad city while Mungishpur is 28 kms away. Mungishpur represents drought prone area which is favourable rainfed during years of high rainfall while Chandpur represents shallow and submergence prone area which is favourable rainfed during the years of low rainfall. In these sites, on-farm experiments on component technologies e.g. varietal trials with a farming systems perspective are being conducted by the research staff of NDUAT, in collaboration with the International Rice Research Institute under the ICAR-IRRI Collaborative Rainfed Rice Program funded by the Ford Foundation and International Fund for Agricultural Development (IFAD).

We interviewed the principal heads (male and female) of 94 households in Chandpur and 78 households in Mungishpur from 1992- 1993 after which we classified them by social status (higher, scheduled caste and backward class).

RESULTS AND DISCUSSION

Social structure of the population

In both villages, majority of the population belongs to the lower castes, 88% in Chandpur and 92% in Mungishpur. However, most of the land is owned by the upper castes.

Gender gap in education, training and extension

There is a wide gap in terms of education by caste and by sex of adult workers. Figure 1 shows that illiteracy rate is high among the lower castes than the higher castes at both villages. In Chandpur, respectivily 92% and 84% of the total female respondents are illiterate. Similarly, in Mungishpur, 98% and 100% of the total female respondents are illiterate. However, the gap is even wider between males and females. The high illiteracy rate of women than men is common in eastern India. There seems to be a relationship between the environment and female illiteracy rates, Five populous states (Andhra Pradesh, Bihar, Madhya Pradesh, Rajasthan and Uttar Pradesh) account for more than half of India's illiterate females. These five states contain 89% of India's districts where the rural female literacy rate is below 5%; 83% of those are with rates of 5- 9%, and with 67% of those between 10-14%. Illiteracy is especially widespread among rural women of the scheduled castes and scheduled tribes. Many parents do not send their daughters to school because their labour is

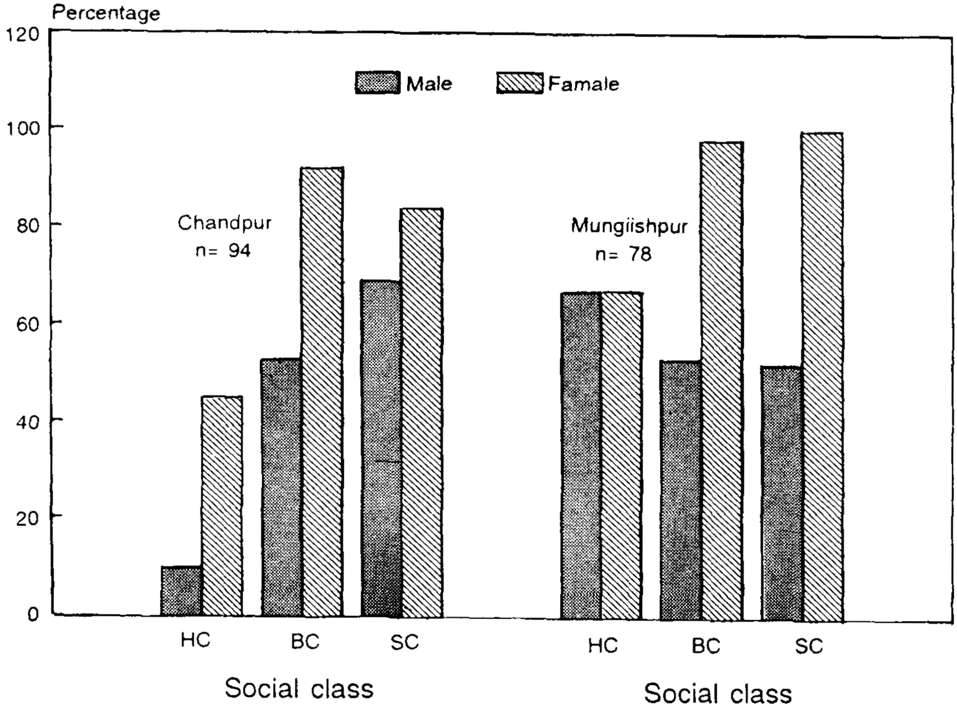


Fig. 1. Illiteracy rates of principal male and female farmers in rainfed villages of Faizabad, Uttar Pradesh, India.

needed for agricultural and household tasks as well as for domestic chores such as cooking and looking after young siblings especially when the mother has to work in the fields. Parents are willing to forego the labour of sons and even incur cash expenses on their education in anticipation of huge dowery in future (earnings and security for the family) since the son will remain with the family even after marriage and contribute to household earnings (Bennett, 1989).

In terms of access to agricultural information, women obtain information about crop cultivation from their husbands, neighbours and other women. Despite the important roles they play in agriculture, scientists include only male farmers when conducting on-farm trials and only recently have begun to include women farmers. Women also perceived themselves as housewives rather than farmers.

Cropping systems

In both villages rice followed by wheat is grown mainly for home consumption. Land preparation for rice is done in June, transplanting or broadcasting in July, weeding in August, harvesting in October and threshing in November. Wheat is sown in January, harvested in March and threshed in April. In June, land is again prepared for rice. Some farmers mix wheat and mustard and grow lentils, grams and peas after rice. Sugarcane is also grown in the upland areas from February to May. The availability of tubewells (8 in Chandpur and 3 in Mungishpur) enables few farmers in Chandpur to grow vegetables which are sold in the market.

Rice area and yields

Fig. 2 shows the average rice area holding across villages and by socioeconomic status. Landholding devoted to rice is higher in Mungishpur than in

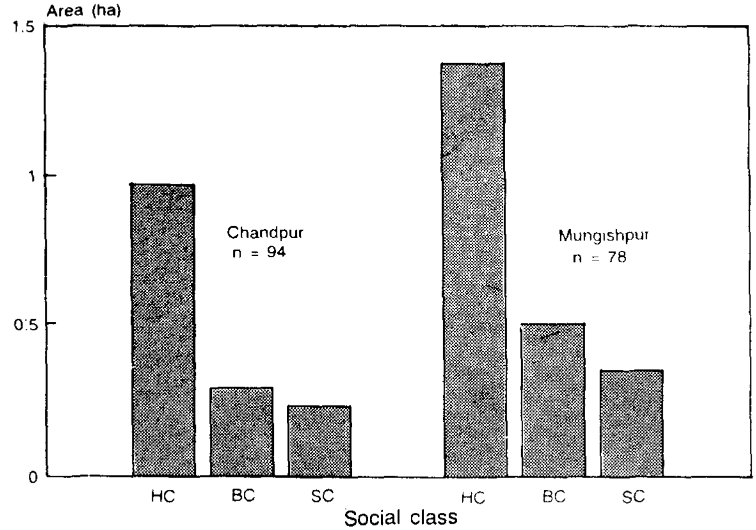


Fig. 2. Average rice area by social class in rainfed villages of Faizabad, Uttar Pradesh, India.

Chandpur. Because of the proximity of Chandpur to Faizabad, the nearest urban centre, farmers diversify their income by growing vegetables and raise cattle for milk production. In Mungishpur, farmers have lesser options for income diversification because they are far from the markets, thus they put more efforts in increasing rice production.

In general, higher castes have larger rice farms (0.97 ha in Chandpur and 1.37 ha in Mungishpur) while the lower castes have smaller areas (0.5 ha and less).

Despite the smaller holding size in Chandpur, the average rice yields are higher (2.0 to 3.24 tons/ha) compared with Mungishpur (less than 2 tons/ha). The farmers from the higher castes obtained higher yields per hectare than the farmers from the lower castes (Fig. 3). Richer farmers not only make more profit because they are "receptive" to new rice technologies but they have cash and capital to purchase for "input intensive" system. On the other hand, small farmers are less willing to take the risks of applying inputs as their lands are often located in less favourable conditions.

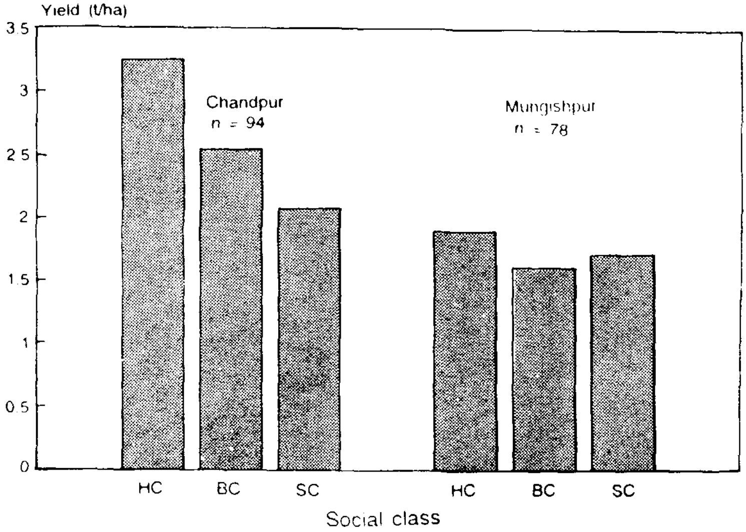


Fig. 3. Average rice yield by social class in rainfed villages of Faizabad, Uttar Pradesh, India

Constraints to increasing rice yields

The lower rice yields in Mungishpur are due to many reasons. Drought is a common environmental constraint which influences rice yields particularly when it occurs during the grain filling stage. The average rainfall in U.P. is around 1,000 mm and total monsoon days are about 125 days in a normal year. However, rainfall is erratic and varies within the year. The coefficient of variability of yearly rainfall in U.P. ranges from 25 to 30%. The approximate probability of deficient rainfall (deficiency in rainfall numerically equal to or greater than 25% of the normal) in

U.P. is once in four years. Percentage occurrence of droughts of moderate class and worse in the Kharif season is in the range of 20-25% in eastern U.P.. In addition, long breaks in rainy days is a common phenomenon in India even during normal years. Such breaks are common in U.P. and they result in contingent and invisible droughts.

Due to the extreme variability in the climatic conditions, farmers, particularly in the drought prone areas are not willing to invest more inputs such as fertilizer and herbicides.

Furthermore, the caste system which creates inequality in access and distribution of resources is prevalent in eastern U.P.

Labour use in rice production

Tables 1 and 2 show the total labour use in rice production. The total labour input is higher in Chandpur than in Mungishpur (188 vs 132 labour days per ha.). The contribution of female labour in rice production is higher than men in both villages (84% in Chandpur and 67% in Mungishpur). The participation of adult female workers is higher in Chandpur because men are more engaged in non-farm jobs than in Mungishpur. In both villages, the social category of households also determines the extent of female labour participation in rice farming. Based on the household surveys, women from the higher caste do not provide physical labour regardless of the size of their landholdings. Informal interviews with women from the higher castes who have small landholdings indicated their desire to work in their own fields or supervise hired labours, but are constrained to do so due to social taboos. However, they are involved in production activities within the confines of their homesteads such as seed management, storage and preparation of dry cowdung

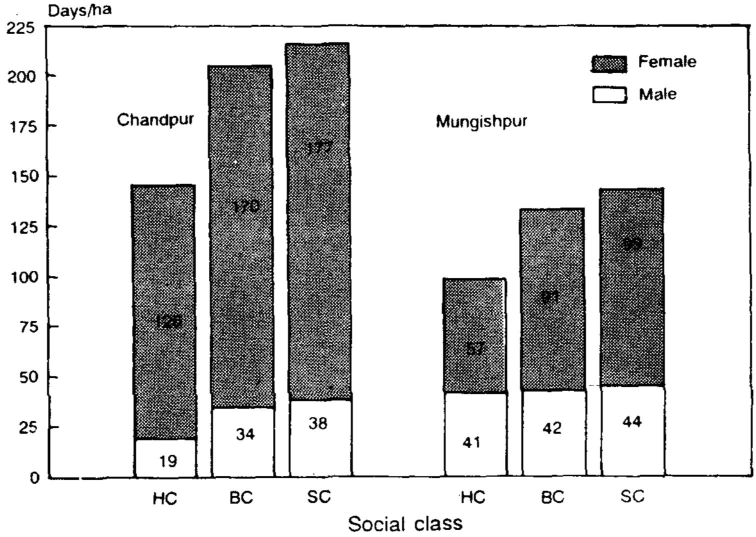


Fig. 4. Total labour use in rice farming by gender and social class in Chandpur and Mungishpur, Faizabad, Uttar Pradesh India.

for fuel. In contrast, female family members among the lower castes work on their farms as well as in other farms as exchange or hired labourers. In Mungishpur, exchange labour is still widely practiced as a strategy for the lack of cash to pay for hired labourers. Fig.4 shows higher labour input of female adult workers in rice cultivation both in higher and lower caste farming families.

Table 1. Labour days per hectare in Chandpur, (rainfed lowland) 1991-92.

Activity	Family			Hired			Total		
	Adult Male	Adult Female	Both	Adult Male	Adult Female	Both	Adult Male	Adult Female	Both
Prepare land	3.23	0.00	3.23	0.95	0.00	0.95	4.18	0.00	4.18
Apply manure/ chemical	3.63	2.29	5.92	0.65	0.12	0.77	4.28	2.41	6.69
Irrigate	1.52	0.27	1.79	2.44	0.00	2.44	3.96	0.27	4.23
Broadcast	3.30	2.41	5.71	0.80	0.06	0.86	4.10	2.47	6.57
Transplant	2.05	7.29	9.34	1.64	40.93	42.57	3.69	48.22	51.91
Weed	1.55	13.42	14.97	0.12	33.02	33.14	1.67	46.44	48.11
Harvest	5.62	10.83	16.45	1.07	15.20	16.27	6.69	26.03	3272
Thresh	1.04	17.16	18.20	0.15	14.81	14.96	1.19	31.97	33.16
Totaln=94	21.94	53.67	75.61	7.82	104.14	111.96	29.76	157.81	187.57
% contribution	30	70	100	7	93	100	16	84	100

Table 2. Labour days per hectare in Mungishpur, (rainfed lowland) 1991-92.

Activity	Family			Hired			Exchange			Total		
	Adult Male	Adult Female	Both	Adult Male	Adult Female	Both	Adult Male	Adult Female	Both	Adult Male	Adult Female	Both
Prepare land	6.66	0.00	6.66	1.56	0.00	1.56	0.00	0.00	0.00	8.22	0.00	8.22
Apply manure/ chemical	3.27	2.52	5.79	0.60	0.00	0.60	0.00	0.00	0.00	3.87	2.52	6.39
Irrigate	2.59	1.06	3.65	0.10	0.05	0.15	0.00	0.00	0.00	269	1.11	3.80
Broadcast	2.97	1.99	4.96	0.55	0.13	0.68	0.00	0.00	0.00	3.52	2.12	5.64
Transplant	3.60	8.66	12.26	4.66	12.07	16.73	0.50	2.16	266	8.76	22.89	31.65
Weed	3.12	12.22	15.34	2.17	7.86	10.03	0.20	1.54	1.74	5.49	21.62	27.11
Harvest	4.18	10.53	14.71	2.06	7.05	9.11	0.35	1.81	2.16	6.59	19.39	25.98
Thresh	2.85	14.28	17.13	1.31	4.15	5.46	0.15	0.98	1.13	4.31	19.41	23.72
Totat n=78	29.24	51.26	80.50	13.01	31.31	44.32	1.20	6.49	7.69	43.45	89.06	132.51
% contribution	36	64	100	29	71	100	16	84	100	33	67	100

Division of labour in rice production

In both sites, the division of labour between male and female workers is very distinct (Fig. 5): Land preparation is exclusively done by men; irrigation and application of fertilizers are predominantly done by men but women also assist particularly when FYM is used as organic fertilizer for crops. Transplanting, weeding, harvesting and threshing activities are highly dominated by female adult workers from the lower caste. The Indian case clearly fits Ester Boserup's hypothesis that where the female labourers come from a caste/ethnic group lower in social status than the families with lands, the women in the latter avoid farm work to maintain status. Similarly in the Philippines, female members in the irrigated farm hire female workers to substitute for them in transplanting and weeding task (Boserup, 1970). In between crop cultivation, women collect animal fodder, cultivate pulses, oilseeds and maize and also perform most of the household responsibilities. These findings indicate the strong correlation between class and gender in rice cultivation and land distribution.

Off-farm and non-farm employment

In Chandpur, the male adult workers from the higher castes showed higher earnings from off and non-farm work than the male adult workers from the lower castes. Male adults from the higher castes have higher paying non-farm jobs because they are better educated. In contrast, male adult workers in Mungishpur earn less than 50% of what the male adult workers in Chandyur earn from off and non-farm employment (Fig.6). These findings indicate that the greater opportunities for non-farm employment for those with better education and skills pull the men away from farm work. The upper caste families in Chandpur are faced with labour shortage since most of their male members go to the cities and their female members do not participate in farming.

While men earn from non-farm employment, women have less opportunities due to their lack of education, mobility, training and skills. The major occupations of male adult members are: teacher, bank manager, labour in iron factory, servant, construction worker, military cook, juice seller, worker in biscuit factory, tailor, casual labour in the university, rickshaw puller, home guard, barber in the military, watchman and driver. A casual labour receives Rs 15 to 20 per day. Because women have less access to paid jobs, they earn supplemental income by gathering, drying and selling "Mahua" fruit flowers and selling them at 6-10 Rs/kg. They earn approximately Rs 500-600 (1US$=Rs30) within 15-30 days in May when the lands are not cultivated. They share 50% of the output if the trees are owned by higher castes.

Agricultural wage rates are higher in Chandpur than in Mungishpur due to its proximity to Faizabad, the nearest urban centre. There is also difference in wage rates for male and female workers for different operations, a male worker with bullock receives Rs 25 per day while female workers receive Rs 10 for transplanting and weeding. Transplanting is either paid on an individual or a contract basis. Harvesters and threshers are paid through share basis. Thus when the yields are low, the share of the harvester/thresher is also low.

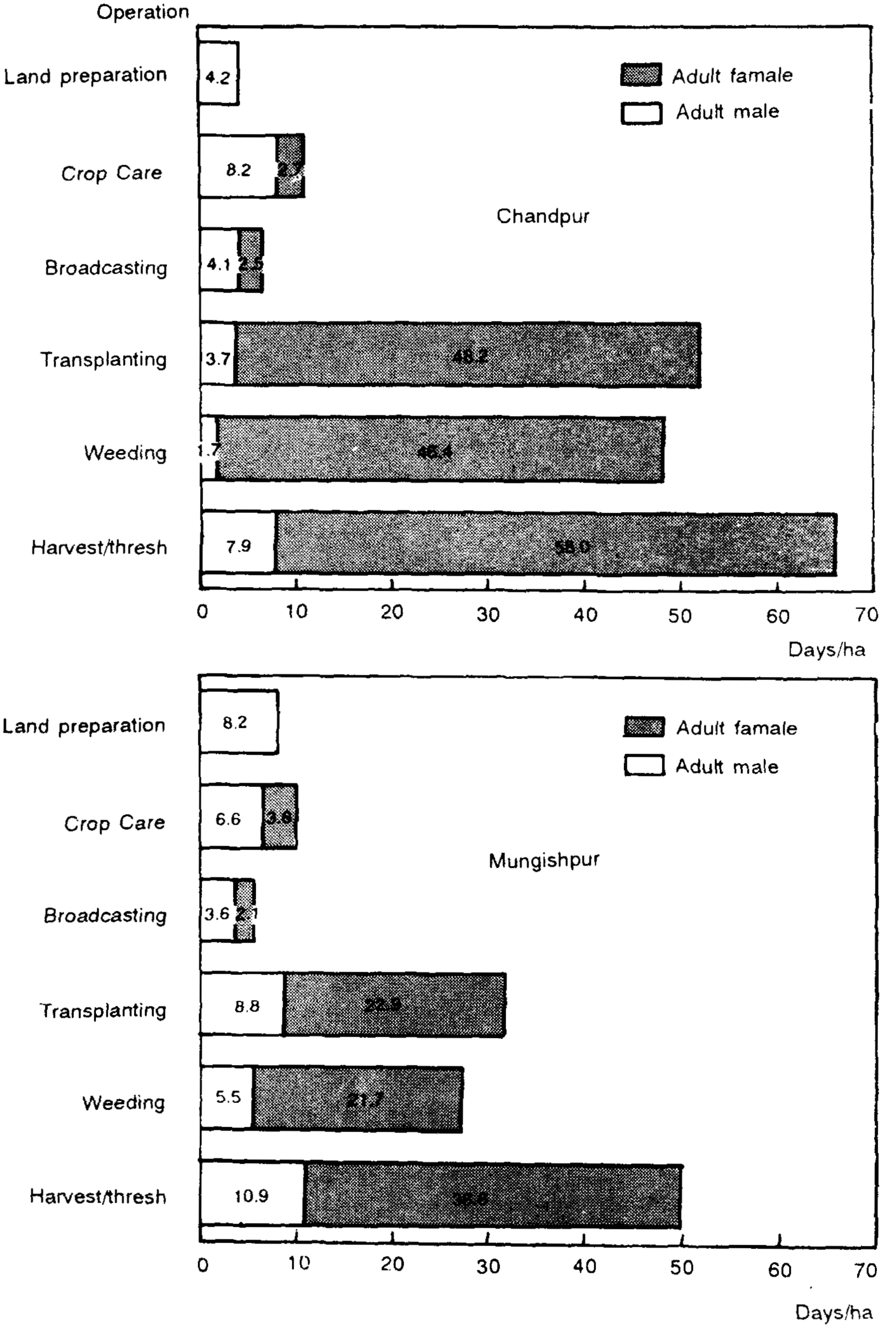


Fig. 5. Labour participation by gender in different rice farming activities, Chandpur and Mungishpur, Faizabad, War Pradesh, India.

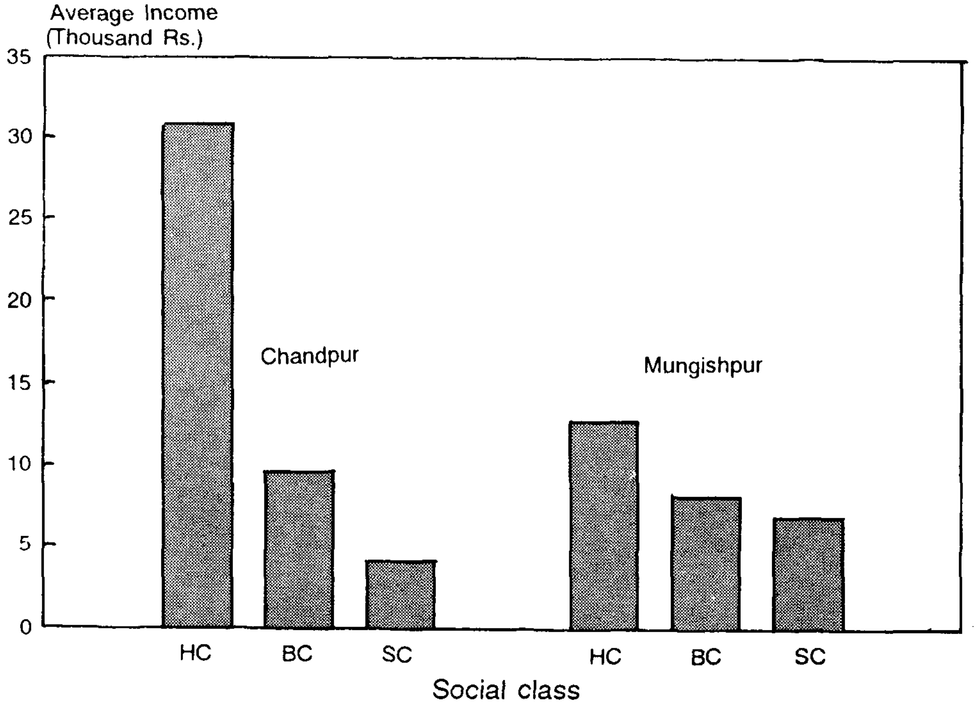


Fig. 6. Average annual off-farm and non-farm income of adult male workers by social class in Faizabad, Uttar Pradesh, India.

Animal systems

In both villages, animals constitute an integral part of a mixed farming systems. Large animals (bullock and cattle) provide draft power for land preparation, manure for crops household fuel and milk for home consumption and income. Ownership of livestock allows farmers to diversify against risks. In Chandpur, more than 50% of the total households interviewed have cattle and less than 38% have bullocks. Because of the proximity of this village to the market, farmers particularly the backward castes (Yadavs), raise cattle for milk which provides them an additional source of income. In contrast, more households in Mungishpur raise bullocks than cattle (Fig. 7). Due to the lower percentage of households which own bullocks in Chandpur, less family male labour, and more income to hire tractors, more farmers in this village use tractors for land preparation. In Chandpur, 41%, 18% and 9% of the backward, scheduled and higher caste households, respectively use tractors. In contrast, in Mungishpur, 15%, 13% and 8% of the backward, scheduled and higher castes, respectively, use tractors (Fig.8).

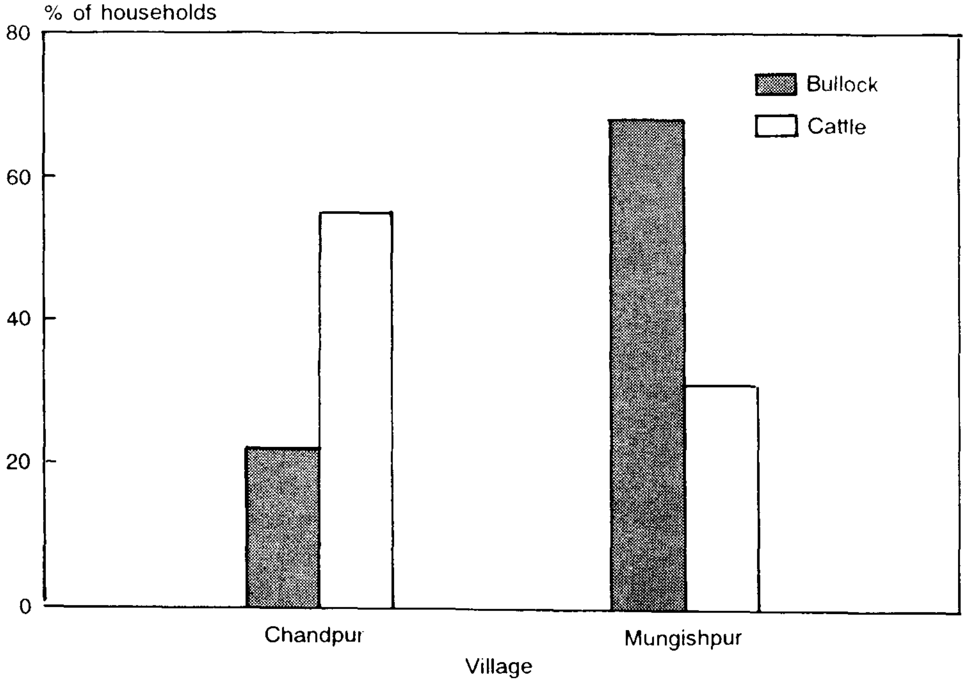


Fig. 7. Percent of households with bullocks and cattles in rainfed villages of Faizabad, Uttar Pradesh, India.

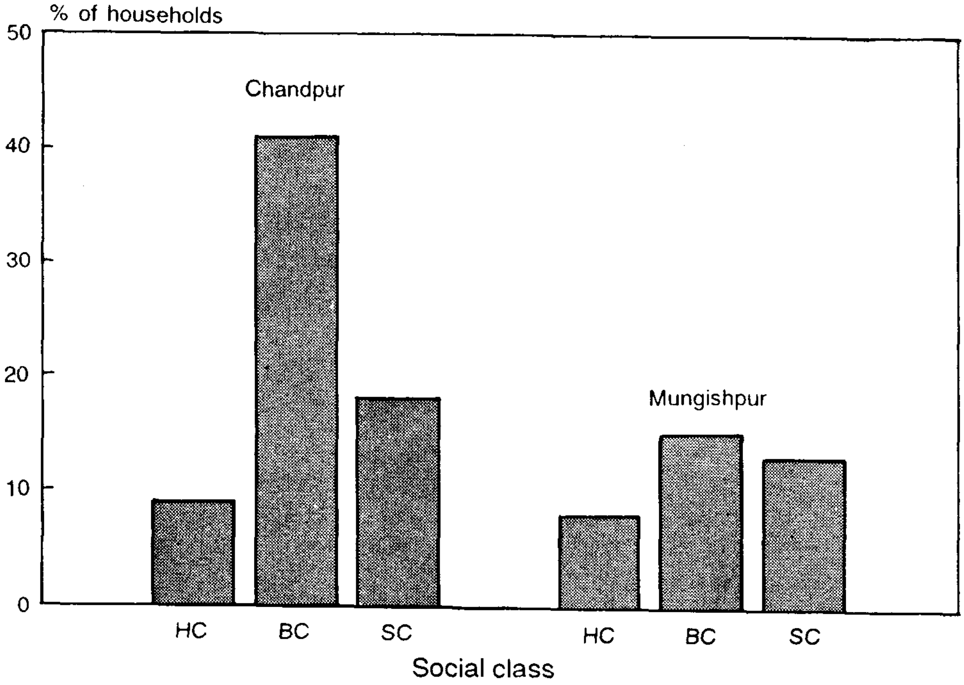


Fig. 8. Percentage of households using tractors in rainfed villages of Faizabad, Uttar Pradesh, India.

At both sites, animals are fed through cut and carry method due to lack of common grazing lands. Farmers use crop residues, grasses and weeds from rice fields to feed their animals. In Mungishpur, farmers grow *”Chari”* and berseem in small plots. During the summer and part of the *“Kharif”* season (March-October), rice and wheat straw are fed to the animals. One animal requires about 6 kgs of straw and 6 kgs of green fodder per day. Green fodder is most scarce from April/May to mid June and available from August to September. Thus, a few farmers grow berseem from October to March while *“Chari”* is grown from March to August/September at about 0.03 ha of land. In Chandpur, very few farmers have sufficient homesteads or field plots for fodder production, thus a few of them rent government owned land to grow berseem or buy foddgr from other farmers. Female family members are mainly responsible in collecting grasses and weeds from distant places. With limited grazing lands, women have to spend half a day daily to collect grasses and weeds, particularly in Chandpur where there are more milch animals which are predominantly cared by female family members. Twice a day they will feed and milk the animals, also clean the shed or area where they are tied and collect the dung to make into fuel cakes. During the drought periods, the only source of fodder and fuelwood is distant forests, thus, women walk farther away from their homesteads to collect animal fodder and fuelwood. With increasing deforestation and the degradation of the common land, the burden falls on women and female children, whose time and energy in gathering firewood has increased substantially.

Social consequences of stressed environments

What emerges from this initial assessment is the need for agricultural scientists to understand not only the consequences of stress environments on rice yields, but also the social consequences of drought on people especially on women who carry the burden of fulfilling their multiple roles as a farmer, farm manager, wage labourer, housewife and mother. With low crop productivity due to the fragile environments, migration of men to the cities in search of work will continue to increase. The number of female *de facto* household heads will also increase and will take over the management of the rice farms. Increasing the demand for female labour in rice production, processing, animal care, collection of animal fodder and fuelwood may lead to changes in cooking habits (fewer meals), less time devoted to child care and breast feeding. During periods of drought, the problem of securing food for the family and fodder for the animals are hardships shouldered by women.

The goal of increasing rice productivity will be difficult to achieve if management, particularly under stressed environments which require new knowledge and skills, will be left to female family members, the majority of whom are illiterate and without access to training and extension services. We also expect that their work burden will increase as they face competing demands on their time between households duties (caring for their children, collecting water, collecting fuelwood, etc.) and agricultural responsibilities (management of crops, animals, collecting animal fodder, processing, etc.) unless their male counterparts or children share in that activities. The greater time spent outside the homes may have detrimental effects on the welfare of the children unless women receive income which they can use to provide the basic needs of their children.

The preliminary results of this study reveal that the environmental stress which cause low crop productivity and income pushes men to engage more of their time and attention in non-farm jobs and consequently, women's work in rice cultivation increases. The low crop productivity will further exacerbate the disparity between the higher and lower castes and women will further be burdened. Women should be given access to education, training and extension services to enhance their role in decision-making and in increasing farm productivity. They should be given knowledge and skills on the timeliness of weeding and transplanting operations which affect rice yields. Since they are the preservers of seeds, their indigenous knowledge and varietal preferences are important in rice breeding programmes.

CONCLUSION

a) The sexual divison of labor is related to the social position of the household and access to non-farm income.

b) Crop production, livestock raising and non-farm activities are interrelated.

c) Farmers can bear more risks in rice cultivation if they have access to income from non-farm sources and would be receptive to input-intensive technologies.

Suggestions for research and extension

a) *Provide female workers access to education, training and extension programs* : Non-involvement of female workers in training and extension programs and the illiteracy of female workers may be important constraints to the adoption of improved farming practices.

b) *Include women farmers in evaluating new rice varieties* : In both villages, improved rice varieties such as NDR-423, NDR- 402, NDR-4001, Mahsuri which are recommended for these rainfed environments have been distributed and planted and are currently being evaluated by women cooperators.

c) *Introduce input-intensive cultivars* : In the village where farmers have access to non-farm employment and income.

d) *Introduce new species of animal fodder* : Seedlings of new species of forage have been introduced to increase the local supply of animal feeds and should be evaluated by male and female farmers.

e) *Strengthen research-extension-farmers linkage* : There are new initiatives in ICAR whereby research-extension-farmer linkage is being strengthened among agricultural universities and other institutions dealing with on-farm experiments, for example, the Project Directorate for Cropping/Faming System.

REFERENCES

Bennett Lynn (1989) Gender and poverty in Asia: Issues and Opportunities Concerning Women in the Indian Economy. The World Bank, Washington, D.C. USA

Boserup Ester (1970) Woman’s role in economic development. St. Martin’s Press, New York, U.S.A..

Singh V P (1992) Rainfed lowland rice-based farming system in eastern India. Paper presented at the Rainfed Lowland Rice Farming Systems Meeting, Yangoon, Myanmar.

DIFFERENTIAL GROWTH IN RICE PRODUCTION IN EASTERN INDIA : AGROECOLOGICAL AND SOCIO–ECONOMIC CONSTRAINTS

☐ *Mahabub Hossain and Alice Laboerte*[1]

SUMMARY

Over the last two decades rice production in Eastern India grew at a satisfactory rate of about 2.7 percent per year. But the growth was uneven across states and districts particularly in Bihar, Orissa and Assam and Eastern Madhya Pradesh where rice production failed to keep up with the population and income induced growth in demand. Production performance was variable even within homogeneous agroecological zones. Performance has been particularly poor in the subhumid plateau regions of Chhotanagpur and Chhatisgarh, which also experienced high rates of rural-urban migration.

Water control and the level of fertilizer use, which are highly correlated, were important factors behind the spatial variation in productivity growth. The level and the growth in rice yield was found to be negatively related with the amount of rainfall, which suggests poor drainage and waterlogging as a significant constraint to growth in rice production. Land tenure is a special social problem as districts with higher incidence of tenancy and landlessness had lower rice yields and slower growth. An inverse relationship is found between the size of farm and the level and growth in rice yield, suggesting that the small size of farm in the region is *not* a serious constraint to the adoption of input-intensive technology. The size of farm, the incidence of irrigation and the instability in rice yield are found important factors behind the spatial variation in fertilizer use and the growth in rice yield.

INTRODUCTION

In the eastern part of India, rice is the principal staple food and agriculture is dominated by the rice-based cropping systems. This geographical area comprises of Assam and the small Northeastern States, West Bengal, Bihar, Orisa and the eastern part of Madhya Pradesh (MT) and Uttar Pradesh (UP) and is inhabited by nearly 500 million people. The region accounts for two-third of total rice area in India, but because of lower productivity, contributes only half to the Indian rice production. Unlike other parts of India where rice is grown under irrigated conditions, rice farmers of the region are

---

[1] International Rice Research Institute. P.O. Box. 933, Manila, Philippines

dependent mainly on monsoon rains which is highly unpredictable, Until recently the growth in rice production was sluggish, and the rice consumers were dependent partly on imports from other parts (mainly Punjab and Haryana) where rice is grown as a commenzial crop (Kumar and Rosegrant, 1993). Since the early 1980s, however, growth in rice production is accelerating, and in the Ganges plain growth in output has surpassed population growth.

In India, poverty and food insecurity are widespread in the eastern region. According to recent estimates the poverty ratio is nearly 60% in Bihar, Orissa and West Bengal, compared to less than 20% in Punjab, Haryana and Gujrat and less than 30% in Tamil Nadu, Andhra Pradesh, Karnataka and Kerala (Dev *et al.,* 1992). The daily calorie intake is less than 2000 per capita in Bihar and Orissa, compared to 2700 in Punjab and between 2400 to 2600 in Haryana, Rajasthan, Gujrat, Kerala and Andhra Pradesh. The high incident of poverty can be partly related to the poor performance of the rice sector which is not only the principal food but also an important source of employment and income for rural population.

Since there is large unmet demand for food, per capita rice consumption is expected to increase with economic prosperity and alleviation of poverty. As the population of the region is still growing at 2.1% per year, the demand for rice may grow by about 3.0% per year, if India could manage a 5% per year growth in gross domestic product for this region. Sustaining a long-term growth of rice production at 3.0% per year, in the face of unfavorable production environment, is a real challenge to rice researchers and development practitioners for this region.

The main objectives of this paper are (a) to estimate the spatial variation in the performance of the rice sector, (b) to understand the role of agroecological factors in spatial variation in the level and growth of rice yields and (c) to assess the interaction between agroecological and socioeconomic factors in constraining the growth in rice productivity.

The study is based on historical data at the district level available from *Agricultural Situation in India* (GOI, 1993) and *Fertilizer Statistics* (Fertilizer Association of India, 1991). The data on agroecological and some socioeconomic characteristics of the districts are taken from Huke and Huke (1982,1990). Growth rates in rice and cereal production have been estimated from the time series data using semi-logarithmic trend lines. To assess the role of agroclimatic and biophysical factors in explaining the differential performance, we have classified the districts into homogenous agroecological regions as defined in India (Sehgal, *et al.,* 1990) and compared the production performance across the zones. We have then applied a multivariate regression analysis on the district level data to estimate the separate impact of selected agroecological and socioeconomic factors. The paper concludes with a summary of major finding and implications for rice research.

REGIONAL VARIATIONS IN PRODUCTION PERFORMANCE

In Eastern India rice production increased at 2.7 percent per year over the last two decades (Table 1). The overall performance was satisfactory considering that population grew at 2.2 percent per year during this period. The per capita availability of rice from regional production increased by about 11 percent over the last two decades. The growth in the productivity of land in rice cultivation (yield rate) was 2.3 percent per year, similar & the performance of Asia as a whole during this period (Hossain and Laborte, 1994). But the absolute level of yield was only 2.2 tons per ha, compared to 5.8 tons in China, 4.5 tons in Indonesia and 2.8 tons in Bangladesh where the production conditions are similar. Within India, the rice yield has reached 4.8 tons in Punjab (in the North) and 4.6 ton in Tamil Nadu (in the south), and in several districts in these two States farmers get more than 5.5 tons per hectare (GOI, 1993).

The production performance was also uneven across the states in Eastern India (Table 1). The growth in production was impressive in Uttar Pradesh, satisfactory in West Bengal, but dismal in Bihar, Orissa and Assam. The annual growth in rice production was about 5.3 percent in eastern UP, and 2.7 percent in West Bengal. Nearly four-fifths of the growth was due to the increase in rice yields made possible through the diffusion of the modern high yielding varieties. In Madhya Pradesh rice production barely managed to keep pace with the growth of population; respectively 2.3 and 2.4 percent per year. In Bihar and Orissa, the growth in rice production was only about 1.6 percent per year. In Orissa, there was an absolute decline in the area harvested with rice, while rice yield increased by 1.9 percent per year.

Since the land frontier has been closing, the future growth in agricultural production in the region must come from the growth in productivity of land. The growth in rice yield was higher than population growth only in Uttar Pradesh and West Bengal. In other states the productivity growth was less than two percent. Assam with a growth in yield at less than one percent per year had the most dismal performance in raising productivity.

An important characteristic of the rice sector in Eastern India is a large year to year fluctuation in rice production due to unreliable monsoons. For some years the production shortfall can be astronomical leading to severe food insecurity for the small and marginal farmers. For example, in Bihar the production shortfall was 67 percent in 1966, 35 percent in 1979, and 24 percent in 1987 compared to the preceding year. In Madhya Pradesh, the harvest failure was 50 percent in 1965, 58 percent in 1979 and 38 percent in 1986 and 1987. Farmers may suffer from both floods and droughts in the same season because of heavy early season rains and prolonged droughts during the end of the monsoon. This makes rice cultivation a risky venture for majority of the farmers who operate at a subsistence level.

Eastern India experienced considerable rural-urban migration of population (Table 1). The average population growth rate over the last two decades was 2.2 percent per year, while the rural population grew at 1.8 percent. The information presented in Table 1 suggests that the rural-urban migration is partly related to the performance of the rice sector. The growth in rural population was almost the same as the total population in UP and West Bengal which experienced an impressive growth in rice production. In Bihar and Orissa which had sluggish growth, 0.3 to 0.4 percent of the people migrated every year to urban areas over the last two decades. The rate of migration from Madhya Pradesh was also substantial. An improved performance of the rice economy can contribute to a reduction in rural-urban migration and help ease pressures on the overburdened cities and urban areas.

Table 1. Growth in rice production and productivity in Eastern India, by states, 1970-91.

	(Percent per year) Rice growth			Population growth	
States	Area	Yield	Production	Rural	Total
Assam	0.94	0.92	1.86	n.a.	2.1
West Bengal	0.45	2.27	2.72	2.1	2.2
Bihar	0.04	1.55	1.59	1.8	2.1
Orissa	-0.34	1.88	1.54	1.4	1.8
Madhya Pradesh	0.62	1.68	2.30	1.5	2.4
Uttar Pradesh	1.03	4.28	5.31	1.9	2.1
Eastern India	0.44	2.27	2.71	1.84	2.2

Source : IRRI Rice Statistics Database.

Note : The growth rates are obtained by estimating semi- logarithmic trend lines on the time series data.

In order to assess the regional variation in growth, we also estimated the production performance at the district level. The districts of Assam were not included in this anslysis due to non- availability of data for many of the variables considered in this study. Many districts have been subdivided into smaller districts since the mid 1970s. Since the data at the subdivided district level was not available for the earlier period, the estimates are obtained at the greater district level. The growth rates are estimated for the 1970-87 period, as the data for the district level was not available for more recent years at the time of the analysis.

The estimated growth in rice and cereal production at the district level are plotted in Figure 1. The extremely variable performance across districts is clearly shown by the figure. Nearly 10 percent of the districts had experienced negative growth, while 20 percent of the districts achieved more than six per cent rate of growth, which must be regarded as highly impressive by any standard. Almost half of the districts achieved a rate of growth of less than three percent year which is needed to meet the population and income growth induced demand for foodgrains in the region . An important point to note from the Fig. 1 is the highly positive correlation between the growth in rice and total cereal production. This signifies the dominant role of rice in achieving food security in Eastern India.

PRODUCTION PERFORMANCE FOR AGROECOREGIONS

To what extent can the diverse performance across districts be attributed to the agroclimatic and environmental factors?. To address this question, we have classified the districts into relatively homogeneous agroecological zones (AEZ) and studied the variations in production performance across and within each zone. If agroecological factors are dominant in influencing rice production we would expect the growth rate to vary across the AEZs, but little variation across districts within each AEZ.

Indian scientists have classified India into 21 relatively homogeneous agroecological regions (Sehgal *et al.,* 1990). The major factors considered in demarcating the zones are water balance and moisture availability, which determine the length of growing period (LGP), elevation of the land, soil characteristics, and the temperature regime as determined by the geographic location of the district. Most of the districts in Eastern India fall under the following five agroecological regions :

Identification of the region	Agroecological region	Land area (million ha)
9	Northern Subhhumid Plains with alluvial soils	12.2
12	Eastern Subhumid Plateau with red and yellow soils (Chhatisgarh)	13.2
13	Eastern Subhumid Plateau with red loamy soils (Chhotanagpur)	27.8
14	Eastern Subhumid Plains with alluvial soils	9.3
16	Eastern Humid Plains with alluvial soils	11.7

The location and characteristics of the zones can be seen from Figs. 2 to Fig. 6, which are reproduced from Sehgal *et al.* (1990).

Table 2 reports the estimates of growth rates in cereal production, and the sources of growth in the production of rice for the five agroecological regions. The production performance is impressive for the three AEZs in the subhumid and humid plains (the Gangetic plain), which increased cereal production at or above 3.5 percent per year over the 1970-87 period. The production of non-rice crops increased at a faster rate than rice, but the growth in rice production itself surpassed population growth.

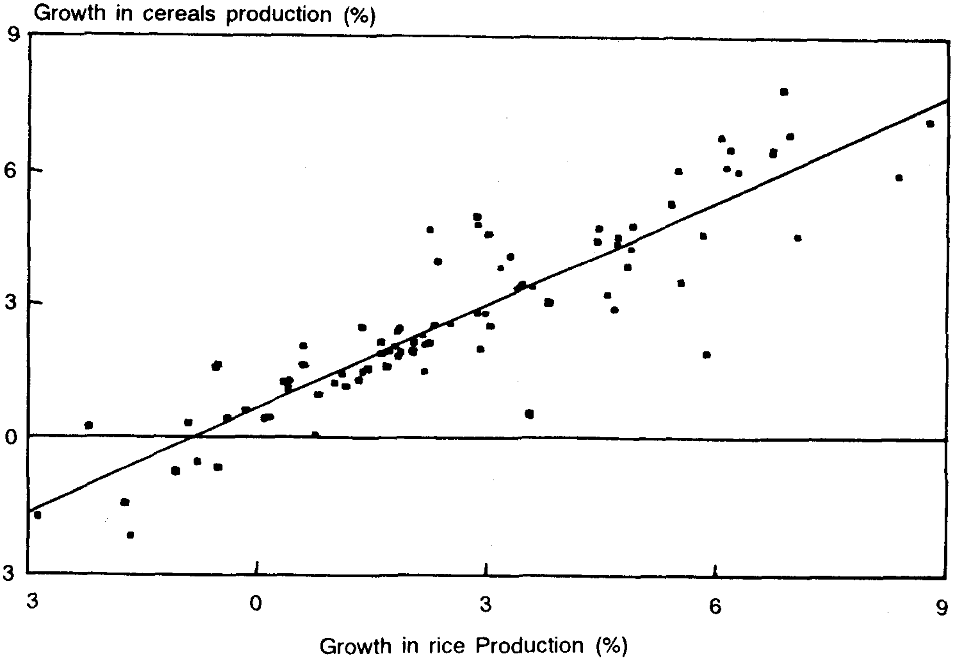


Fig. 1. Growth in cereals production Vs growth in rice production, 1970-87.

The impact of technological progress in rice cultivation can be assessed from the growth in rice yield. For Northern subhumid plains (AEZ 9) and Eastern humid plains (AEZ 16), rice yield increased at 2.8 percent per year, a record superior to that for Asia as a whole (Hossain and Laborte, 1994). In the Eastern subhumid plains (AEZ 16, North Bihar), nearly one-fourth of the growth on rice production was due to area expansion, but the absolute level of the growth in rice yield was respectable at 2.1 percent per year. The Chhotanagyur and Chhatisgarh plateau performed poorly. It will be noted from the standard errors of the estimates (Table 2) that the growth in rice yield was fairly stable in the Eastern subhumid and humid plains, but was highly variable in the Chhatisgarh and Chhotanagpur plateau (AEZ 12) and in the Northern subhumid plains. The variation in the level and the growth in rice yield across districts in different agroecological zones can be reviewed from Tables 3 and 4. Yield levels are fairly low. Only in two out of 60 districts in the region, the average yield for the 1985-87 period was higher than 3.0 tons per hectare, and in 17 districts the yield was less than 1.5 tons per hectare. The majority of the districts in the Eastern humid plains, and Northern subhumid plains had yields over 2.0 tons per hectare, while most of the districts in the other three AEZs had yields below that level. The important point to note is that there is a large variation in the level of yield across districts in all five agroecological zones.

Table 2. Growth of foodgrains and rice production in Eastern India, by agroecological zones, 1970-87. (Figure in percent per year)

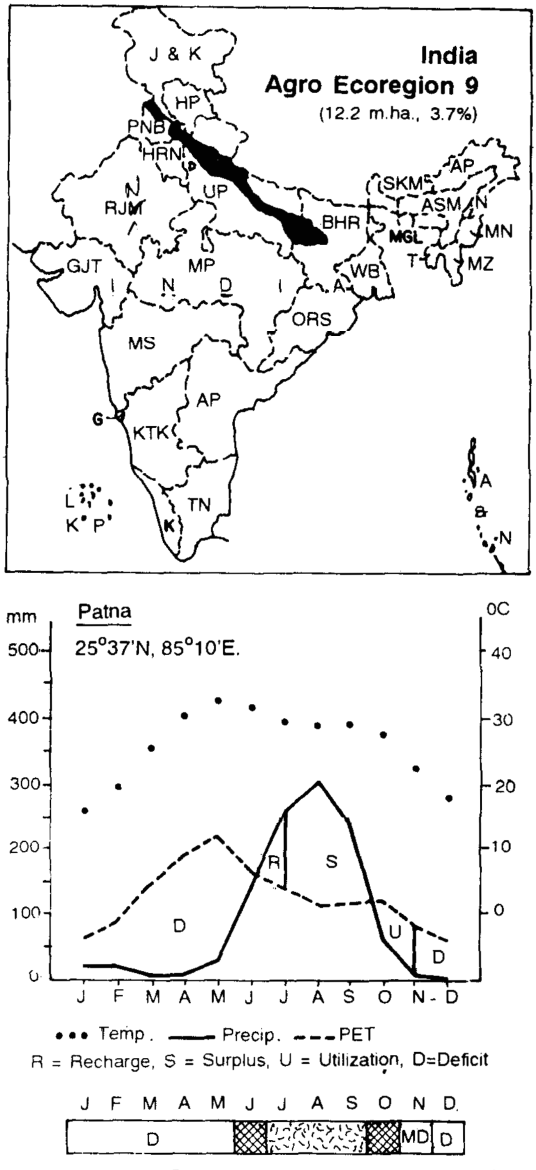
Major agroecoregions		Rice		Cereals	
					production
		area	Yield	Production	
9	Northern Subhumid Plains with alluvial soils	0.72 (0.29)	2.68 (0.97)	3.43 (1.08)	4.32 (0.62)
12	Eastern Subhumid Pleateau with red and yellow soils (Chhatisgarh)	0.54 (0.05	1.68 (1.11)	2.22 (1.13)	2.24 (1.06)
13	Eastern Subhumid Pleateau with red loamy soils (Chhotanagpur)	-0.28 (0.20)	1.21 (0.65)	0.92 (0.81)	1.03 (0.75)
14	Eastern Subhumid Plain with alluvial soils	0.72 (0.19)	2.05 (0.47)	2.78 (0.53)	3.47 (0.36)
16	Eastern Humid plains with alluvial soils	0.45 (0.19)	2.76 (0.40)	3.22 (0.51)	3.45 (0.48)

Note: Estimated by fitting semi-logarithmic trend lines with times series data available at the district level.

Figures within parentheses are standard errors of the estimates. But the record is dismal for the Chhotanagpur plateau where cereal production grew at only 1.0 percent per year and rice production at 0.9 percent. The Chhatisgarh plateau managed to keep pace with the growth of population with a 2.2 percent per year growth in both rice and cereal production. But since the region is characterised by widespread poverty, the income growth induced demand for rice must be significant, and hence the supply of rice has not been able to keep pace with demand.

The performance with respect to the growth of rice yield also varied widely across districts. In 19 of the sixty districts under study, the growth in rice yield was more than 3.0 percent per year; while in nine districts the growth rate was negative, and most of them are located in the Chhotanagpur plateau. Again, the inter-district variation in the growth of rice yield was large for each of the AEZ's.

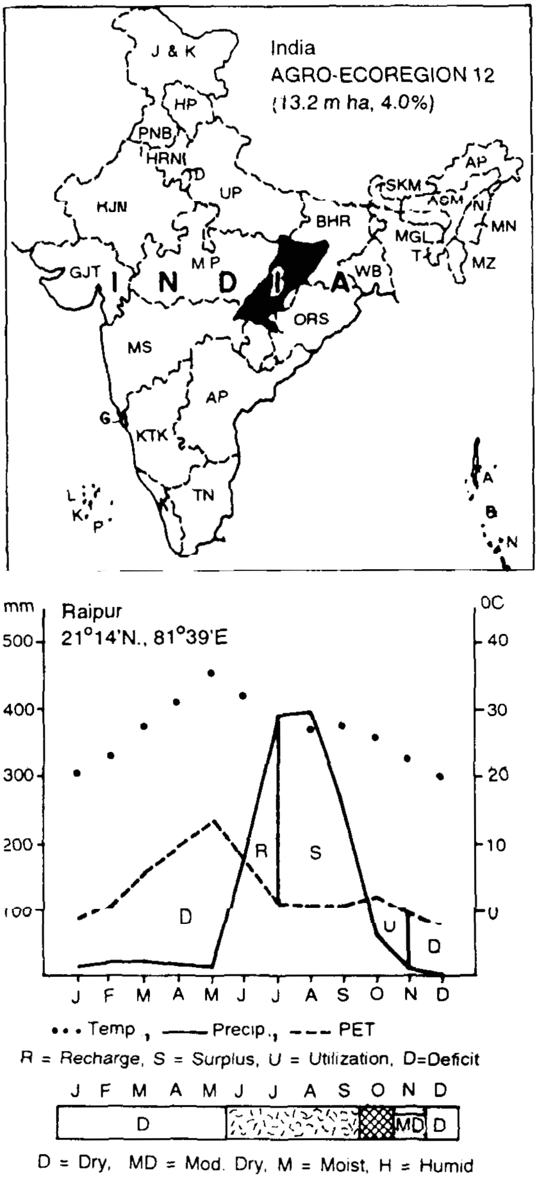
Characteristics :
LGP = 150-180 days
Water deficit = 500-700 mm
Cropping pattern :
Rice - wheat
Maize - wheat
Constraints :
Waterlogging
Salinity



'Water balance & moisture availability
Growing Period (GP) at Patna, Bihar

Fig. 2. Northern sub-humid plain with alluvial soils.

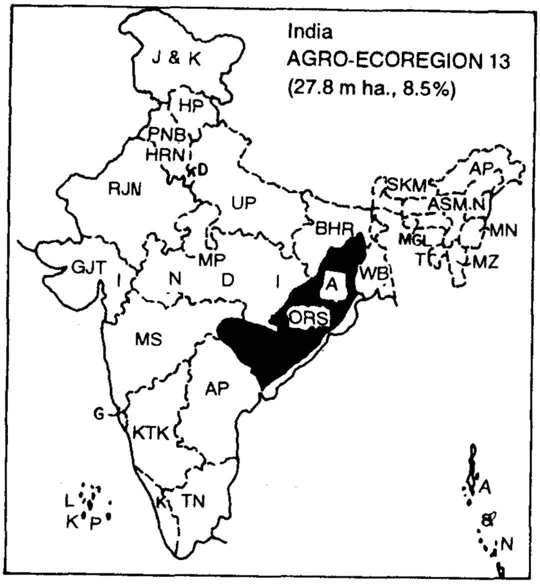
Characteristics :
LGP = 150 days
Water deficit = 700 mm
Cropping pattern :
Rice-pulses
Rice-wheat
Constraints :
Soil erosion
N, P, Zn deficiency
Drought

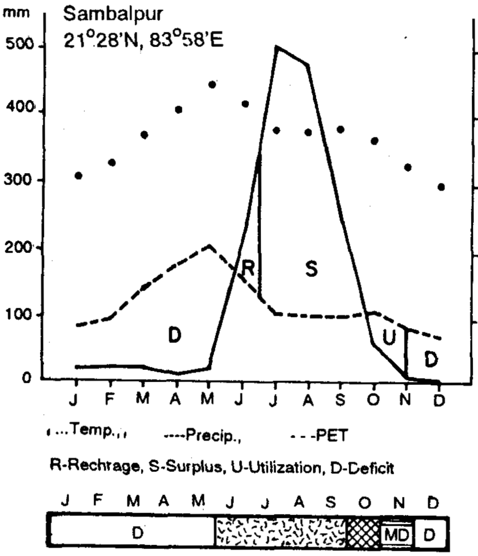


Water balance & moisture availability period at Raipur, Madhya Pradesh.

Fig. 3. Eastern sub-humid plateau with red and yellow soils.

Characteristics :
LGP = 150 days
Water deficit = 700 mm
Cropping pattern
Rice-pulses
Millet-pulses
Constraints :
Soil erosion
Drought
N, P, Zn deficiency
Moderate P fixation

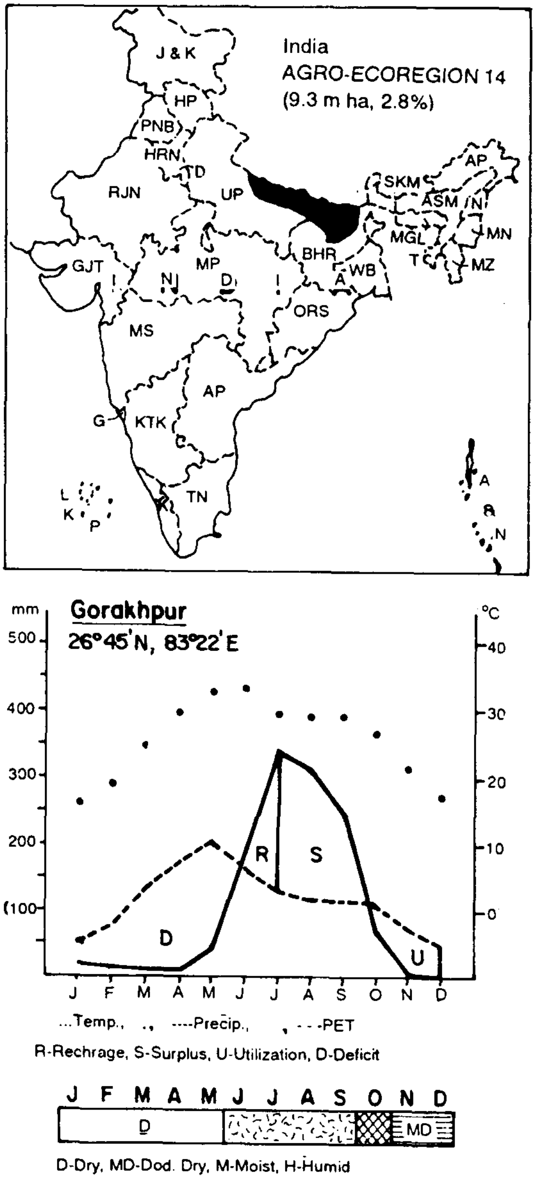




Water balance & moisture availability period at Sambalpur, Orissa

Fig. 4. Eastern sub-humid plateau with red loamy soils.

Characterstics :
LGP = 180-210 days
Water deficit = 400 mm
Cropping pattern :
Rice-wheat
Maize-wheat
Sugarcane Constraints :
Flooding Poor drainage
Salinity/sodicity
N, P, Zn deficiency
Nutrient imbalance



Water balance & moisture availability. period at Gorakhpur, Uttar Pradesh

Fig. 5. Eastern sub-humid plains with alluvial soils.

Characteristics :
LPG = 270 days
Water deficit = nil
Cropping pattern
Rice-Rice
Jute-Rice
Rice-Wheat
Constraints :
Flooding
Poor drainage
Leaching of nutrients
Nutrien imbalance

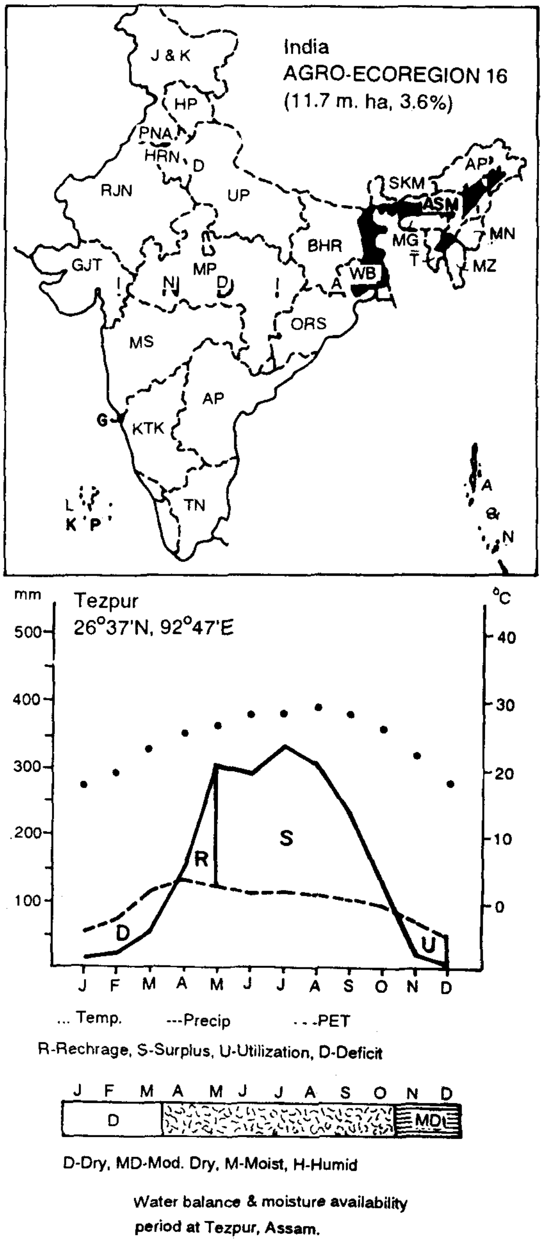


Fig. 6. Eastern humid plains with alluvial soils.

We conclude from the findings that agroecological factors alone cannot explain the diverse production performance of the rice sector across districts in Eastern India.

IMPACT OF AGROECOLOGICAL AND SOCIOECONOMIC FACTORS

We used a multivariate regression analysis to assess the importance of different agroecological and socioeconomic factors in explaining the variation in the level and the growth of rice yield across districts in Eastern India.

Table 3. The variation in rice yield by agoecological zones, Eastern India 1985-86.

	Average rice yield (t / ha)				
Agroecological zones	< 1.5	1.5-2.0	2.0-3.0	3.0 & over	Total
Northern Subhumid Plains with alluvial soil		3	7		10
Eastern Subhumid Plateau with red and yellow soils	4	4			8
Eastern Subhumid Plateau with red loamy soils	7	10	3		20
Eastern Subhumid Plains with alluvial soil	6	3	3		12
Eastern Humid Plains with alluvial soil		3	5	2	10
Total	17	23	18	2	60
(Percent)	28.3	38.3	30.3	3.3	100.0

Source : Estimated from IRRI Rice Statistics Database.

The socioeconomic factors considered in the analysis are the average size of the farm in the district, the pattern of distribution of land (measured by the share of landless agricultural laborers and tenants in total farm population), the incidence of poverty (measured by the per capita calorie intake of the population for the base period), and the economic capacity of the farmers (measured by the amount of chemical fertilizer used per hectare of land in the district). The smaller the size of farm, the higher the pressure of population on land and hence higher would be the need to increase foodgrain production. But the size of farm also determines the availability of labour input and its opportunity cost to the farm household. Small farms may use more labor and hence achieve higher levels of productivity than large farms (Berry and Cline, 1979). Small farms may however be economically unable to afford relatively capital intensive modern technology, and hence the growth in rice yields may be slower in districts with smaller farm size. The effect of farm size on productivity would depend on the relative strength of these two oppositive forces. The unequal distribution of land ownership and the high incidence of tenancy may provide disincentives to production, and hence is expected to have a negative impact on the growth of rice yield. The subsistence pressure on the growth of rice production is expected to be captured by the incidence of poverty at the base period.

Table 4. The variation in growth in rice yield by agroecological zones, Eastern India, 1970-87.

Agroecological zones	Annual growth in rice yield (%)					
	Negative	Up to 1.0	1-0 2.0	2.0-3.0	Over 3.0	Total
Northern Subhumid Plains with alluvial soil	1	0	2	0	7	10
Eastern Subhumid Plateau with red and yellow soils	0	2	4	2	0	8
Eastern Subhumid Plateau with red loamy soils	7	3	4	6	0	20
Eastern Subhumid Plains with alluvial soil	0	6	0	4	2	12
Eastern Humid Plains with alluvial soils	1	0	2	3	4	10
Total	9	11	12	15	13	60
(Percent)	15.0	18.3	20.0	25.0	21.7	100.0

Source: Estimated from IRRI Rice Statistics Database.

The nonavailability of data at the district level was a major constraint to incorporate in the analysis important agroecological factors that affect rice production. Climate is an important factor estimated by the average annual rainfall in the district. The proportion of upland rice area was included to capture the effect of land elevation. The data on this variable have been taken from Huke and Huke (1982). For lowlands, farmed control over water supply would be an important variable affecting the risk of adoption of new technology and investment in modern agricultural inputs. The percent of rice area under irrigation was included to capture this effect. We considered flooding depth as another variable affecting rice production, but it was found highly correlated with the incidence of irrigation and hence was dropped in the final estimation of the equation.

There are many other bio-physical factors that would affect agricultural production. Particularly important are soil types, temperature, and pressure of pests and diseases. Data on these variables are not available at the district-level. In order to capture the effect of some of the variables, we used dummy variables using the location of the districts in different agroecological zones. The Eastern humid plains zones was taken as control (with value o) for assessing production conditions in other agroecoregions (with value 1).

The regression coefficients were estimated using the ordinary Leasts square method. The results are reported in Table 5.

Table 5. Factors affecting variation in the level and growth of rice yields across districts: Regression estimates.

	Rice yield (kg/ha)		Growth of rice yield (%/year)	
Explanatory variables	Eq(1)	Eq(2)	Eq(3)	Eq(4)
1	2	3	4	5
Farm size (ha)	-100	-103	-0.61	-0.62
	(1.15)	(-1.10)	(-1.66)	(-1.62)
Incidence of landlessness and tenancy	-73	-96	-3.67**	-3.11**
(ratio of total workers)	(–0.20)	(-0.25)	(-2.37)	(1.95)
Per capita energy intake at base	121	77	-0.37	-0.51
period (10^2 calorie)	(1.32)	(0.79)	(-0.95)	(1.29)
Fertilizer use	3.3**		0.011**	
(kg of materials/ha)	(2.97)		(2.32)	
Area under irrigation	855**	1183**	0.95	2.04*
(ratio of total area)	(3.26)	(4.62)	(0.86)	(1.94)
Area under upland rice	314	272	6.78**	6.64**
(ratio of total area)	(0.65)	(0.52)	(3.30)	(3.10)
Annual rainfall (cm)	-3.62**	46.6**	0.15**	-0.19**
Agroecoregion dummy	(-2.76)	(-3.41)	(-2.72)	(-3.32)
(Eastern Humid Plain =0)				
Northern SubHumid Plains	-814**	-1054**	-0.41	-1.290
	(-3.92)	(-5.12)	(-0.57)	(-1.42)
Eastern SubHumid Plains	-909**	-1420**	-1.30	-2.07**
	(-5.20)	(-6.79)	(-1.76)	(-3.08)
Chhotanagpur Plateau	-510**	-867**	-0.82	-2.00**
	(-2.46)	(-4.79)	(-0.94)	(2.69)
Chhatisgarh Plateau	-620**	-976**	-0.54	-1.72*
	(2.63)	(-4.45)	(-0.54)	(-1.92)
Constant term	2.26**	2.82**	5.29*	7.12
	(5.77)	(7.60)	(3.19)	(4.69)
R^2	0.77	0.73	0.61	0.56

Note : Figures in parentheses are estimated 't' values. ** denotes that the regression coefficient is statistically significant at 5% probability level and l at 10 percent.

The rice yield is found to be negatively correlated with the amount of rainfall. The districts with higher rainfall are also found to have slower growth in rice yield. The regression coefficient for this variable is statistically highly significant. The results suggest that poor drainage and flooding is a major constraint to increase in rice yield in Eastern India.

As expected, irrigation is an important factor affecting rice production. The conversion of rainfed to irrigated land is found to increase rice yield by about 1.2 tons per hectare. Irrigation contributes to the growth in rice yield partly through facilitating adoption of modern high yielding varieties and larger use of chemical fertilizers. When the fertilizer variable is included in the model along with the irrigation variable, the value of the regression coefficient for irrigation is substantially reduced (Table 5). In fact, in the equation on growth of rice yield, the irrigation coefficient becomes statistically insignificant as the fertilizer variable picks up the effect of irrigation. The value of the regression coefficient of fertilizer suggests that at the farmers level, one kg of additional use of fertilizer (materials) increases rice production on the margin by 3.3 kg.

Other factors unchanged, the average rice yield is found to be higher in districts with larger proportion of area under uplands. The positive and statistically significant regression coefficient for this variable in equations 3 and 4 (in Table 5) suggests that these districts achieved higher rates of growth in rice yield than the districts with larger proportion of rainfed lowlands. This finding is contrary to the prevailing notion that the progress in increasing rice productivity has been extremely limited in the uplands. This issue needs further investigation.

The association between the level of rice yield and the per capita energy intake is positive but statistically insignificant. The positive relationship suggests that the causality may be working the other way - the higher the rice yield, the higher the per capita energy intake, ie., the lower the incidence of poverty. This result signifies the importance of increasing rice yield for achieving food secutity. However, the districts with higher levels of food security have achieved slower growth in rice yields, as shown by the negative coefficient of the energy intake variable in the equations for the growth in rice yields.

The districts with smaller size of farms have achieved higher levels of rice yields and also have higher rates of growth in yields. This is contrary to the notion that small farms cannot particitate in the adoption of input-intensive technology as much as the large farms (Griffin, 1974; Pears, 1980). The finding rather supports the inverse farm size-productivity relationship documented by large number of micro-studies for South Asia.

The regression coefficient of the landlessness and tenancy variables is negative and statistically significant in the equation for the growth in rice yields. The value of the coefficient suggests that the districts with more skewed distribution of land have lower rice yields and had slower growth in yields than the districts with relatively less unequal land distribution. This finding points to the importance of land reforms for providing incentives to growth in agricultural production.

The dummy variables for the agroecoregions are statistically highly significant in the equations for the level of rice yield. The results suggest that there are many other bio-physical variables which could not be included in the analysis have had impact on rice yield. Compared to the Humid Plains (mostly in West Bengal) rice yield are substantially lower not only in the Chhotanagpur and Chhatisgarh Plateau, but also in the Subhumid Plains in the Upper Ganges Delta. The growth in rice yield was significantly lower in the two plateau regions and also in Eastern Subhumid Plains compared to the Humid Plains, even after accounting for differences in rainfall, irrigation, land levels and the land tenure situation, (eq (4) in Table 5). But when fertilizer variable is included, the value of the coefficients of the regional dummy variables declines and becomes statistically insignificant (eq 3). Presumably, the negative effect of the biophysical constraints in these agroecoregions is partly offset by larger use of fertilizer input.

What are the factors that influence the use of chemical fertilizers? To address this issue we conducted another multi- variate analysis relating fertilizer use across districts to some of the agroecological and socioeconomic variables mentioned above. We added the standard error of the estimated growth in yield as another explanatory variable to represent a measure of risk involved in rice cultivation which is a common problem in Eastern India. The results can be reviewed from Table 6.

Fertilizer use is found to be highly negatively correlated with the instability in rice production and the relationship is statistically significant. Districts with more unstable growth in rice yield have lower levels of use of chemicals fertilizers. As expected, the relationship between irrigation and fertilizer use is positive and statistically significant. Better water control reduces the risk in rice cultivation and encourages farmers to apply more fertilizer and adopt fertilizer responsive varieties.

The coefficient of the farm size variable is negative. It indicates that districts with smaller farm size have higher intensity of fertilizer use, contrary to a *priori* expectation. When the regional dummy variables are introduced the negative coefficients of farm size and the instability in rice yield turn out to be statistically insignificant, presumably due to high levels of collinearity between these two sets of variables. Thus, the lower levels of fertilizer use in the subhumid plains and plateau regions compared to the humid plains is partly due to larger size of farms with low subsistence pressure and the higher risks in rice cultivation (Table 2).

In a recent study on research prioritization for eastern India, major technical constraints to increase rice production are reported as drought, weeds, yellow stem borer, acid soils, bacterial leaf blight, lodging, blast, submergence, zinc deficiency and, army worm in order of importance (Widawsky and O' Toole, 1990). The study estimates that these top 10 problem areas account for 60 per cent of the losses due to technical constraints that contribute to nearly 45 per cent of the gap between the average farm level yield and the yield obtained from on-farm experiments under optimal environmental conditions. The study on agroecological zoning for India mentions flooding, poor drainage and water-logging as key constraints to agricultural production in the humid and subhumid plains in the Gangetic Delta;

and drought, problem soils and soil erosion as key constraints in the Chhotanagpur and Chhatisgarh plateau (Sehgal *et al.,* 1990).

Table 6. Factors affecting variation in fertilizer use across districts in Eastern India: Regression Estimates.

Factors	Fertilizer use (kg/ha)	
	Eq(1)	Eq(2)
1	2	3
Farm size (ha)	-36.15** (-3.79)	-8.04 (-0.74)
Instability in yield (SE)	-36.17** (-2.47)	-13.15 (-0.90)
Annual rainfall (cm)	-1.00 (0.58)	-3.77* (2.34)
Area irrigated (ratio of total rice area)	97.13** (3.33)	83.95** (3.08)
Area under upland rice (ratio of total rice area)	33.78 (0.50)	-46.12 (-0.77)
Agroecoregiondummy (Humid Plains = 0)		
Northern Subhumid Plains		-72.0** (2.93)
Eastern Subhumid Plains		-68.9** (3.26)
Chhotanagpur Plateau		-112.2** (5.08)
Chhatisgarh Plateau		-103.8** (-3.52)
Constant term	140.36** (3.30)	207.9** (5.22)
R^2	0.56	0.71

Note : Figures within parentheses are estimated 't' value of the regression coefficents. ** denotes statistical significance at 5 percent level.

Mechanism of tolerance to drought particularly at the anthesis stage, is crucial to increased productivity not only in the plateau regions but also in the humid and subhumid plains which suffer frequent late season moisture stress. Submergence tolerance is crucial not only for areas with problems of flooding and poor drainage (in Ganges Delta) but also for the Chhatisgarh and Chhotanagpur plateau where rainfall suddenly picks up with frequent heavy rains for a number of consecutive days during the months of July and August and then the monsoon abruptly ends in the month of September (See Figs. 3 and 4). Elongating varieties tend to lodge after the flood water recede. So, semi-dwarf varieties with abilities to short- term submergence could prove beneficial to large areas of Eastern India.

Development of resistant cultivars to prolonged moisture stress and short period submergence can stabilize yields and reduce the risk in rice cultivation, and thereby induce low-income farmers to adopt input-intensive technologies. The rainfed Lowland Rice Research Consortium is on the right track in emphasizing stress physiology as the priority area of research for this region.

REFERENCES

Berry A R, Cline W R (1979) *Agrarian Structure and Productivity in Developing Countries.* Baltimore: Johns Hopkins University Press.

Dev S, Suryanarayana M H, Parikh S (1992) "Rural poverty in India: Incidence, Issue and policies", *Asian Development Review,* **10** (1) :35-66.

Fertilizer Association of India (1991) *Fertilizer Statistics,* 1990-92. New Delhi, India.

Government of India (GOI) (1993) *Agricultural Situation in India.* September 1993 (earlier issues), Directorate of Economics and Statistics, Ministry of Agriculture, New Delhi, India.

Griffin K (1974) *The Political Economy of Agrarian Change: An Essay on the Green Revolution.* Cambridge: Harvard University Press.

Hossain M, Laborte A (1994) "Rice Economy in Asia: Recent Progress and Emerging Trends", *Food and Fertilizer Technology Centre Newsletter,* **101.** Taipei, Taiwan.

Huke R, Huke E (1982) *Rice Area by Type of Culture: South, Southeast and East Asia.* International Rice Research Institute, Los Banos, Philippines.

Huke R, Huke E (1990) *Human Geography of Rice in South Asia.* International Rice Research Institute, Los Banos, Philippines.

Kumar P, Rosegrant M W (1993) "Productivity and sources of growth in rice in India", paper presented at the Second Workshop on Rice Supply and Demand Project, International Rice Research Institute and International Food Policy Research Institute, 13-15 April 1993, Los Banos, Philippines.

Pears A (1980) *Seeds of Plenty, Seeds of Want: Social and Economic Implications of the Green Revolution Oxford:* Clarendon Press.

Sehgal J L, Mandal D K , Mandal C, Vadivelu S (1990) *Agro-Ecological Regions of India,* NBSS Publication No. 24, National Bureau of soil Survey and Land Use Planning, Nagpur, India.

Widawsky, D, OToole J C (1990) "Prioritizing the Rice Biotechnology Research Agenda for Eastern India", The Rockefeller Foundation.

Printed at Prakash Packagers, 257-Golaganj, Lucknow.