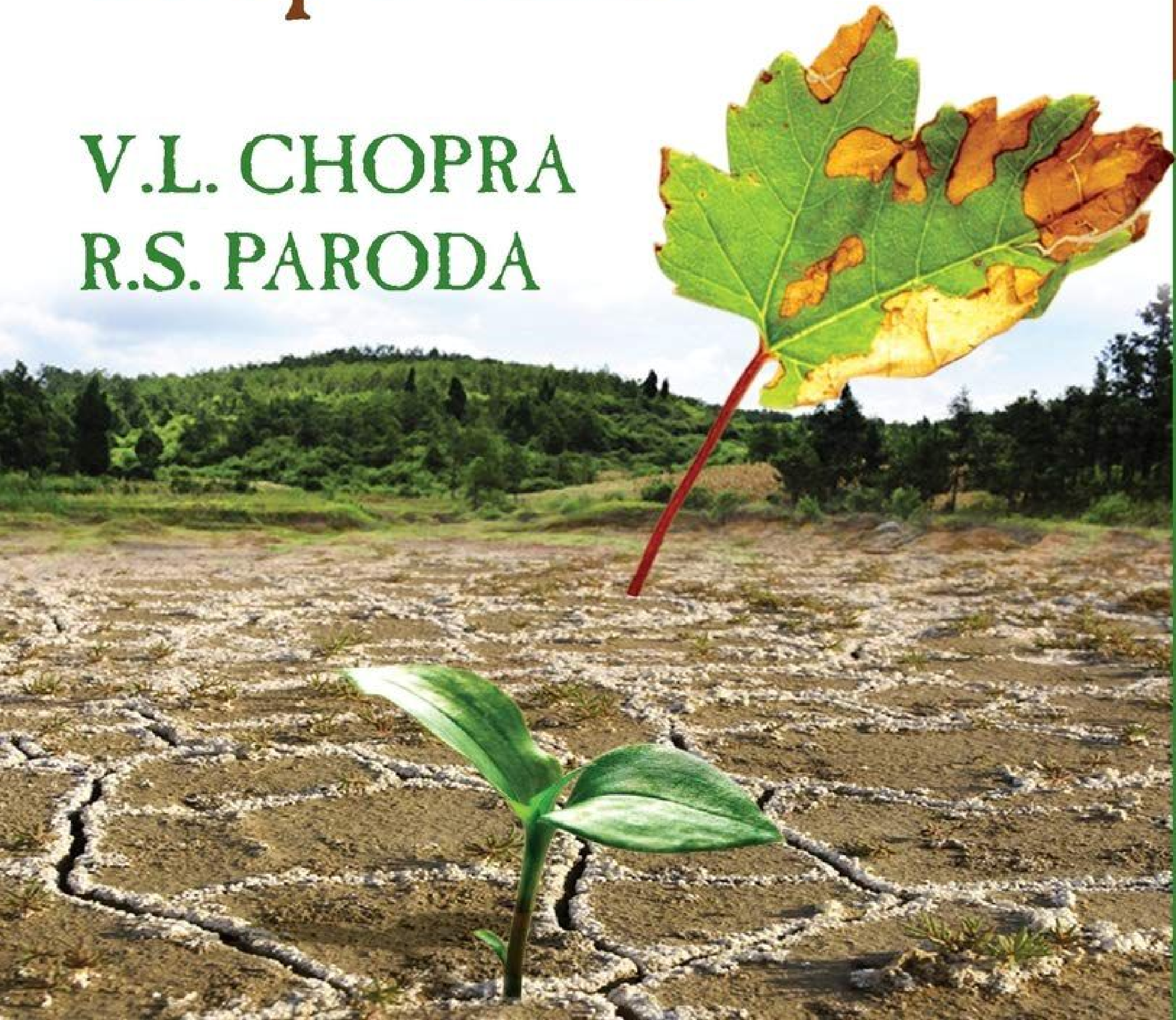
Approaches for Incorporating Drought & Salinity Resistance in Crop Plants

V.L. CHOPRA
R.S. PARODA



APPROACHES FOR INCORPORATING DROUGHT AND SALINITY RESISTANCE IN CROP PLANTS

Approaches for Incorporating Drought and Salinity Resistance in Crop Plants

Editors ed. by
V.L. CHOPRA
R.S. PARODA

OXFORD & IBH PUBLISHING CO. PVT. LTD.
New Delhi Bombay Calcutta

ISBN 81-204-0151-4

Published by Mohan Primlani
for Oxford & IBH Publishing Co. Pvt. Ltd.,
66 Janpath, New Delhi 110001 and printed at
Vishal Printers, Navin Shahadara, Delhi 110032

Foreword

Between 1965, when the large-scale testing of high yielding varieties of wheat, rice and hybrids of maize, *Sorghum* and pearl millet began, and 1985 when the country harvested over 150 million tonnes of food grains, the capacity to produce an additional quantity of 70 million tonnes of food grains per year was developed. Such an additional production capacity was the result of a suitable blend of technology, services and government policies in input and output pricing and rural infrastructure development. Between 1986 and 2000 A.D. India will have to develop the capacity of producing at least 75 million tonnes more of food grains, so as to reach an annual production target of 225 million tonnes in the year 2000. Thus, we have to achieve more than what became possible during the "green revolution" period to maintain a satisfactory population-food production equation.

We can achieve the desired production goal by the end of the century only if we can elevate and stabilise crop yields in rainfed, drought-prone areas and under unfavourable soil condition. Salinity is one of the more serious constraints restricting soil productivity. The present publication is hence a timely contribution.

The book brings together very valuable information on different aspects of breeding for drought and salinity tolerance in crop plants. In addition, the management aspects of soil salinity have also been dealt with. This book will hence be of help in intensifying on-going research designed to extend agricultural progress to areas suffering from disadvantaged climatic and soil environments.

We owe a deep sense of gratitude to Prof. V.L. Chopra and Dr. R.S. Paroda for making such valuable data and insights available to all scientists and scholars interested in this important area of research.

Director General
International Rice Research Institute
Los Banos, Manila, Philippines

M.S. SWAMINATHAN

Preface

World agriculture today presents two contrasting production systems. On the one hand is the highly mechanised, input intensive and highly productive agriculture exemplified by the agri-business approach of North America. On the other, is the agriculture with numerous limitations as operated in less developed countries. In the former, high productivity is achieved without much regard to investment in energy; there is also no dearth of cultivable area. In the less fortunate agriculture, obtainable in countries of Asia for example, there are numerous constraints on production and productivity. In most cases the possibilities of bringing additional land under cultivation are excluded. In fact, the cultivable land resource gradually shrinks under pressure of urbanisation and population increase. The economic position of the cultivators does not allow investments in costly agricultural inputs (machinery, fertiliser, agrochemicals, irrigation). Worst still, varying proportion of land is unproductive because of hostile factors like stresses of moisture, temperature, soil texture and composition. Since land is a scarce resource, devising procedures and practices that will improve production from stressed soil assume great relevance.

Some countries, of which India is a good example, have made remarkable progress in improving their agricultural productivity. The productivity increases, however, have been restricted to irrigated agriculture and have utilised the avenue of genetic upgradation of the productivity potential of crop varieties. The improved genotypes make more efficient use of the applied agricultural inputs and partition a large proportion of their photosynthetic products into seed. The elevated yield levels of the new high yielding genotypes are consistently realised only for those crops which grow under stable environment.

For example, high yielding varieties have been produced in India both for wheat and rice but the translated effects have been conspicuous only in the case of wheat. The diversity of specific environment in which rice grows and the limiting influences of 'Kharif' environment combined with incidence of pests and pathogens has not allowed the effect of the achieved genetic upgradation of production potential of rice to become perceptible uniformly at the national level. From the scientific and sociological viewpoints the challenge is to overcome the limitations to the above-mentioned factors of productivity increase. It is imperative that the benefits of improved agricultural technology become available to all sections of the farming community. The production and economic requirements demand that agriculture, even in areas suffering from one or the other kind of stress, becomes productive and remunerative. Unfortunately, research efforts for the improvement of agriculture in areas suffering from water and soil composition stresses have so far not been as vigorous as the problem demands. One of the possible causes for this has been the anxiety to increase production in areas suited for intensive agriculture so as to buy time for mounting efforts for tackling a relatively more difficult situation. A more scientific reason is our lack of knowledge of the mechanisms by which crop plants cope with a stress situation and of the operational parameters which can be employed for identifying more productive genotypes under stress situation. Experience has shown that the assumption of a productive type under favourable conditions also being productive under stress situations is not uniformly valid. Evolution of crop varieties suitable to stress situation specifically can, therefore, no longer be ignored. For this objective to be realised, it is essential to proceed in a systematic way both to clearly and scientifically define the stress and to mount basic research for gaining an understanding of the physiological and biochemical pathways that express in plants when subjected to stress. Equally important will be to understand the genetics of resistance to the relevant stresses. Only when this information is available, it will be possible to systematically devise selection criteria that can be applied for identifying donors for resistance and develop breeding strategies and methodologies useful for making selections that combine stress resistance with other required agronomic characteristics.

The present volume is an attempt to present the relevant information and the state-of-the-art for two predominantly prevalent stresses i.e. drought and salinity. It is our hope that this information will provide the spring board from which major advances will be reached in the future.

V.L. CHOPRA
R.S. PARODA

Contents

Salt-affected Soils : An Overview

I.P. ABROL

Introduction

Accumulation of excess soluble salts in the root zone of soils resulting in partial or complete loss of soil productivity is a worldwide phenomenon. The problems of soil salinity are widespread in the arid and semi-arid areas but salt-affected soils also occur extensively in the sub-humid and humid climates particularly in the coastal regions where the ingress of sea water through estuaries and rivers and through ground water movement causes large scale soil and water salinisation. Soil salinity is also a serious problem in areas where ground waters of high salt content are the only source of water available for irrigation. By far the most serious problems of salinity are being faced in the irrigated, arid and semi-arid regions of the world. Our ability to manage salt-affected soils and waters both in the irrigated and in the unirrigated regions will constitute a major effort in meeting potential food requirements. The magnitude of the problem can be appreciated from the following.

Salt-affected Soils in the World

Table 1 gives the world's potentially arable land resources and Table 2 gives the distribution of salt-affected soils in the major continents of the world. It is observed that whereas only about 10.6 per cent of the total land area of the world is cultivated at present, cultivation can be increased to about 24.2 per cent of the total land area. This means that there is more land avail-

Table 1. Total land area and arable land by continents

Region	*Total land area (million ha)*	*Cultivated land area (million ha)*	*Land area cultivated (%)*	*Potential arable land (million ha)*	*Ratio of cultivated to potential land (%)*
Africa	3,010	158	5.2	734	22
Asia	2,740	519	18.9	627	83
Australia and New Zealand	820	32	3.9	153	21
Europe	480	154	32.1	174	88
N. America	2,110	239	11.3	465	51
S. America	1,750	77	4.4	681	11
USSR	2,240	227	10.6	356	64
Total	13,150	1,406	10.6	3,190	44

Source: The World Food Problem, A Report of the President's Science Advisory Committee, Vol. II; Report of the Panel of World Food Supplies (USA).

able for being brought under cultivation in the future than is cultivated at present in the world as a whole. The largest area of potentially arable land not used currently for crops is in Africa, mostly south of the Sahara. The next largest area is in South America. In the continents of Europe and Asia more than 80 per cent of the potentially arable land is already being cultivated. It would, therefore, appear that each region or country will have to develop its own strategies for increasing food production considering the availability of resources, levels of technology and other socio-economic factors. It is apparent that although much of the increased food production will have to come through increased yields and through intensified cropping, it will also be imperative to bring into production the potentially productive lands which are now not under cultivation. According to an FAO study (Massoud 1974) salt-affected soils occupy nearly 7 per cent of the world's land area with great differences between continents, countries and climatic regions (Table 2). Again, while considering the region or a continent as a whole, the extent of salt-affected soils may not appear large but when considering a particular agricultural district or a region the problems of salinity may pose a serious threat to the well-being of the people of the region. An understanding of the nature of the salt-affected soils and their poten-

Table 2. Distribution of salt-affected soils

Region	*Area* *(thousand ha)*	%
Europe	80,454	4.6
N. America	16,285	0.9
C. America	1,965	0.7
S. America	129,163	7.6
Africa	98,521	3.5
S. Asia	85,108	21.0
N & C. Asia	211,686	
SE Asia	19,983	
Australasia	357,330	42.3

Source: Massoud FI (1974). Salinity and alkalinity as soil degradation hazards, FAO/UNDP Expert Consultation on Soil Degradation, 10-14 June 1974 FAO, Rome, 1974. 21 pp.

tial for meeting food requirements, therefore, needs urgent attention.

Salinity Problems in India

Tables 3 and 4 give the land utilisation statistics in India and the major constraints faced in the utilisation of potentially arable land. Table 5 gives the broad distribution of salt-affected soils in the country. These estimates are only approximate and the magnitude of the problem is becoming increasingly severe because an additional 15-20 million hectares of land in the canal irrigated tracts already run the risk of being degraded through the influence of salts. Salinity problems are also widespread in the arid regions where saline ground waters are the

Table 3. Land utilisation statistics of India (area in million ha)

Total geographical area	328.048
Total area for which land use statistics are available	305.506
Area under urban and other non-agricultural use	18.000
Areas which are barren and unculturable (e.g. perpetually snow bound, rocky etc.)	21.000
Culturable wastes (potentially arable)	40.000
Area under forests (35.0) and permanent pastures (48.0)	83.000
Agricultural lands	143.000

Source: Indian Agriculture in Brief. Directorate of Economics and Statistics, Ministry of Agriculture, Government of India, New Delhi.

only source of irrigation. The problems of salinity will further intensify as efforts are made to use water more efficiently on farms, industrial activities are increased and land use intensified.

Table 4. Approximate area and major constraints in the reclamation of potentially arable areas

Major constraint	*Approximate area (million ha)*
Waterlogging	6.0
Salinity and alkali	7.0
Ravines	3.7
Lateritic soils	12.0
Riverine lands, coastal sandy areas, stony and gravel lands, high altitude and steep sloping lands	11.3
Total	40.0

Source: Compiled from Report of the National Commission on Agriculture 1976, Ministry of Agriculture and Irrigation, Government of India, New Delhi.

Table 5. Distribution of salt-affected soils in India (Abrol and Bhumbla 1971)

Broad group	*States in which the soils occur*	*Approximate area (million ha)*
1. Coastal salt-affected soils		
a) Coastal salt-affected soils of the arid regions	Gujarat	0.714
b) Deltaic coastal salt-affected soils of the humid regions	West Bengal, Orissa, Andhra Pradesh and Tamil Nadu	1.394
c) Acid salt-affected soils	Kerala	0.016
2. Salt-affected soils of the medium and deep black soil regions	Karnataka, Madhya Pradesh, Andhra Pradesh, Maharashtra	1.420
3. Salt-affected soils of the arid and semi-arid regions	Gujarat, Rajasthan, Punjab, Haryana and Uttar Pradesh	1.000
4. Alkali soils of the Indo-Gangetic plains	Haryana, Punjab, Uttar Pradesh, Bihar, Rajasthan, Madhya Pradesh	2.500
	Total	7.044

Objectives

There are several approaches to the management of salt-affected soils. Breeding crop varieties for higher salinity tolerance has, in the past few years, received considerable attention the world over. This paper presents views on the scope and limitations of this approach and draws attention to some of the problems that those engaged in such research efforts may tend to ignore.

Kinds of Salt-affected Soils

In the course of accumulation of knowledge on the distribution, nature, characteristics and plant growth relationships in salt-affected soils, two main groups have been differentiated. These are : (a) Saline soils, and (b) Alkali soils. These two groups of salt-affected soils differ not only in their chemical characteristics but also in their geographical distribution as well as in their physical, chemical and biological properties. The mechanisms which adversely affect plant growth in the two cases are also different and the two categories require different approaches for their reclamation and agricultural utilisation. For this reason, it is imperative that plant improvement programmes categorically define their objective regarding the kind of stress that is intended to be overcome through breeding programmes. The distinguishing features of these two groups of soils are discussed below.

SALINE SOILS

These are soils which contain sufficient neutral soluble salts to adversely affect the growth of most crop plants. The salts that largely contribute to salinity include the chlorides and sulphates (and somewhat rarely, nitrates) of sodium, calcium, magnesium and potassium. The salts in saline soils may be indigenous. More commonly, salts are brought into an area from outside by irrigation waters. For purposes of definition, saline soils are those the saturated soil paste extract of which has an electrical conductivity of more than 4 dS/m. The unit of measurement, dS/m (decisiemens per metre) is numerically equal to the earlier units used for salinity measurement mmhos/

cm (millimhos per centimetre). The following salinity classes (Table 6) are usually recognised in relation to the growth of most crop plants.

Table 6. Effect of soil salinity on crop plants

Soil salinity, class	*Conductivity of saturation extract (dSm^{-1})*	*Effects on crop plants*
Nonsaline	0—2	Salinity effects negligible
Slightly saline	2—4	Yields of sensitive crops may be restricted
Moderately saline	4—8	Yields of many crops restricted
Strongly saline	8—16	Only tolerant crops yield satisfactorily
Very strongly saline	>16	Only a few very tolerant crops yield satisfactorily

ALKALI SOILS

These are soils with sodium salts which, upon hydrolysis, impart a high pH factor to the soils. Sodium carbonate is a common salt present in these soils. Presence of even small amounts of sodium carbonate results in accumulation of the element sodium on the soil exchange complex leading to high pH levels in the soil. Excess exchangeable sodium and high pH in turn impart poor physical properties to the soils which adversely affect plant growth. For purposes of definition, alkali soils are those which contain sufficient, usually more than 15 per cent, exchangeable sodium (ESP) to affect plant growth adversely. The saturated paste pH of alkali soils is nearly always more than 8.2. In scientific literature, alkali soils are also called sodic soils. Table 7 gives the approximate alkali hazard with respect to soils of varying ESP classes.

The distinguishing chemical and physical properties, plant growth relationships and related characteristics of these two important groups of soils are summarised in Table 8.

It must be pointed out here that although the above two categories account for a very large fraction of salt-affected soils the world over, undoubtedly there are borderline formations which are likely to have properties somewhat intermediate between those of the two categories. A mention must also be

Table 7. Exchangeable sodium percentage (ESP) and alkali hazard

ESP classes	*Alkali hazard*	*Remarks*
0-15	None to slight	The adverse effect of exchangeable sodium on the growth and yield of crops in various classes occurs according to the relative crop tolerance to excess sodicity. Whereas the growth and yield of only sensitive crops are affected at ESP levels below 15, only extremely tolerant native grasses grow at ESP above 70 to 80.
15-30	Light to moderate	
30-50	Moderate to high	
50-70	High to very high	
70 and above	Extremely high	

made of a few other categories of salt-affected soils which, though less extensive are commonly met with in different parts of the world. These include the acid-sulphate soils, the degraded alkali soils and soils rich in or dominated by a particular salt species, or a profile morphological feature.

Management of Salt-affected Soils

In practice two broad approaches to the utilisation of these soils have been adopted. These are: (a) Reclamation, and (b) Adoption of appropriate management practices.

a) RECLAMATION

The term reclamation of salt affected soils refers to the methods used to remove soluble salts and/or excess exchangeable sodium from the root zone which render the relatively unproductive soils more productive. The methods commonly adopted to accomplish this include leaching of the soluble salts, application of soluble calcium amendments to remove excess exchangeable sodium, installation of appropriate drainage measures to drain out the waters containing excess salts from an area into a regional drainage system and ultimately into the sea etc. However, complete reclamation of salt-affected soils is generally a capital intensive proposition and often availability of appropriate outlets for disposal of the drain waters and the absence of regional drainage systems pose serious problems.

Table 8. Distinguishing features of saline and alkali soils

Characteristics	*Saline soils*	*Alkali (sodic) soils*
1	*2*	*3*
Chemical	a. Dominated by neutral soluble salts consisting of chlorides and sulphates of sodium, calcium and magnesium	a. Appreciable quantities of neutral soluble salts are generally absent. Measurable to appreciable quantities of salt capable of alkaline hydrolysis e.g., Na_2CO_3 is present.
	b. pH of the saturated soil paste is less than 8.2.	b. pH of the saturated soil paste is more than 8.2.
	c. An electrical conductivity of the saturated soil extract of more than 4 dSm^{-1} at 25° is thegenerally accepted limit above which soils are classed as 'saline'.	c. An exchangeable sodium percentage (ESP) of 15 is the generally accepted limit above which the soils are classed as 'alkali' or 'sodic'. Electrical conductivity of the saturated soil extract is generally less than 4 dSm^{-1} at 25°C but may be more if appreciable quantities of Na_2CO_3, $NaHCO_3$ etc. are present.
	d. There is generally no well defined relationship between pH of the saturated soil paste and the exchangeable sodium percentage (ESP) of soil or the sodium adsorption ratio (SAR) of the saturation extract	d. There is a well defined relationship between pH of the saturated soil paste and the exchangeable sodium percentage (ESP) of soil or the SAR of the saturation extract for an otherwise similar group of soils such that the pH can serve as a good measure of soil sodicity/alkali status.

	e. Although Na is generally the dominant soluble cation, the soil solution contains appreciable quantities of divalent cations e.g. Ca and Mg f. Soils may contain significant quantities of sparingly soluble calcium compounds e.g. gypsum	e. Sodium is the dominant soluble cation. High pH of the soils results in precipitation of soluble Ca and Mg such that their concentration in the soil solution is very low. f. Gypsum is nearly always absent in these soils.
Physical	a. In the presence of excess neutral soluble salts the clay fraction remains flocculated and the soils have a stable structure b. Permeability of soils to water and air and other physical characteristics are generally comparable to normal soils	a. Excess exchangeable sodium and high pH result in the dispersion of clay and the soils have an unstable structure. b. Permeability of soils to water and air is restricted. Physical properties of the soils become worse with increasing levels of exchangeable sodium and pH.
Effect on plant growth	In saline soils plant growth is adversely affected through a. chiefly, the effect of excess salts on the osmotic pressure of soil solution resulting in reduced availability of soil water. b. toxicity of specific ions e.g. Na, Cl, B, etc.	In alkali soils plant growth is adversely affected through a. chiefly the dispersive effect of excess exchangeable sodium resulting in poor soil physical properties. b. the effect of high soil pH on nutritional imbalances including a deficiency of calcium. c. toxicity of specific ions e.g., Na, B, Mo, etc.

Table 8. (*Contd.*)

1	*2*	*3*
Soil improvement	Improvement of saline soils essentially requires removal of soluble salts from the root zone through leaching and drainage. Application of amendments is generally not required.	Improvement of alkali soils essentially requires the replacement of sodium on the soil exchange complex by calcium through use of soil amendments and leaching and drainage of salts resulting from reaction of amendments with exchangeable sodium.
Geographic distribution	Saline soils tend to dominate in the arid and semi arid regions	Alkali soils tend to dominate in the semi-arid and sub-humid regions.
Ground water quality	Ground waters in areas dominated by saline soils have generally a high electrolyte concentration and have a potential salinity hazard.	Ground waters in areas dominated by alkali soils have a generally low to medium electrolyte concentration and some of them may have residual alkalinity to have a potential alkali/sodicity hazard.

b) ADOPTION OF APPROPRIATE MANAGEMENT PRACTICES

Management practices that can aid in obtaining better crop production include choice of crops that are more tolerant to salt-affected conditions and other practices such as method and time of planting, irrigation application rates, agronomic and cultural practices that minimise the salt concentration in the root zone of growing crops. Adoption of proper management practices helps attain satisfactory levels of production in areas with a medium salinity problem although with some reduction in the potential yield. In practice, both the approaches viz. reclamation and appropriate management practices are important depending on the geographical setting, soil conditions, source of irrigation water etc. However, with increasing development, salinity problems are likely to become more serious particularly when the cropping becomes more intensive and water efficiency is increased by re-use of water. It is in this context that breeding crop varieties for improved salt tolerance will gain importance for the optimal management of resources.

Crop Tolerance in Saline and Alkali Soils

Although saline and alkali soils are distinct in relation to plant growth, in the following sections the term salt-affected/salinity has been used to cover both the situations. Crop plants differ widely in their ability to survive and yield satisfactorily when grown in salt-affected soils. Information on the relative tolerance of crops to saline or alkali soil environment is of practical importance in planning cropping schedules for optimum returns. There are several situations where the farmers have to live with salinity problems. These situations include areas having saline water as the only source of irrigation, areas where adequate quantities of good quality water is not available to completely desalinise soils or where the land surface is continuously subjected to influence of salts, as is the case in coastal areas.

There is extensive published literature on the relative tolerance of different crops to salinity conditions. The task of evaluating the relative tolerance of a species is difficult because investigations have been carried out under a wide range of soil, climate and salinity conditions. Notwithstanding the difficulties involved in evaluating and normalising the extensive published data worldwide, Mass and Hoffman (1977) compiled and reviewed available salt tolerance data of over 30 years to arrive at the best assessment of the relative tolerance of agricultural crops. Information on the relative yield of a crop as a function of the electrical conductivity of the soil saturation extract is plotted in Fig. 1 and crops classified according to their place in this chart (Table 9). The information compiled by Mass and Hoffman (1977) has now been extensively quoted and used for practical purposes. Fig. 1 shows that, in general, crop yields were not reduced significantly until a threshold salinity level

Table 9. Relative salt tolerance of crop plants based on the yield response boundaries of Fig. 1 (Mass and Hoffman 1977)

CATEGORY			
Sensitive	*Moderately sensitive*	*Moderately tolerant*	*Tolerant*
Almond	Alfalfa	Barley (forage)	Barley (grain)
Apple	Bentgrass	Beet	Bermuda grass
Apricot	Broadbean	Brocoli	Cotton
Avocado	Cabbage	Bromegrass	Date
Bean	Clover	Canarygrass	Sugar beet
Blackberry	Corn	Fescue, tall	Wheatgrass (tall)
Boysenberry	Cowpea	Olive	Wildrye (Altai)
Carrot	Cucumber	Ryegrass (perennial)	Wildrye (Russian)
Grapefruit	Flax	Safflower	
Lemon	Grape	Sorghum	
Okra	Lettuce	Soybean	
Onion	Lovegrass	Wheat	
Orange	Millet (Foxtail)	Wheatgrass (crested)	
Peach	Orchardgrass	Wildrye (beardless)	
Plum	Peanut		
Raspberry	Pepper		
Strawberry	Potato		
	Radish		
	Rhodesgrass		
	Rice		
	Sesbania		
	Spinach		
	Sugar cane		
	Sweet potato		
	Timothy		
	Tomato		
	Vetch		

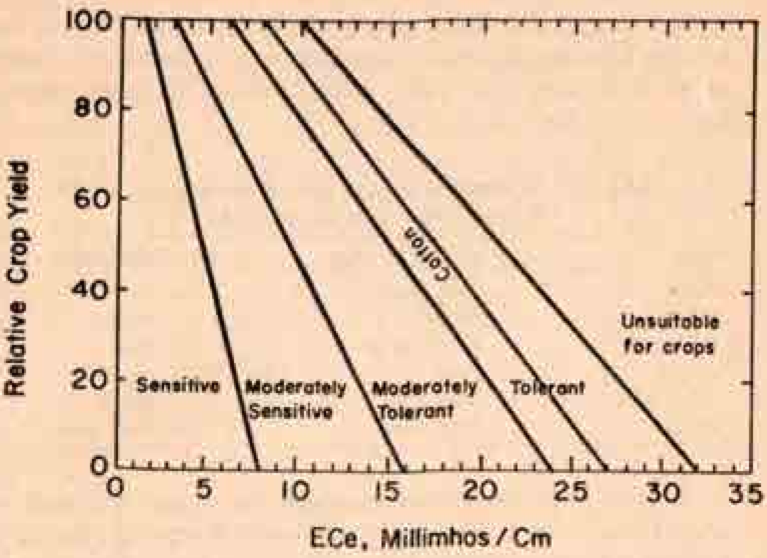


Fig. 1. Classification of crop tolerance to salinity based on relative crop yield as a function of the electrical conductivity of soil saturation extracts (EC*e*). (Mass and Hoffman 1977)

was exceeded, and then the yields decreased almost linearly with increased salinity. The salt tolerance curve for each crop was obtained by calculating a linear regression equation for the yield beyond the threshold point. From the curve for any crop, relative yield (*Y*) at any given soil salinity can be calculated by the equation:

$$Y = \frac{100\,(EC_0 - ECe)}{EC_0 - EC_{100}}$$

where EC_{100} is the salinity threshold value (ECe where $Y = 100$) and EC_0 is the salinity at zero yield (ECe where $Y = 0$). Values of EC_{100} and EC_0 for a given crop can be taken from the appropriate curve. Taking cotton as an example, $EC_{100} = 8$ dS/m and $EC_0 = 27.0$ dS/m (Fig. 1). Therefore, the relative yield at an *ECe* of say, 10 dS/m will be:

$$\begin{aligned} Y &= 100\,(27.0-10.0)/(27.0-8.0) \\ &= 100\,(17.0)/(19.0) \\ &= 89\% \end{aligned}$$

The tolerance of crops to alkali conditions has not been studied extensively. Based largely on studies at the Central Soil Salinity Research Institute, crops have been classified in respect of their tolerance to alkali conditions and the information is presented in Table 10 and Fig. 1.

Table 10. Tolerance of crops to salts at two stages of growth (Canada Department of Agriculture 1977)

Crop	*Germination stage*	*Established stage*
Barley	Very good	Good
Corn	Good	Poor
Wheat	Fairly good	Fair
Alfalfa	Poor	Good
Sugar beet	Very poor	Good
Beans	Very poor	Very poor

It needs to be emphasised here that the relative tolerance of crops to saline or alkali conditions does not represent the absolute salt tolerance independent of other factors. Tolerance is strongly influenced by factors other than the salinity and/or alkali status of soils. It also needs to be pointed out here that most often tolerance to saline and alkali conditions is not adequately differentiated and this can lead to very inappropriate conclusions. The data in Table 10 is for saline conditions and does not apply to alkali conditions. For example, while barley is known to be a very tolerant crop of saline conditions, it is not tolerant of alkali or sodic conditions to the same degree. Similarly, while cotton tolerates high salinity conditions moderately, it is not tolerant of alkali conditions.

Factors Influencing Salt Tolerance

Tolerance of plants to saline and/or alkali conditions is not a fixed characteristic of a crop species or a variety but may vary considerably with the environmental conditions. Tolerance may also vary with the stage of crop growth for the same species. Efforts to breed crop varieties for improved tolerance require a proper understanding and appreciation of these and other factors.

1) GROWTH STAGE

The tolerance of a crop varies with the growth stage. Most plants are more sensitive to salinity during germination than at the later growth stages. However, there are large variations in sensitivity of germinating seeds to salinity. In Fig. 2, percentage germination of four species is plotted against the *ECe* of soil extract. It is seen that sugar beet, which is considered a very tolerant crop, is more sensitive to salts at germination than are alfalfa and barley. Table 10 depicts large variations that exist in the tolerance of crops at two growth stages.

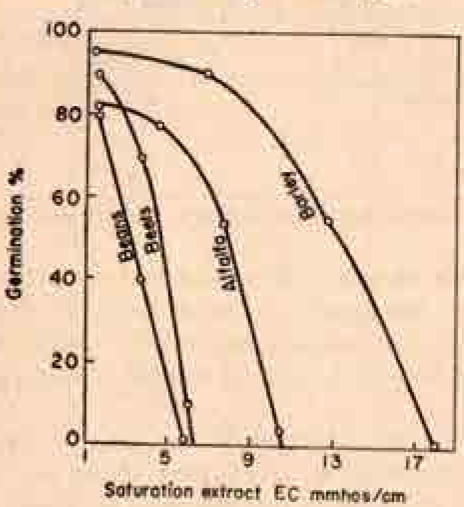


Fig. 2. Per cent germination of four crops as affected by salinity of soil under laboratory conditions. (Ayers and Hayward 1949)

2) CLIMATIC CONDITIONS

Climatic conditions greatly influence plant responses to substrate salinity. Plants tend to tolerate higher salinity levels when the atmospheric evaporative demand is low and lower salinities when the atmospheric evaporative demands are high. Table 11 illustrates this point. Similar observations were recorded (Table 12) on rice (Murthy and Janardhan 1971). It is seen that the yield reductions due to salinity were much more when the crop was grown in the dry season as compared to when the crop was grown in the wet season.

Sinha and Singh (1974) related the observed differences in tolerance due to evaporative demand to accumulation of ions

Table 11. Response of three crops to salinity in sand culture experiments at two locations (Magistad et al. 1943)

Crop	*Solution salinity at which 25% yield reduction was observed* dSm^{-1}	
	Cool location	*Hot location*
Bean pods	4.0	3.0
Garden beet roots	11.1	6.6
Onion bulbs	12.5	3.3

Table 12. Effect of season on the relative rice yields (Murthy and Janardhan 1971)

Salinity of root zone dSm^{-1} *(approximate range)*	*Relative yield*	
	Wet season	*Dry season*
Control (non-saline)	100	100
2—4	93	81
4—8	63	53
10—12	39	11

Note: Relative yields are comparable only within the same season.

near the root surface. Their studies showed that the concentration of ions was linearly related to water uptake per unit root length. These observations strengthen the contention that the relative tolerance of a crop is strongly influenced by climatic conditions.

Apart from the atmospheric evaporative demand, some workers (Hoffman et al. 1975) have shown that air pollution may increase the apparent salt tolerance of many crops. For example, it was observed that for alfalfa grown in Ozone concentrations often prevalent in several agricultural areas, yields were highest at moderate salinity levels that normally reduced growth.

Nutrient Interactions

Crop responses to salinity are strongly modified through the influence of nutrient status of soils. Generally, at a given level of salinity, growth and yield of crops are likely to be depressed more when nutrition is disturbed than when the nutrition is normal. At moderate salt concentrations in the soil solution, plants tend to exclude unwanted ions and promote the uptake of nutrients. With increasing salt concentration the uptake of sodium and chloride ions increases sharply and is responsible for growth retardation. Excessive uptake of such ions, in turn, results in reduced uptake of essential plant nutrients, causing nutrient imbalances and deficiencies. Thus, although the available status of a nutrient in soils might not be deficient *per se*, its application might compensate for the decreased uptake by plants as a result of the antagonistic effect of excess uptake of certain ions. The inverse relationship was observed (Fig. 3) between soil available phosphorus status and the chloride content of wheat straw (Singh et al. 1979). Based on such studies, a suggestion has been made that judicious application of phosphorus fertilisers in saline soils can help improve crop yields by directly providing phosphorus and by decreasing absorption of toxic elements like chloride.

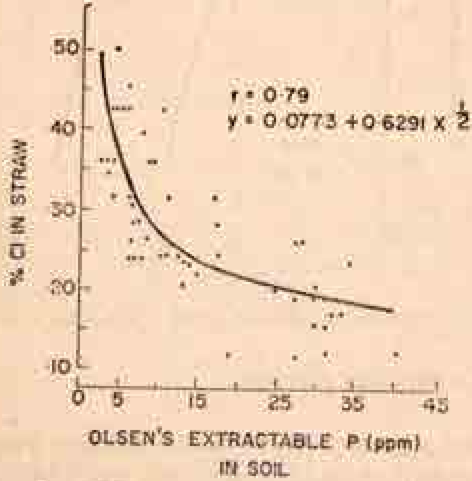


Fig. 3. Effect of available soil phosphorus as the chloride content of wheat straw (Singh et al. 1979)

It has been suggested that deficiency of the elements potassium and calcium may play an important role in the observed growth depression in many saline soils (Finck 1977). High salinity may also interfere with the growth and activity of soil microbial population and thus indirectly affect the transformations of essential plant nutrients and their availability to the plants.

Nutrient interactions are particularly significant for crop growth in alkali soils. High pH levels of alkali soils strongly influence the availability and transformations of several plant nutrients. Apart from the high pH level influencing the nutrient availability, direct influence of applied nitrogen on yield and relative uptake of sodium and calcium has been reported (Fig. 4, Abrol 1968). Interactions between salinity and sodicity and nutrients are only now being understood and, therefore, caution needs to be exercised when evaluating salinity/sodicity tolerance data of crops grown under widely different conditions of nutrient use.

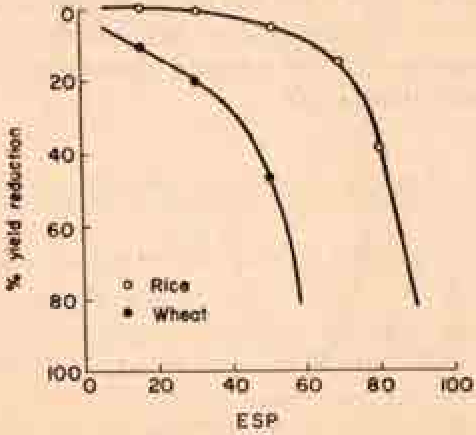


Fig. 4. Tolerance of rice and wheat to exchangeable sodium.

Interaction with Other Stresses

There is strong interaction of salinity/sodicity with other stresses in influencing observed crop growth and yield. A particular mention here must be made of the oxygen stress or of the oxygen supply to the plant roots. High salinity, in many cases, is accompanied by high water table conditions which limit oxygen supply to the growing roots. Similarly, in alkali soils short term oxygen deficiencies are almost a rule. Plant responses to salinity and sodicity under these conditions are likely to be entirely different. Therefore, objectives of any selection programmes will need to be very clearly defined in terms of the stress/stresses to which the tolerance is desired.

Dynamic Nature of Salts in the Root Zone

Soluble salts are highly dynamic in nature and move with each irrigation/drying cycle. Concentration of salts, therefore, may vary several fold both in time and space. After a pre-sowing irrigation, salts move to the soil surface due to evaporation and accumulate in the upper soil layers where seeds are often sown. Thus, the seeds are normally subjected to much higher concentration of salts than is indicated by the mean concentration of salts in the root zone. Similarly, plants that produce rapidly growing deep roots will avoid surface salts better than plants with a relatively shallow root system confined to the surface layers. Inadequate attention to, and appreciation of, these aspects may often lead to misinterpretation of data from studies intended to evaluate the tolerance of plants at different growth stages etc.

Varietal Differences in Tolerance

Differences in varietal tolerance to salinity and other adverse soil conditions have been known to exist. Testing the tolerance of varietal collections has been resorted to for selecting tolerant lines. In India, for example, a large number of cultivars of rice have been identified in different coastal states for their tolerance to salinity (Bhattacharyya 1976). Some of these are listed in Table 13. Similarly for wheat, cultivar 'Kharchia' from Rajasthan has been identified as highly tolerant (Rana et al. 1980).

Table 13. Some salt-tolerant rice cultivars

State	*Cultivar*
Andhra Pradesh	MCM1, MCM2
Kerala	Pokkali
Maharashtra	Kala Rata, Bhura Rata
Orissa	SR 22 B
West Bengal	Matla, Hamilton, Getu, Dasal, Damodar
Tamil Nadu	PVR I

It has been observed that, in general, those varieties of a crop which are more tolerant to adverse soil conditions have a somewhat lower yield potential under relatively non-stress conditions. In Fig. 5, B is a tolerant cultivar while A is relatively less tolerant of salinity but of a high yield potential under relatively non-stress conditions. Similar observations were made by Pasternak et al. 1979 whose data on response to salinity of four varieties of tomato are reproduced in Table 14. This data again shows that varieties which had the highest relative dry weight had almost the lowest scoring under non-stress conditions. Although this appears to be a common trend

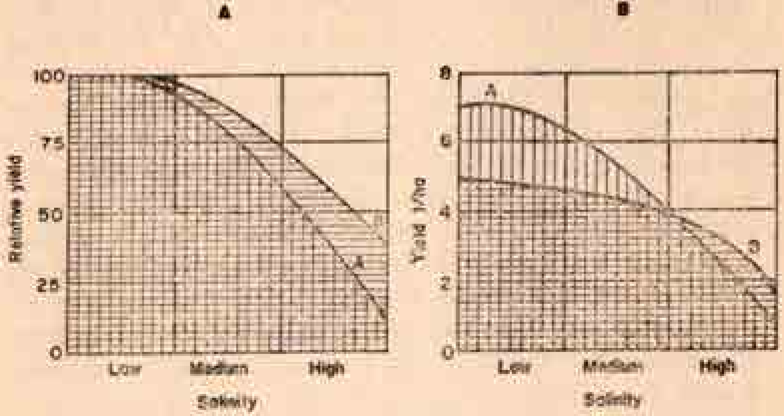


Fig. 5. Relative and absolute yields of high yielding dwarf (A) and tolerant tall (B) varieties of rice.

Table 14. Dry weight of 58-day-old tomato seedlings grown in nutrient solutions containing 8000 ppm NaCl (The four varieties were selected from 42 tested varieties)

(Pasternak et al. 1979)

Variety name	*Absolute dry weight (mg)*	*Scoring no.*[b]	*Relative dry weight (%)*[c]	*Scoring no.*
Marmande	860 a[a]	1	59.1 b	28
VF 145 B7879	520 b	15	81.2 a[b]	3
NCX 322 Niagara	400 b	25	61.5 b	22
Early VF 39	203 c	39	88.3 a	1

[a] Parameters with same letters within columns do not differ significantly at the 5% level.

[b] Scoring no. refers to the score of the parameters in relation to the other 41 varieties.

[c] Ratio to dry weight of seedlings grown in nutrient solutions without NaCl.

under natural conditions yet induced tolerance coupled with ability to yield high will be the major objective of plant improvement programmes in future.

Breeding for Enhanced Tolerance

Breeding of crops for enhanced tolerance to salinity/sodicity stress has received considerable attention of bio-scientists in recent years and a number of excellent articles and reviews including books have appeared (Downton 1983; Noble 1983; Staples and Toennisen 1984). Essentially two general approaches are being pursued. These are : (1) improving the tissue tolerance of plants; (2) manipulating the physiology of yield formation. The existing knowledge on the subject and evaluation of different approaches will be made in a companion paper in this volume by Dr. R.S. Rana. It would be appropriate here to mention that major success in breeding programmes depends on the adoption of proper selection criteria from amongst the populations. It has been suggested that if closely related genotypes that differ markedly in salt tolerance can be identified, such populations would be useful in determining the physiological basis of salt tolerance in a species (Epstein 1980). Such studies could provide plant breeders with physiological or morphological criteria for selecting for increased tolerance. The future research efforts on the genetic control of salt tolerance in a crop species, the physiological basis of tolerance and its variation with ontogeny and newer plant breeding techniques should lead to development of cultivars with greater tolerance to stress conditions improved by salinity (Noble 1983).

Conclusions

Based on the results already achieved, there are tremendous possibilities of increasing and stabilising agricultural production in areas where salinity is a perpetual problem through plant breeding programmes. In order that sound contributions be made on a long terms basis, the research programmes will necessarily require a large input from plant physiologists and soil scientists. In short, this will come about only by concerted team work. Although steady improvements will be possible in obtaining the better yields of crops through breeding programmes, at the present state of knowledge it would not appear reasonable to expect spectacular breakthroughs in the yield barriers that stress conditions impose.

REFERENCES

Abrol, I.P. (1968). A study of the effect of added nutrients on plant growth on a sodic substrate. Trans. 9th Int. Congr. Soil Sci. 2:585-595.

Abrol, I.P. and D.R. Bhumbla (1971). Saline and alkali soil in India—their occurrence and management. Paper presented at FAO/UNDP Seminar on Soil Survey and Soil Fertility Research. Feb. 15-20, 1971, New Delhi, *FAO World Soil Resources Report* 41:42-51.

Ayers, A.D. and H.E. Hayward (1949). A method for measuring the effects of soil salinity on seed germination with observations on several crop plants. *Soil Sci. Soc. Amer. Proc.* 13:224-226.

Bhattacharyya, R.K. (1976). New salt tolerant rice varieties for coastal saline soil of Sunderbans, W. Bengal. *Sci. and Cult.* 42:122-123.

Downton, W.J.S. (1983). Salt tolerance of food crops : Prospective for improvements. *CRC Critical Reviews in Plant Sciences* 1 (3): 183-201.

Epstein, E. (1980). Responses of plants to saline environments. In : *Genetic engineering of osmo regulation*, Eds. D.W. Rains, R.C. Valantine, and A. Hollanden, Basic Life Sci., Plenum Press, N.Y. 14:293-309.

Finck, A. (1977). Soil salinity and plant nutritional status. In: Managing saline water : *Proceedings of the International Salinity Conference*, Texas Tech Univ Lubbock Texas, pp. 199-210.

Hoffman, G.J., E.V. Maas and S.L. Rawlins (1975). Salinity-ozone interactive effects on alfalfa yield and water relations. *J. Environ. Quality* 4:326-331.

Magistad, O.C., A.D. Ayers, C.H. Wadleigh and H.G. Gauch (1943). Effect of salt concentration, kind of salt and climate on plant growth in sand culture. *Plant Physiol.* 18:151-166.

Mass, E.V. and G. Hoffman (1977). Crop salt tolerance—current assessment. *J. Irrig. Drain Div. Proc. Am. Soc. Civil Engg.* 103:115-134.

Massoud, F.I. (1974). *Salinity and alkalinity as soil degradation hazards.* FAO/UNDP—Expert consultation on soil degradation. June 10-14 1974, FAO, Rome, pp. 21.

Murthy, K.S. and K.V. Janardhan (1971). Physiological considerations for selection and breeding of varieties for saline and alkaline tracts. *Oryza J.* 8:85-99.

Noble, C.L. (1983). The potential for breeding salt tolerant plants. *Proc. Royal Soc. Vict.* 95:133-138

Pasternak, D., M. Twersky and Y. de Malach (1979). Salt resistance in agriculture In: Stress physiology in crop plants. Ed. H. Mussell and R. Staples, John Wiley and Sons, N.Y., pp. 128-142.

Rana, R.S, K.N. Singh and P.S. Ahuja (1980). Chromosomal variation and plant tolerance to sodic and saline soils. In : *International Symposium on Salt Affected Soils*, 18-21 February, Karnal, pp. 487-493.

Singh, A., R. Chhabra and I.P. Abrol (1979). Effect of flourine and phosphorus applied to sodic soil on their availability and on yield and chemical composition of wheat. *Soil Sci.* 126:90-97.

Sinha, B.K. and N.T. Singh (1974). Effect of transpiration rate on salt accumulation around corn roots in a saline soil. *Agron J.* 66:557-560.

Staples, R.C. and G.H. Toenniessen (1984). *Salinity tolerance in plants*, John Wiley and Sons, N.Y., pp. 443.

Breeding Crop Varieties for Salt-affected Soils

R.S. RANA

Expression of genetic potential for growth and yield of a crop variety is directly dependent upon the environment comprising both climate (weather) and soil components. As discussed in the preceding chapter, the term 'salt-affected soils' encompasses a broad group of adverse but distinct soil conditions, namely, saline, alkali (sodic) and acid soils with further variations such as coastal and inland locations as well as arid and water-logged situations (Swaminathan 1977; Bresler et al. 1982). Factors limiting growth and yield of crop plants in various categories of problem soils are different and specific. Likewise, adaptive strategies evolved by plants to cope with the prevailing edaphic stresses, such as salt stress, also vary a great deal as indicated in Table 1. It is not unexpected therefore, that even varieties within a crop often show notable differences regarding tolerance to adverse soil conditions (Epstein et al. 1980; Devine 1982; Shannon 1984; Sayed 1985). Hence, it is essential that the breeder must understand the inherent characteristics of the problem soil with which he is concerned and should also simultaneously appreciate that basically it is the sensitivity of crop variety, rather than the soil parameters *per se*, that essentially determines the occurrence as well as the magnitude of actual soil problem (Rana 1977). Since the degree of tolerance (adaptation) of crop varieties to different kinds of salt affected soils is genetically controlled, it is axiomatic that it can be improved through genetic manipulations by adopting suitable breeding procedures.

While efforts to adjust edaphic environment to suit crop production are continuing on a massive scale, there is a growing

Table I. Simplified patterns of plant response and adaptation to salt stress

Response patterns	*Major consequences*	*Adaptation strategies*
A. High ion uptake by roots	Ion excess, toxicity, adverse effects on metabolism	1. Coping with high internal ion build up: Turgor maintenance through compartmentation of ions into vacuoles, and accumulation of compatible solutes in the cytoplasm.
		2. Avoidance of excess ion build up in shoots: Control of toxic ion's uptake by roots; Control of ion transport to the shoot; Removal of toxic ions from the shoot through salt glands, bladders, or via phloem; Increase in shoot volume (succulence).
B. Low ion uptake by roots	Water deficit nutritional deficiency; decrease in expansion growth; decrease in CO_2 fixation	1. Avoidance of cellular water deficit: Turgor maintenance through synthesis of organic solutes.
		2. Survival with minimal growth and reduced reproduction (yield) capacity.

realisation now that a more effective, less costly, non-polluting and longer lasting adaptive contingency lies with genetic modification of the plant itself (Epstein 1976; Rana 1977; Epstein and Norlyn 1977; Epstein et al. 1980; Downton 1984). This challenging task may be best achieved by the application of classical genetics in combination with modern techniques of tissue culture, somatic hybridisation, molecular biology and genetic engineering (Hollaender et al. 1979; Rains et al. 1980; Swaminathan 1983). It is not surprising, therefore, that proceedings of several international symposia and workshops, held on this subject in recent years, have emphasised the need to develop improved crop varieties best suited to specific adverse soil conditions (Wright 1976; Muhammed et al. 1977; Jung 1978; CSSRI 1980; Christiansen and Lewis 1982; Staples and Toenniessen 1984).

It is remarkable in this context that plant physiologists and geneticists are now actively engaged in studying genotypic differences in salt resistance in terms of capacities for exclusion, absorption, translocation, isolation, exclusion, and metabolic tolerance of potentially toxic ions (Fitter and Hay 1981; Saric and Loughnan 1983). If these efforts are to make any real headway, however, it is essential that plant breeders must be actively involved in these projects to ensure proper and speedy utilisation of the basic research findings.

Basic Concepts

RESISTANCE

A pre-requisite for undertaking a project on breeding for salt stress resistance, to cite one edaphic stress factor, is to properly understand the notion of such resistance. The term resistance was originally used in case of animals to indicate their specific reactions to particular infective organisms and implied an antigen-antibody concept. The usage was subsequently extended to plants' reactions to biotic stresses with a view to categorising host-parasite interactions as followed in case of rust infection based on the type and intensity of postules. In marked contrast, however, plant resistance to abiotic stress factors (such as salinity, drought and temperature) denotes *a relative rating* of the plant's response to a given level of stress factor under defined soil and weather conditions.

Plant resistance in the context of salt-affected soil is thus not a simple reaction but it is a complex interaction between the plant and the operating soil stress factor and its expression is effected considerably by numerous variables relating to the plant itself (genotype, ploidy level, growth stage, maturity period, etc.), the soil status (texture, topography, fertility, groundwater table, irrigation schedule, management level, etc.) and the atmospheric conditions (temperature, humidity, light, rainfall, wind, pollution, etc.). The salt-stress resistance rating of a crop/variety is thus meaningful only when soil status and atmospheric conditions are mentioned and, wherever relevant, the growth stage is also specified. In other words, terms like "salt-resistant" and "salt-sensitive" crops or varieties do not convey any useful information to the breeder unless the stress as well as the response parameters are also stated.

In general, the Salt Stress Resistance (SSR) denotes a plant's ability to prevent, reduce or overcome the possible injurious effects caused directly or indirectly by the excessive presence of soluble salts/toxic ions in its root zone. It follows that the SSR mechanisms present in a plant result in a measurable increase in the soil stress level that is required to produce a specified quantum of strain (as measured by the stress-caused visible injury or reduction in germination/growth/yield) and they also lead to a decrease in the quantum of strain induced by a specified level of edaphic stress like salinity.

Although a plant cannot modify an edaphic stress that is exerting on it externally yet it may prevent or decrease the stress penetration into its tissues. This type of resistance is called "stress avoidance". Even when the stress enters a plant's tissues, it may show resistance if it has the capability to eliminate, reduce or repair the injurious strain. This ability of the plant is termed "stress tolerance". In practice, however, the terms tolerance and resistance have been used interchangeably (See Levitt 1980 for a discussion on terminology).

TOXICITY

It may also be useful to distinguish between unfavourability and toxicity. Whereas the former denotes simply a slowing down of metabolism because of deficiency of nutrient ions/

water as experienced under conditions of drought or low fertility, the latter involves excess of specific ions that interfere actively with the plant metabolism as happens largely in the case of alkali, acid and saline soils. Osmotic effects as well as specific ion effects cause reduction/inhibition of plant growth in problem soils. Toxic ions affect not only a plant's ability to acquire resources (i.e., acquisition of water, nutrients, CO_2, light energy) but they also influence its ability to utilise those resources through inhibition of enzyme action, cell division, and loss of respiratory substrates.

RESISTANCE MECHANISMS

It has become increasingly clear in recent years that there is no single mechanism operating in glycophytes, the group to which most crop plants belong, conferring adaptation to saline and other problem soils (Bernstein 1975; Greenway and Munns 1980). Different species and species-groups appear to have developed their own strategies based on certain anatomical, morphological and developmental features to cope with their environmental demands while genotypes within a species often show notable variations of the specific scheme extending the range of adaptation of that species. Thus, despite the preponderance of unwanted or even potentially toxic ions in the soil liquid phase surrounding the root cells, a resistant type of plant tries to maintain its own characteristic ionic composition in its tissues so as to survive, grow and reproduce (yield). This objective is achieved through avoidance (selective exclusion of specific ions), tolerance, or more often, a subtle combination of both these mechanisms.

Halophytes like some species of the family Chenopodiaceae, on the other hand, respond to salinity by taking up sodium and chloride at high rates and then accumulating these ions and isolating them in vacuoles of leaf cells. This compartmentation has great significance for the performance of halophytes in a saline environment (Flowers et al. 1977).

Plants have also evolved a variety of mechanisms for adaptation to osmotic stress, one of which is osmoregulation that is cellular adaptation. This osmotic adjustment in the cytoplasm is accomplished mainly by means of dissolved substances that are compatible with the cell's enzymes and its metabolic processes. These compatible solutes are mostly organic compounds (of the photosynthetically fixed carbon and nitrogen, both valuable resources) such as the nitrogenous compounds glycinebetaine and proline and, in some plants, sugar alchohols such as sorbitol (Paleg and Aspinall 1981). In addition, a high concentration of potassium is also maintained. Nevertheless, when a plant adjusts osmotically to a saline medium or osmotic stress, the increased rates of ion uptake (and transport) and the synthesis of organic solutes require additional expenditure of energy that would have otherwise been used for growth processes. In other words, actual yield levels of even osmoregulatory genotypes will be lower under stress condition as compared to those under favourable environments.

Measurement of Salt Stress Resistance

MONITORING OF SALT STRESS

To begin with, soil salinity in the plant's root zone needs to be monitored periodically throughout the duration of the experiment. It is conveniently measured as electrical conductivity of the saturated soil extract ECe and it is directly proportional to the salt concentration in the soil liquid phase. Unit of measuring electrical conductivity is decisiemens per metre (dS/m) and it has replaced the earlier used expression of millimhos per cm; one dS/m is equal to one mmhos/cm. A routine method used for this purpose comprises sampling the soil within the root zone, preparing a saturated extract or 1:2 soil-water solution, and measuring the EC of the soil water. Because of the usual variation in soil salinity with depth, measurements are made of samples taken from several depths within the root zone and the values are averaged. Another technique employs salinity sensors or probes which are inserted in the soil for a direct measurement of the EC of the soil water. Determination of pH and exchangeable Sodium is also necessary for the alkali soils. In addition, estimation of Ca^{+2}, Mg^{+2}, Cl^{-}, SO_4^{-2}, CO_3^{-2} and HCO_3 is done for a more precise characterisation of the soil problem.

Since soil-water-plant-atmosphere is a continuvum, variations in respect of all the four component systems interact, thereby modifying the operating stress level and, consequently, the resultant strain induced in the plant. It is, hence, essential that variables concerning these interacting components are also monitored to ensure valid interpretation of data and meaningful comparison of results reported by different workers.

MEASUREMENT OF RESISTANCE

Several methods are used for measurement of resistance, choice depending upon the objective of study. Avoidance, for example, is measured by determining the ratio of salt (or ion) concentration in the external medium to that in the plant tissue. This may be done for specific salts like NaCl or would be measured separately for the cation (Na^+) and the anion (Cl^-). Avoidance by the shoot is usually measured by determining translocation from root to shoot. Osmoregulation may be measured by the length of time required by the plant to adjust to a specific increase in osmotic concentration of the root medium. Another possibility is to determine the highest external concentration to which a species or variety can adjust.

DIRECT STRAIN

Primary direct strain is measureable at the tissue level and also in seedlings and adult plants. For this purpose, tissue sections are immersed in a graded series of saline solutions for 24 hours and then proportion of living cells is determined by * plasmolysis with hypertonic glucose solutions. This method is considered to give the best measure of salt tolerance since it is based on survival rather than on growth and yield. Sometimes "salinity tolerance indices" are worked out by combining both mortality and biomass production.

SEEDLING TESTS

Seedling evaluation for salt resistance is done by awarding visual score values, at the tillering and stem elongation growth phases, based on percentage leaf area damaged or killed in seedlings growing in saline media in greenhouse, saline field or salinised microplots. Standard checks, representing both resistant as well as susceptible types, are also included to take note of general growth conditions as well as effectiveness of the salinity level chosen for evaluation of resistance. Since problem soils are mostly heterogenous under field conditions, several replications are necessarily scored for obtaining precise comparisons. Special experimental layouts, such as the grid design, and technique of unusually long rows are also adopted to take care of such field heterogeniety. Besides recording relative leaf tissue damage caused by a chosen salinity level, some workers compute salinity levels that cause a 50 per cent reduction in chlorophyll content of different crops and their varieties.

INDIRECT STRAIN

Salt resistance of crop varieties is tested more commonly on the basis of primary indirect strain and this is measured by computing the specific conductance of a soil saturation extract corresponding to a standard percentage of reduction (usually 50 per cent) in seed germination, seedling growth, dry matter production or grain yield. Mass and Hoffman (1977) analysed the published data on salinity-caused yield reductions in 76 crops and prepared averaged yield response curves. This information was then used for comparing relative salinity tolerance of those crops on the basis of the following two criteria:

1) The maximum salinity level, represented by the plateau part of the yield response curve, which does not cause significant yield reduction in comparison to the yield level obtained in nonsaline favourable soil conditions. This salinity level is the threshold level beyond which yield begins to decline significantly.

2) Per cent yield decrement per unit (dS/m) increases in salinity beyond the threshold level.

It is noteworthy in this context, however, that these computed values in respect of the above mentioned two criteria merely serve the purpose of providing general guidelines since the actual values observed at any location will vary from the computed figures depending on climate, soil conditions and cultural practices. In addition, there is often a strikingly large range of genetic diversity regarding salinity tolerance in varieties of the same crop. In addition, linearity of the yield response curve, that serves as the basis for computing salt tolerance ratings, has been contested by many workers. CSSRI experience reveals that determination of the threshold salinity point and the salinity level causing a 50 per cent yield reduction (also seedling emergence in case of directly seeded crops) is a more relevant and reliable guideline. It needs to be appreciated that the research data, required for calculation of these indices, must be generated for representative locations of salt-affected areas in our country for the relevant crops of the concerned region. Location-specific data are expected to be more dependable as these will take care of the variations with regard to soil, climate, crop variety and cultural practices. Usefulness of such information will, however, depend upon the precision and validity of the experimental data.

Genetic Diversity for Salinity Stress Resistance

There is a great diversity of biological life adapted to habitats of high salinity extending from the extreme halophilic bacteria and algae to mangrove vegetation of estuaries and coastal belt. Green alga *Dunaliella viridis*, for example, thrives in the highly saline Dead Sea (its salinity is nearly eight times that of normal ocean water whose average salinity level is around 35 dS/m) and it is being tried in Israel for extraction of glycerol, that occurs in this species in high concentration, on a commercial scale. Mangrove swamps of highly productive large trees growing in sea water are examples of higher plants adapted to perform remarkably well in a saline environment.

INTER-SPECIFIC DIFFERENCES

A survey of reported data on response of crop plants to increasing salinity levels reveals about eight fold differences among them regarding tolerance to salinity stress. Threshold salinity level (SY_{100}) beyond which yield begins to decline significantly, for example, varies from nearly 1.0 dS/m for Beans to around 8 dS/m in case of barley, cotton and some *Agropyron* species. Again, salinity level causing 50 per cent reduction in yield (SY_{50}) is less than 4 dS/m in the case of beans and onions while it is above 15 dS/m for barley, cotton, sugar beet, tall wheatgrass and some forage grasses.

An interesting point that has emerged from the work done at the CSSRI is that some allopolyploid crop species turned out to be remarkably more tolerant to both alkali soil as well as saline soil conditions as compared to their putative diploid work in this area (Epstein et al. 1980; Devine 1982; Downton 1964; Shannon 1984; Kingsbury and Epstein 1984; Sayed 1985).

Table 2. Grain yield of seven wheat varieties grown in reclaimed and partially reclaimed alkali soil

	Average grain yield (t/ha)		
	Reclaimed soil	*Partially reclaimed soil*	
Varieties	*pH 8.0*	*pH 8.9*	*pH 9.3*
HD 2009	4.58	2.94	1.63
WL 711	4.56	3.18	1.87
WH 157	4.32	3.50	2.20
HD 2177	4.31	2.59	1.47
HD 1982	4.15	3.41	1.89
HD 1553	4.02	2.92	1.46
Kharchia 387	2.96	2.75	2.28
CD at P = 0.05	0.77	0.86	0.53

The CSSRI has made sizeable collections of indigenous cultivars of rice, wheat and barley materials that have for a long time been grown traditionally in different situations of salt-affected soils under little management care. Evaluation of these materials, along with large stocks of germplasm collections of these crops built up over the years, regarding their response to soil salinity/alkalinity under comparable conditions in micro-plots designed for such testing, has led to four significant inferences which are being verified by studying the responses of more recent accessions. Parameters used for monitoring varietal response to edaphic stress included seed germination, rate of seedling emergence, seedling growth rate, plant height, dry matter production and grain yield. The aforementioned inferences are stated in the following paragraphs.

First, the highest level of salt tolerance was found in indigenous cultivars of salt-affected areas. Outstandingly salt-tolerant wheat materials comprised of red-grained selections made from locally-adapted Kharchia wheats of Rajasthan and Rata wheats of Bhal tract of Gujarat. Two such lines, namely, KR 375 and KR 387 have been extensively used in our hybridisation programmes designed to combine superior salt tolerance with high grain yield potential. Data on mineral analysis of plants at the tillering phase, growing in alkali (sodic) soil, have revealed that their outstanding tolerance is largely due to their superior ability for potassium uptake under competition with sodium (Table 3). Rice cultivars, identified to be highly salinity/alkalinity tolerant, included Nona Sail, Nona Bokra, Damodar (CSR 1), Getu (CSR 3), Jhona 349, SR 3-9, Kala Rata, Bhura Rata, Karekagga, Bilekagga, Orpandy and Ormundkan (Fig. 2).

Table 3. Response of four wheat varieties to soil alkalinity (sodicity)

	Soil grades		Content in dry matter at tillering phase			Grain yield
			Na	*K*	*K/Na*	
Varieties	pH_s	*ESP*	*%*	*%*	*index*	*(g/pot)*
Kharchia KR 387	7.6	8	0.09	3.81	42.33	34.69
	9.1	32	1.05	2.44	2.32	26.12
	9.5	46	1.56	1.59	1.02	18.74
WH 157	7.6	8	0.08	3.73	46.62	35.27
	9.1	32	1.67	1.79	1.07	19.61
	9.5	46	2.49	0.88	0.35	4.92
HD 2009	7.6	8	0.08	3.69	46.12	36.71
	9.1	32	2.05	1.32	0.64	13.43
	9.5	46	2.71	0.89	0.33	0.00
HD 4530	7.6	8	0.16	3.52	22.00	29.86
	9.1	32	2.41	0.98	0.41	6.81
	9.5	46	3.19	0.51	0.16	0.00
C.D. at $p = 0.05$			0.31	0.26		3.01

Second, the maximum level of tolerance to salinity stress among rice materials, particularly observed at the seedling stage, was found among tall, photo-sensitive and coarse-grained cultivars of long duration. Efforts to obtain this level of tolerance in dwarf and photo-insensitive forms through recombination breeding have not succeeded as yet.

Third, evaluation of several hundred varieties of both Breadwheats (hexaploids) and durums (tetraploids) for tolerance to alkali soil conditions revealed that the former group was far superior in this respect, particularly in terms of foliar damage and grain yield reductions. Fourth, both genetic variability for tolerance to alkali and saline soil conditions was found to be remarkably higher among wheat materials than in case of barley accessions screened so far under this programme. Though barley materials showed a distinct superiority over wheats under

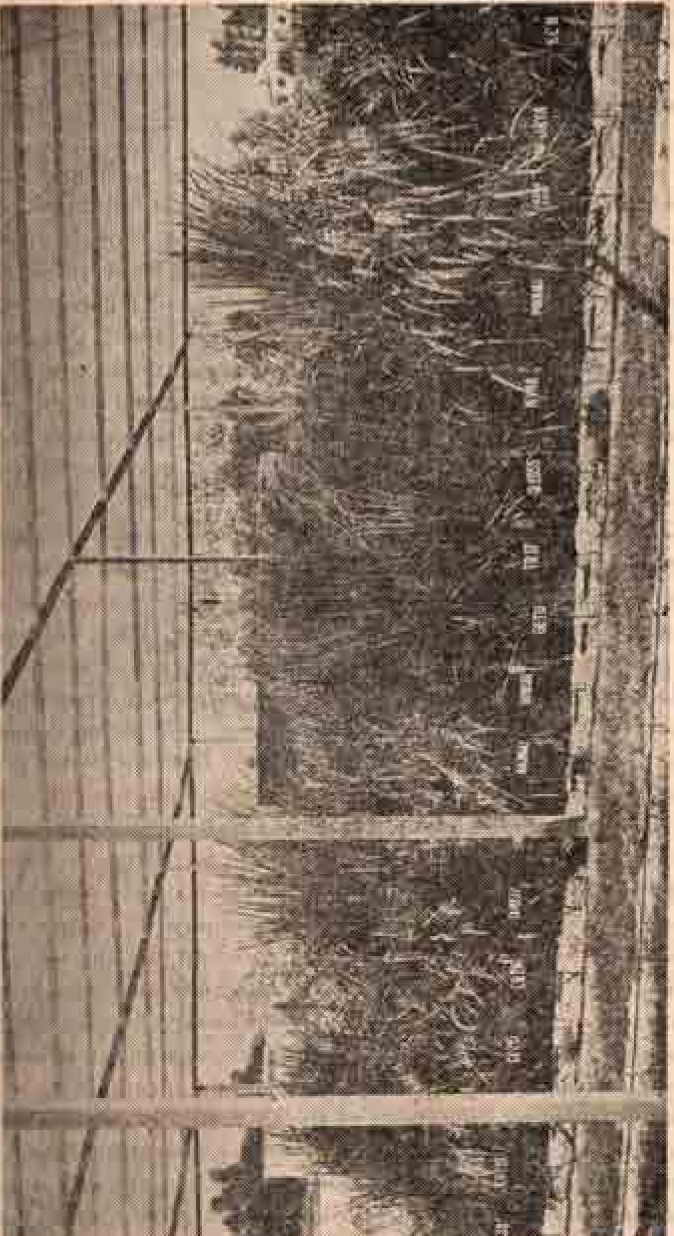


Fig. 2. Comparative response of rice varieties to mild salinity stress.

conditions of NaCl-based salinity and limited water availability yet the magnitude of varietal differences in the former was relatively much lower.

Genetic Control Mechanisms

The subject of plant tolerance to problem soils and the efficiency of nutrient uptake, as well as utilisation, has been reviewed comprehensively from time to time though critical information on genetic mechanisms governing plant responses to edaphic stresses is still limited (Epstein and Jefferies 1964; Epstein 1972, 1976; Foy et al. 1978; Shannon 1984). Whereas ion uptake and transport in plants can be monitored with high precision in nutrient cultures grown under controlled conditions, the methodology of measuring plant tolerance to problem soils still lacks reasonable accuracy and, hence, reproducibility of tolerance ratings.

Salinity, in particular, interacts rather strongly with other environmental factors and this often diffuses/masks the genotypic differences in tolerance making inheritance studies uncertain as the sharp boundaries between classes fade away. Thus, unavoidable heterogeniety under field conditions makes it necessary for the geneticists to develop a suitable experimental set up where salinity/alkalinity may be reasonably maintained within defined limits. Such a system should also ensure that the plants performance is as close to that under field conditions as possible. In this context, microplots designed at the CSSRI have been found to work satisfactorily under Karnal conditions (Fig. 3). Since breeders employ a tolerance rating based on yield-reductions caused by a specified stress level under otherwise comparable growth conditions, it is also essential to ensure that the selected edaphic stress level is sufficiently discriminatory to resolve genetic differences in tolerance and the yield levels obtained under favourable (non-stress) soil conditions are maximised to make the computation of yield reductions valid and meaningful.

Besides inherent limitations of working with soil media such as complexity of interactions among operating stress factor(s) and nutrients, lack of availability of clearcut varietal differences of sufficient magnitude in currently available genetic stocks of some crops as well as want of efficient criteria for precise tole-

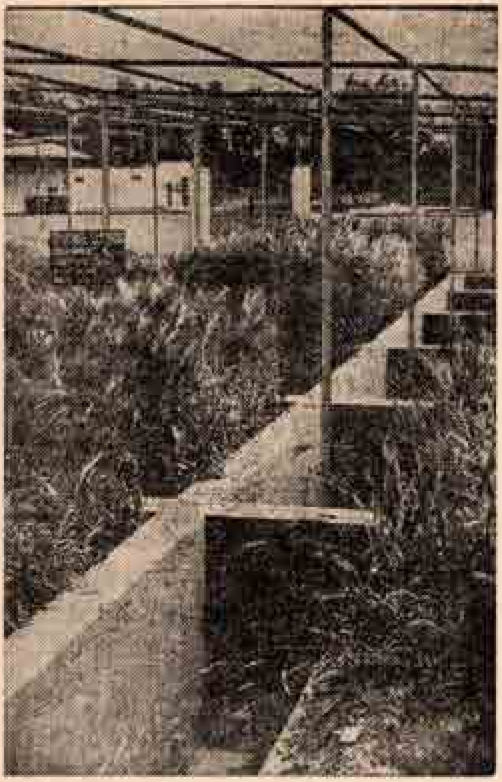


Fig. 3. Experimental set up at the CSSRI for studying varietal response to soil alkalinity and salinity under monitored conditions.

rance rating of individuals in large segregating populations are also the bottlenecks in undertaking the genetic analysis required for formulation of breeding strategy.

GENE ACTION AND HERITABILITY

An understanding of genetic mechanisms, that control varietal response to a particular edaphic stress factor, will not only help in evolving a suitable breeding methodology but it is also expected to accelerate the pace of progress. Thus, the choice of breeding procedure will depend upon knowledge of the trait's pattern of inheritance (qualitative or quantitative), number of genes with major effects and the nature of gene action involved.

A survey of published information on this aspect reveals that resistance to specific ion effects in most cases shows a qualitative type of inheritance governed by single or a few genes with major effects. In marked contrast to this, resistance to osmotic effects follows usually a quantitative pattern of inheritance with polygenic control. This situation obviously complicates the task of plant breeders and poses a challenge to the development of appropriate breeding methodology with a view to combining superior salt tolerance with improved yield potential.

Heritability estimates are required in case of quantitatively inherited traits to know how much of the phenotypically expressed variation is genetic (Heritability in a broad sense) and to what degree a particular trait can be modified by direct selection and fixed because of additive gene action (Heritability in a narrow sense). Estimates of heritability of varietal responses to edaphic stresses have been reported by many workers in respect of grain yield and several other parameters that are usually employed for measurement of salt tolerance (Singh and Rana 1983; Lehman et al. 1984). Since expression of genetic information depends upon its interaction with the environment, heritability estimates for the same trait may be expected to vary and, hence, general statements regarding heritability of response to edaphic stresses would not be meaningful. Strength of association of some of these parameters with the grain yield has also been reported revealing their reliability as selection criteria for predicting yielding ability under saline soil conditions as shown in Table 4. It has been concluded that salt tolerance at the seedling stage and at the reproductive phase are two sepa-

Table 4. Correlation coefficients between grain yield and four other criteria used for measurement of salt resistance in rice. (Based on 55 varieties grown in saline soil ECe 8-10 dS/m)

Criteria for salt resistance	*Seedling dry wt.*	*Survival*	*Seed sterility*	*Grain yield*
Seedling leaf injury	0.425**	0.512**	0.124	0.129
Seedling dry wt.	—	0.316*	0.158	0.279
Survival	—	—	0.145	0.162
Seed sterility	—	—	—	0.702**

* significant at 5 per cent P level.
** significant at 1 per cent P level.

rate inherent characteristics suggesting thereby that screening for salt tolerance should be based on two criteria representing both the growth stages (Rana 1981). For example, salinity-induced reduction in seedling growth and salinity-caused seed sterility have proved to be reliable parameters for measurement of salt resistance.

GENES AND CHROMOSOMES WITH MAJOR EFFECT

Genes which have a major effect on varietal responses to edaphic stress factors have been reported in many crops, mostly controlling uptake/utilisation of nutrients or exclusion of toxic ions (Devine 1982; Tal 1984). A summary of some of these reports is provided in Table 5 by way of illustration to indicate the possibility of genetic manipulation of the listed traits through breeding. Where major gene effects are not discernable, some cytogeneticists have resorted to genomic and aneuploid analysis of resistance to abiotic stresses with a view to identify-

Table 5. Genes with major effects influencing ion uptake/use

Gene	*Reported effect*	*Reference*
fe	Controls efficiency of Fe utilisation in soybeans. Recessive homozygotes lack ability to reduce Fe^{+3} to Fe^{+2} at the root surface.	Weiss (1943) *Genetics* 28: 253-268
np	Determines sensitivity to excess P in soybeans. Recessive homozygotes develop severe splotching and chlorosis.	Bernard & Howell (1964) *Crop Sci*. 4 : 298-299.
Ncl	Controls chloride exclusion from plant tops in soybeans. Recessive homozygotes accumulate Cl more than seven times of dominants.	Abel (1969) *Crop Sci.* 9 : 697-698.
ys_1	Yellow stripe mutant (recessive) in maize lacks efficient utilisation of ferric iron supplied to roots.	Bell et al. (1958) *Bot. Gaz.* 120 : 36-39
Alp	Confers resistance to Al toxicity in winter barley.	Reid (1970) *Barley Genetics* II: 409-413.
fer	Recessive homozygotes show Fe-inefficient response in tomato.	Brown et al. (1971) *Physiol Plant*. 25: 48-53.
Ku	Enhances potassium uptake and accumulation in leaves of wheat plants grown in alkali (sodic) soil.	Rana (Unpub.).

ing genomes or individual chromosomes contributing significantly towards the observed resistance. Some instances of this approach are listed in Table 6.

Table 6. Chromosomal regulation of plant response

Author (s)	*Reported conclusion*	*Reference*
Naismith et al. (1974)	—Loci influencing Ca, P, Mn accumulation located on chromosome 9 in maize.	*Crop Sci.* 14 : 845-849.
Slootmaker (1974)	—Resistance to high soil acidity conferred by D genome in wheats.	*Euphytica* 23 : 505-513.
Prestes et al. (1975)	—Al tolerance factor carried on chromosome 5 D in wheats.	*Agron. Abst.* 67: 60.
Cacco et al. (1976).	—Root uptake efficiency of SO_4^{-2} and K^+ increased with ploidy level in wheat and sugarbeet.	*J. Agri. Sci.* Camb. 87 : 585-589.
Rana et al. (1980)	—Resistance to alkali and saline soil conditions increased with ploidy level in *Triticum* and *Brassica* spp. —Wide adaptation of bread-wheats to salt affected soils owing largely to D genome (2D, 3D, 5D).	Internatl. Symp. CSSRI, Karnal. pp. 487-493.

BREEDING TECHNIQUES

To recapitulate from what has been mentioned so far, it may be stated that physiological effects of salinity and other edaphic stresses have not been fully understood, the measurement of salt resistance is not yet precise, plant mechanisms imparting resistance to salinity and other soil stresses are not properly elucidated, and reliable markers for such resistance are not so far available. What is documented authentically so far, however, is that considerable interspecific genetic diversity for resistance to salts and several other edaphic stress factors exists in several crops holding promise for genetic manipulations through breeding efforts to combine superior resistance to specific edaphic stress factor(s) with better yielding ability. Inspiration to undertake such a challenging assignment comes from the knowledge of genes with major effects controlling uptake and utilisation of nutrients, and also exclusion of potentially toxic ions, reported in several crops. Optimism in this line of work stems from some notable advances already made in some crops such as barley, wheat, rice, soybean and tomato.

Barley lines, for example, have been developed that survive and yield grain (averaged nearly 1118 kg/ha) under irrigation with undiluted sea water (Epstein 1976; Ramage 1982).

A redeeming feature of developing crop varieties to suit specific situations of salt-affected soils is that many edaphic stresses are now much better understood than other abiotic stresses such as drought and their monitoring as well as simulation can also be done more satisfactorily. It is not surprising, therefore, that noteworthy progress has been made towards this objective in several crops following conventional breeding procedures involving cycles of rigorous testing, selection and hybridisation. Since growth and yield reductions are quantitative parameters, data analysis employing modern methods of biometrical and quantitative genetics has helped in handling and evaluation of breeding materials on a large-scale and with greater precision.

The pivotal step in breeding for resistance to edaphic stresses is a reliable and efficient screen capable of isolating the resistant genotypes. A method, advocated by Dewey (1962) and elaborated by Kingsbury and Epstein (1984), involves isolating genotypes that survive at very high salinities (seedling test in nutrient culture for 6 weeks), rather than picking those which are most productive at a lower salinity. Productivity (yield) of the surviving selections is then tested over a range of salinities and compared with that of other lines, ranging from salt-resistant to salt-sensitive. This method with some modifications is being followed by many workers but others do not subscribe to this view of very severe initial rejection (over 90 per cent) and prefer to work with a wide genetic base keeping their options open during early generations. It is also argued that narrowing down the genetic base too much in the beginning may lead ultimately to lines having outstanding survival and biomass production under conditions of high salinity but their grain yield potential may be low and difficult to improve upon.

While screening germplasm collections at the CSSRI for tolerance ratings, criteria of seedling emergence index and early vigour are used for cutting down the number of entries to manageable numbers but selections for advancement of generation are based primarily on spike weight which is strongly correlated with yielding ability in alkali/saline soils. There are reports, on the other hand, that heritability of single plant yield is low and selection for grain yield on a single plant basis is ineffective. Rosielle and Hamblin (1981) discussed theoretical aspects of selecting for yield under stress and non-stress environments and concluded that selection should be made for increased mean productivity (i.e., for the average yield under stress and non-stress environments) rather than solely for the tolerance to stress (i.e. for the yield difference between stress and non-stress environments). Although a standard breeding methodology for developing crop varieties best suited to problem soils is obviously not available at present yet it is heartening to note that over 60 research centres, spread in many countries facing salinity and related problems, are actively engaged in this challenging task.

New Approaches

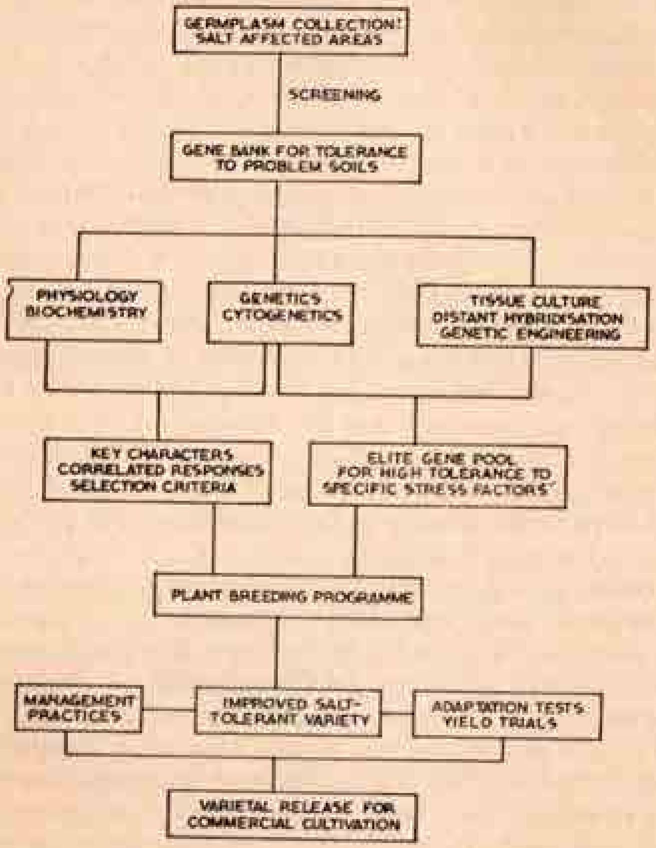
Use of cell culture techniques in developing salt tolerant crop plants, and also in studying salt tolerance at cellular level, has aroused considerable excitement in recent years. It has been shown that salt tolerance, manifested in callus cultures of tomato, barley and sugarbeet, is also reflected in the whole plant (Tal et al. 1978; Orton 1980; Smith and McComb 1981). Although the application of these techniques has proved effective in selecting cell lines for salt tolerance in several systems yet there are still many unsolved problems pertaining to cell culture systems and, consequently, there has been limited success of this approach so far (See Rains et al. 1980; Swaminathan 1981; Stavarek and Rains 1984; Hanson 1984). Nevertheless, protoplast culture technique is being increasingly employed to generate genetic diversity for salt tolerance at the cellular level by: (i) passage through cell, (ii) mutagenesis, and (iii) fusion with other protoplasts. It is now widely appreciated that the techniques of culturing tissue, cells and protoplasts have provided the much needed link between classical genetics and molecular genetics (Swaminathan 1983).

It may be recalled that conventional plant breeding methods for the improvement of grain crops are essentially based upon the sexual cycle to recombine genetic information (DNA) through an independent assortment of chromosomes and crossing over. Mendel's laws (with appropriate modifications and additions) and the relationship of genes with chromosomes comprise classical genetics that serves as the backbone of plant breeding procedures. Genetic engineering (including cellular and molecular approaches), on the other hand, involves genetic manipulations that bypass the sexual cycle and aim at producing an individual having a new combination of inherited properties. The cellular approach involves *in vitro* culturing of haploid cells and hybridisation of somatic cells while the molecular approach is based on direct manipulation of DNA. This latter approach employs recombinant DNA molecules that are constructed outside living cells by joining additional (natural or synthetic) DNA segments to known DNA molecules of primary interest. In this context, techniques for cleaving and annealing DNA molecules with precision and the development of host-vector systems for carrying foreign DNA into the host cells have led to demonstrable advances in bacteria as illustrated by the transfer of osmoregulatory gene(s), *osm*, governing production of osmoprotective molecules.

Using the recombinant DNA technique, a nitrogen-fixing strain of *Rhizobium*, normally highly sensitive to osmotic stress, was converted into a tolerant type with the help of a broad-host-range plasmid by transferring a DNA segment (of about 10,000 base pairs) from *Escherichia coli* carrying the *osm* gene(s) that led to proline over-production and consequent osmotic tolerance (Valentine 1984). This technology for genetic manipulation of cellular adaptation to salinity (i.e., osmoregulation) must, however, be suitably integrated with standard plant breeding procedures if this approach is to be gainfully employed for genetic improvement of salinity tolerance in crop plants as suggested in Table 7.

Breeding crop varieties suited to specific situations of edaphic stresses is far more difficult than developing varieties suited to favourable and relatively stabilised environments. This challenge could be best met by the application of classical genetics in combination with the techniques of tissues culture, molecular biology and recombinant DNA. The stage is already set for exciting developments in this new area of research.

Table 7. Integrated approach to breeding for adaptation to salt-affected soils



Conclusion and Outlook

To sum up, the ability of a crop variety to tolerate a given level of salinity/alkalinity has now become a paramount proposition in managing salt-affected soil and water resources. For this reason, there has been an upsurge of interest in recent years in tailoring crop plants to suit salt-affected edaphic environments. This new outlook contrasts the past approaches which exploited a greater abundance of better quality water and cheaper energy resources (soil amendments) to modify the soil environment to suit the plant. Current research efforts are mainly focussed upon critical assessment of inter-varietal genetic variability and its exploitation for improving crop salt-tolerance both by conventional breeding (intra-specific hybridisation and recovery of desired recombinations) and by *in vitro* methods that include tissue culture technique and recombinant DNA technology.

Notwithstanding the reported genetic variability for tolerance to alkali/acid/saline soil conditions in several crop species, there is an urgent need to collect and evaluate more indigenous cultivars (and also wild relatives of the cultivated species) from areas where salt stress is recurrent and has been exerting a selection pressure over the years both in coastal and inland situations. In this context, indigenous locally-adapted cultivars of rice have been successfully utilised by Indian breeders for obtaining salt-resistant selections (Table 8). Apart from their use for direct cultivation, these selections have also been widely used in recombination breeding programmes as donors for salt resistance (Table 9). Moeljapawiro and Ikehashi (1981) crossed two salt-

Table 8. Some promising salt-resistant selections from locally adapted indigenous rice cultivars

S. No.	*Locally adapted parent material*	*Salt-resistant selection*	*Region of adaptation*
1.	Jhona	Jhona 349	Punjab/Haryana/ Western UP
2.	Kalambank	SR 26B	Wide adaptability
3.	Budda molagolukulu	MCM-2	Andhra Pradesh
4.	Kala Ratta	KR 1-24	Maharashtra
5.	Bhura Ratta	BR 4-10	Maharashtra
6.	Arya	Arya 33	Karnataka
7.	Chattivirippu	Mo. 1	Kerala
8.	Kalladachampavu	Mo. 2	Kerala
9.	Kunjathikkara	Mo. 3	Kerala
10.	Choottupokkali	Vytilla 1	Kerala
11.	IRON germplasm	AU-1	Tamil Nadu
12.	Patnai	Patnai 23	West Bengal
13.	Damodar	CSR-1	West Bengal
14.	Getu	CSR-3	West Bengal
15.	Dasal	CSR-2	West Bengal
16.	Nonasail	CSR-6	West Bengal
17.	Beni sail	Matla	West Bengal
18.	Nona Bokra	Hamilton	West Bengal

Table 9. Some salt tolerant rice varieties evolved in India through recombination breeding

S. No.	*Variety developed*	*Original cross*	*Institution*
1.	PVR-1 "Kallar Ottu"	SR 26B/MTU-1	State Agri. Dep. Tamil Nadu
2.	MCM-1	Co. 18/Kuthir	Rice Res. Sta. Machilipatnam (A.P.)
3.	SR 10022	SR 26B/MTU-1	
4.	SR 1-2-1	Jaya/SR 10022	
5.	MR-18	SR 26B/Wannar-1	Rice Res. Sta., Mandya (Karnataka)
6.	Co. 43	Dasal/IR 20	TN Agri. Univ. Coimbatore (TN)
7.	Usar 1	Jaya/Getu	CSA Univ., Kanpur (UP).

tolerant rice cultivars and noted overdominance for salt tolerance in the F_1 and also found many progeny lines of the F_2 that were more tolerant than either parent. It looks quite promising that multiple crosses involving tolerant cultivars may lead to upgrading of salt tolerance in economically more important crop plants.

Many wild relatives of the cultivated plants, growing naturally in salt-affected areas over long periods, are reported to be highly tolerant to soil salinity, alkalinity and other associated adverse conditions (Tsitsin 1962; Stalker 1980). Distant hybridisation thus offers another promising possibility for genetic improvement of crop plants through selective transfer or addition of desired adaptive gene complexes from relevant sources. Attempts are already underway for exploiting the outstandingly superior salt tolerance of the wheatgrass genus *Elytrigia* (=*Agropyron*) for enhancing adaptation of wheat cultivars to salt-affected soils (Dvorak et al. 1985; Storey et al. 1985). Diploid *E. elongatum* ($2n=2x=14$) and the decaploid *E. pontica* ($2n=10x=70$) have been reported to survive salt concentrations as high as 1.5 times sea water (Dewey 1960; Shannon 1978; McGuire and Dvorak 1981). Materials derived from Wheat × Barley crosses, mostly in the form of disomic addition lines ($2n=44$) carrying individual barley chromosome pairs (Fig. 4), are also being studied intensively in this context (Islam et al. 1975, 1981; Rana

1984). Somatic hybridisation technique is expected to open up new vistas to this approach.

Fig. 4. Six disomic addition lines ($2n = 42W + 2B$) carrying individual chromosome pairs of barley in 'Chinese Spring' background. Addition line having barley chromosome 5 is not represented. (Source material : Islam et al. 1981).

Elucidation of plant mechanisms that impart salt tolerance is likely to accelerate selection and breeding programmes aimed at developing crop varieties suited to specific situations of salt-affected soils. Although substantial information is already available on the physiology and biochemistry of glycophytes as well as of halophytes yet it is only recently that researchers have begun to study closely related plant genotypes in a comparative way to determine mechanisms underlying heritable differences in salt tolerance. At present, plant breeders do not have suitable markers for salt tolerance and this handicap has greatly affected the progress of their efforts. Since physiologists, biochemists and geneticists now have at their disposal a greater range of plant materials differing in salt tolerance, both at the intra and inter-specific levels, they should be able to elucidate plant mechanisms/processes conferring salt tolerance and also their genetic control. It may, however, be emphasised that confirmation of the initially reckoned markers of salt resistance, worked out by the inter-disciplinary efforts of concerned specialists, will necessarily require close cooperation with the plant breeders if breeding crop varieties for resistance to edaphic stresses is to make an impact.

In conclusion, a word of caution may be added for the plant breeder, namely, that the breeding efforts should aim at realistic and attainable goals. Although plant yields under salt stress cannot be expected to equal those obtainable under non-saline environment yet it appears quite feasible now to develop crop varieties that may withstand moderate increases in soil salinity without undergoing a significant yield loss. It also seems within reach to evolve varieties capable of growing and giving some economic yield at salinity levels which are well beyond their survival range at present.

REFERENCES

Bernstein, L. (1975). Effects of salinity and sodicity on plant growth. *Ann. Rev. Phytopath.* 13: 295-312.

Bresler, E., B.L. McNeal and D.L. Carter (1982). *Saline and sodic soils: Principles—dynamics—modelling*, Springer-Verlag, Berlin.

Christiansen, M.N. and C.F. Lewis (eds.) (1982). *Breeding plants for less favourable environments*, John Wiley, New York.

CSSRI (1980). Symposium Papers—*International Symposium on Salt Affected Soils.* Central Soil Salinity Research Institute, Karnal.

Devine, T.E. (1982). Genetic fitting of crops to problem soils. In: *Breeding plants for less favourable environments*, Eds. M.N. Christiansen and C.F. Lewis, John Wiley, New York, pp. 143-173.

Dewey, D.R. (1960). Salt tolerance of twenty-five strains of *Agropyron. Agron. J.* 52: 631-635.

Dewey, D.R. (1962). Breeding crested wheatgrass for salt tolerance. *Crop Sci.* 2: 403-407.

Downton, W.J.S. (1984). Salt tolerance of food crops: Prospectives for improvements. *CRC Critical Reviews in Plant Sciences* 1: 183-201.

Dvorak, J., K. Ross and S. Mendlinger (1985). Transfer of salt tolerance from *Elytrigia pontica* (Podp.) Holub to wheat by the addition of an incomplete *Elytrigia* genome. *Crop Sci*. 25: 306-309.

Epstein, E. (1972). Physiological genetics of plant nutrition. In: *Mineral nutrition of plants: Principles and perspectives*. Ed. E. Epstein, John Wiley, New York, pp. 325-344.

Epstein, E. (1976). Genetic potentials for solving problems of soil mineral stress: Adaptation of crops to salinity. In: *Plant adaptation to mineral stress in problem soils*. Ed. M.J. Wright, Cornell Univ., Ithaca, New York, pp. 73-82.

Epstein, E. and R.L. Jefferies (1964). The genetic basis of selective ion transport in plants. *Ann. Rev. Plant Physiol.* 15: 169-184.

Epstein, E. and J.D. Norlyn (1977). Seawater-based crop production: A feasibility study. *Science* 197: 249-251.

Epstein, E., J.D. Norlyn, D.W. Rush, R.W. Kingsbury, D.B. Kelley, G.A. Cunningham and A.F. Wrona (1980). Saline culture of crops: A genetic approach. *Science* 210: 399-404.

Islam, A.K.M.R., K.W. Shepherd and D.H.B. Sparrow (1975). Addition of individual barley chromosomes to wheat. Barley Genetics III, *Proc. 3rd Internatl. Barley Genetics Symp.*, Garching, pp. 260-270.

Islam, A.K.M.R., K.W. Shepherd and D.H.B. Sparrow (1981). Isolation and characterization of euplasmic Wheat-Barley chromosome addition lines. *Heredity* 46: 161-174.

Fitter, A.H. and R.K.M. Hay (1981). *Experimental physiology of plants*. Academic Press, London.

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

Foy, C.D., R.L. Chaney and M.C. White (1978). The physiology of metal toxicity in plants. *Ann. Rev. Plant Physiol.* 29: 511-566.

Greenway, H. and R. Munns (1980). Mechanisms of salt tolerance in nonhalophytes. *Ann. Rev. Plant Physiol.* 31: 149-190.

Hanson, M.R. (1984). Cell culture and recombinant DNA Methods for understanding and improving salt tolerance of plants. In: *Salinity tolerance in plants : Strategies for crop improvement.* Eds. R.C. Staples and G.H. Toenniessen, John Wiley, New York, pp. 335-359.

Hollaender, A., J.C. Aller, E. Epstein, A. San Pietro and O.R. Zaborsky (eds.) (1979). *The biosaline concept : An approach to the utilization of underexploited resources.* Plenum Press, New York.

Jung, G.A. (ed.) (1978). *Crop tolerance to suboptimal land conditions.* Madison Wis, ASA Special Publication No. 32.

Kingsbury, R.W. and E. Epstein (1984). Selection for salt-resistant spring wheat. *Crop Sci.* 24: 310-315.

Lehman, W.F., J.N. Rutger, F. E. Robinson and M. Kaddah (1984). Value of rice characteristics in selection for resistance to salinity in an arid environment. *Agron. J.* 76: 366-370.

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

Maas, E.V. and G.J. Hoffman (1977). Crop salt tolerance—Current assessment. *J. Irrig. Drain. Divn. Amer. Soc. Civil Engg.* 103: 115-134.

McGuire, P.E. and J. Dvorak (1981). High salt tolerance potential in wheatgrass. *Crop Sci.* 21: 702-705.

Mashhady, A.S. and M.S. Heakal (1983). Performance of a potentially salt tolerant wheat cultivar under non-steady state soil salinity. *Plant and Soil* 74: 407-416.

Moeljopawiro, S. and H. Ikehashi (1981). Inheritance of salt tolerance in rice. *Euphytica* 30: 291-300.

Muhammed, A., R. Aksel and R.C. von Borstel (eds.) (1977). *Genetic diversity in plants.* Plenum Press, New York.

Nelson, L.E. (1983). Tolerances of 20 rice cultivars to excess Al and Mn. *Agron J.* 75: 134-138.

Noble, C.L., G.M. Halloran and D.W. West (1984). Identification and selection for salt tolerance in lucerne (*Medicago sativa* L.) *Aust. J. Agric. Res.* 35: 239-252.

Norlyn, J.D. and E. Epstein (1984). Variability in salt tolerance of four triticale lines at germination and emergence. *Crop Sci.* 24: 1090-1092.

Orton, T. J. (1980). Comparison of salt tolerance between *Hordeum vulgare* and *H. jubatum* in whole plants and callus cultures. *Z. Pflanzenphysiol* 98: 105-118.

Paleg, L.G. and D. Aspinall (eds.) (1981). *The physiology and biochemistry of drought resistance in plants.* Academic Press, Sydney.

Rains, D.W., R.C. Valentine and A. Hollaender (eds.) (1980). *Genetic engineering of osmoregulation : Impact on plant productivity for food, chemicals and energy.* Plenum Press, New York.

Ramage, T. (1982). New variety yields 1.2 tonnes/ha when irrigated from the ocean. *Internatl. Agril. Dev.* 2: 29.

Rana, R.S. (1977). Plant adaptation to soil salinity and alkalinity. *Proc. Indo-Hungarian Sem. Management of Salt Affected Soils,* Central Soil Salinity Res. Institute, Karnal, pp. 177-191.

Rana, R.S. (1978). Wheat variability for tolerance to salt-affected soils. In: *Genetics and wheat improvement.* Ed. A.K. Gupta, New Delhi, Oxford & IBH Publishing Co., New Delhi, pp. 180-184.

Rana, R.S. (1981). Studies on plant adaptation to stress environments. Criteria for salt resistance. *Ann. Rept., CSSRI,* Karnal, pp. 74-79.

Rana, R.S. (1984). Genetic and cytogenetic studies for improvement of plant adaptation to stress environments. *Ann. Rept. CSSRI,* Karnal, pp. 88-89.

Rana, R.S., K.N. Singh and P.S. Ahuja (1980). Chromosomal variation and plant tolerance to sodic and saline soils. In: *Symposium Papers—International Symposium on Salt-Affected Soil,* Central Soil Salinity Res. Institute, Karnal. 1980.

Rosielle, A.A. and J. Hamblin (1981). Theoretical aspects of selection for yield in stress and nonstress environments. *Crop. Sci.* 21: 943-946.

Saric, M.R. and B.C. Loughnan (eds.) (1983). *Genetic aspects of plant nutrition.* Martinus Nijhoff, The Hague.

Sayed, H.I. (1985). Diversity of salt tolerance in a germplasm collection of wheat (*Triticum* spp.). *Theor. Appl. Genet.* 69: 615-657.

Schaller, C.W., J.A. Berdegue, C.W. Dennet, R.A. Richards and M.D. Winslow (1981). Screening the world barley collection for salt tolerance. Barley Genetics IV: *Proc. 4th Internatl. Barley Genet. Symp.*, Edinburgh, pp. 389-393.

Shannon, M.C. (1978). Testing salt tolerance variability among tall wheatgrass lines. *Agron J.* 70: 719-722.

Shannon, M.C. (1984). Breeding, selection and the genetics of salt tolerance. In: *Salinity tolerance in plants—Strategies for crop improvement.* Eds. R.C. Staples and G.H. Toenniessen. John Wiley, New York, pp. 231-254.

Singh, K.N. and R.S. Rana (1983). Genetic variability and path analysis in triticales grown in alkali soil. *Indian J. Agric. Sci.* 53: 1-4.

Singh, K.N. and R.S. Rana (1984). Stability of wheat varieties suitable for cultivation in normal and salt-affected soils. *Indian J. Agric. Sci.* 54: 950-954.

Singh, K.N., P.S. Ahuja and R.S. Rana (1984). Combining ability in wheat grown in alkali soil. *Indian J. Genet.* 43: 441-444.

Smith, M.K. and J.A. McComb (1981). Effect of NaCl on the growth of whole plants and their corresponding callus cultures. *Aust. J. Pl. Physiol.* 8: 267-275.

Stalker, H.T. (1980). Utilization of wild species for crop improvement. *Adv. Agron.* 33: 111-147.

Staples, R.C. and G.H. Toenniessen (eds.) (1984). *Salinity tolerance in plants: Strategies for crop improvement.* John Wiley, New York.

Stavarek, S.J. and D.W. Rains (1984). Cell culture techniques: Selection and physiological studies of salt tolerance. In: *Salinity tolerance in plants: Strategies for crop improvement.* eds. R.C. Staples and G.H. Toenniessen. John Wiley, New York, pp. 321-334.

Storey, R., R.D. Graham and K.W. Shepherd (1985). Modification of the salinity response of wheat by the genome of *Elytrigia elongatum. Plant and Soil* 83:327-330.

Swaminathan, M.S. (1977). Combating desertification by 2000 A.D. Recommendations of the UN Conference on Desertification, Nairobi.

Swaminathan, M.S. (1981). *Plant breeding in preparation for* *the 21st Century.* Meghnad Saha Medal Lecture, Indian National Science Academy, New Delhi, pp. 17.

Swaminathan, M.S. (1983). *Agricultural progress—Key to third world prosperity.* Third World Foundation Monograph, No. 11, London, pp. 14.

Tal, M., H. Heikin and K. Dehan (1978). Salt tolerance in the wild relatives of the cultivated tomato. Response of callus tissue of *Lycopersicon esculentum, L. peruvianum* and *Solanum pennellii* to high salinity. *Z. Pflanzenphysiol.* 86: 231-240.

Tal, M. (1984). Physiological genetics of salt resistance in higher plants: Studies on the level of the whole plant and isolated organs. In: *Salinity tolerance in plants: Strategies for crop improvement.* Eds. R.C. Staples and G.H. Toenniessen, John Wiley, New York, pp. 301-320.

Tsitsin, N.V. (ed.) (1962). *Wide hybridization of plants.* Israeli Programme of Scientific Translations, Jerusalem.

Valentine, R.C. (1984). Genetic engineering. *California Agri.* 38 (10): 36-37.

Yeo, A.R. and T.J. Flowers (1983). Varietal differences in the toxicity of sodium ions in rice leaves. *Physiol. Plant.* 59: 189-195.

Wright, M.J. (ed.) (1976). *Plant adaptation to mineral stress in problem soils.* Agency for International Development, Washington.

Drought Resistance in Crop Plants: A Physiological and Biochemical Analysis

SURESH K. SINHA

Introduction

Drought is the most common adverse environmental factor which limits crop production in different parts of the world. Often drought is accompanied by relatively high temperatures, which promote evapotranspiration, and hence could accentuate the effects of drought and thereby further reduce crop yields. Since these events occur more frequently in tropical and semi-tropical regions where most of the developing countries are situated, droughts are often associated with food shortages and an overall setback to developmental activities. Therefore, raising of drought-resistant crops is common sense to achieve stability in production and to enhance the possibility of self-sufficiency in food. Consequently, breeding for drought resistance is a major objective of many research programmes in the international and national institutions. This has been so for the past several decades. But, it is disappointing that, there has not been any measurable success in these programmes compared with the success achieved in breeding for yield; or breeding for disease resistance or breeding for quality attributes. In fact, this was amply expressed by Arnon (1980) when he stated "Breeding for drought resistance has been a consistent theme for as long as I remember and probably the greatest source of wasted breeding efforts in the whole field of plant breeding." However, the fact remains that we do hear of drought resistant varieties in many crops. For example, C-306 in wheat, Lalnakanda in rice and M

35-1 in Sorghum are some of the better known examples in India. It is also claimed that a large number of cultures among the Assam Rice Collection exhibit a considerably high degree of drought tolerance. Many land races and wild relatives of several crop species are said to contain drought resistant traits, which could be profitably utilised in breeding programmes. This situation is not unique to India alone but is a common experience in different parts of the world. However, to affirm a conviction a short questionnaire to assess the current state-of-art on breeding for drought resistance was distributed to 75 distinguished plant breeders and plant physiologists all over the world. The questionnaire and a summary based on the responses is as follows:

QUESTIONNAIRE

1) Name of crop

2) Variety or varieties identified/recognised as drought resistant

3) Duration of these varieties (seeding to maturity) in comparison with other popular high yielding varieties

4) Yield in a good rainfall and in a drought year

5) Any special morphological or physiological characteristics of the tolerant variety

6) Water use in comparison with susceptible varieties

7) Was the variety specifically bred for drought tolerance or was it a selection from the existing types?

8) Is there any variety/which has specially been produced for drought tolerance through hybridisation?

Response from many scientists in India and abroad were received and are summarised as follows :

1) Some varieties are identified/recognised as drought tolerant in wheat, barley, Sorghum, oats and rice.

2) Mostly, the varieties are of medium or long duration. In Sorghum, the hybrid CHS-6 is of short duration, but it escapes drought period. It is not successful in the *rabi* season when the crop actually experiences drought. Under drought prone *rabi* conditions, an average yielding variety, M 35-1 is the most stable.

3) In good rainfall years, these drought tolerant varieties do not take sufficient advantage of available water. The average

yield is between 2.5 and 3 tonnes ha^{-1} and is reduced to 1 tonne ha^{-1}.

4) Some varieties such as Olympia of wheat in Australia have early vigour, whereas C 306, has slow vegetative growth in the initial stages but both tiller reasonably.

5) The drought-tolerant varieties use the same or more water as susceptible types, such as Olympia and C 306 in wheat, Lalnakanda in rice and others.

6) Most of the drought-tolerant varieties are local selections or selections from some other breeding programmes.

7) No one has developed a variety which may have been produced through a hybridisation programme aimed at breeding for drought resistance. It was however claimed that some drought-tolerant varieties were in the process of development. For rice, the upper limit of yield would be around four tonnes in good years and 1.5-2 tonnes in lean years.

It is thus seen that while considerable success has been achieved in breeding for disease resistance, a comparable success is yet to be achieved in breeding for drought resistance.

Defining Drought and Drought Tolerance

The definition of drought, and drought tolerance, has differed depending upon whether the defining is done by a biochemist, physiologist, an agronomist or a plant breeder. It is important, therefore to set the reference point with clarity.

Gotoh et al. (1979), in their review on adaptation of crop plants said "Breeding crop plants for drought prone conditions requires an appreciation and knowledge of the environmental factors which interact with rainfall deficits to create the array of complexes collectively referred to as 'drought'. The variability (across and within seasons) and range of these salient environmental factors are extremely location specific." Thus, it is being increasingly realised that 'drought' from the point of view of a crop, is the state when water adequate in quantity and distribution is not available to express its full yield potential. Since the availability of water during the whole plant life is not determined by rainfall alone, but is dependent on soil characteristics and evaporative demand, the intensity and duration of drought become highly location specific. The pattern of rainfall distribution adds to the uncertainty of stage specificity for experiencing drought. Therefore, in a country like India, where most of the rainfall is received between late June and early September, the concept of drought would be different for *kharif* and *rabi* seasons. Past experience, particularly of rainfall and evapotranspiration, could serve as a guide but is not entirely dependable, since from the past 30 or 50 years meteorological data, no individual year can be termed a 'normal' year. Nonetheless, these records may help in defining drought at specific locations. Thus, a working definition of drought would be *the inadequacy of water availability, including precipitation and soil moisture storage capacity, in quantity and distribution during the life cycle of the crop to restrict expression of its full genetic yield potential.*

Drought resistance, according to Passioura (1983), is a nebulous term that appears to become more nebulous, the more closely it is examined. There are a large number of morphological and physiological traits associated with plants growing naturally in arid environments that, it is believed, confer drought resistance on these plants. These include a long list of characters as given in Table 1. Whether these traits in part or full are relevant to crops and how many plant breeders would venture to incorporate them into an agronomically desirable genetic background is not yet certain. Further, the consequences of such hybridisation programmes aimed at obtaining desirable segregants are not yet known. It is however evident that some cultures such as Assam Rice Collection, diploid and tetraploid species of wheat, wild-oats, and local collections of several crop plants, are described as drought resistant. In all these instances, survival or recovery after a period of water stress and maintenance of greenness for a longer time are the basis of assessment of their drought resistance. Most of these cultures/genotypes, produce very few seeds/grains and have a poor sink potential.

An important approach to assess drought resistance of a variety is by determining its stability index on the lines of the methods described by Finlay and Wilkinson (1963) and Eberhart and Russell (1966). According to this, a large number of varieties are grown in a range of environments which presumably differ in water availability. The variety which shows maximum stability is considered as drought resistant; the criterion of stability

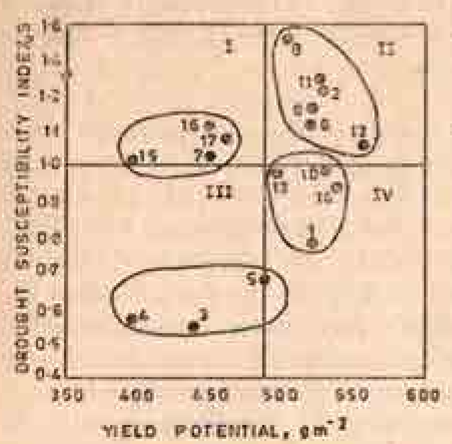
Table 1. Factors controlling water use which may be amenable to genetic regulation

Leaf	Roots
orientation	water absorption
hairs	water transport
reflectance	hairs
color	ability to grow in dry soil
leaf area index	aeration (internal)
size	penetration
orientation	size (diameter and length)
duration	branching
thickness	respiration
retention	reaction to temperature
Stomata	Awns
frequency	
size	Maturation
behaviour	Photosynthesis intensity
Shoots and stems	
length	C_3 vs C_4 pathway
crust penetration	Respiration photo versus dark
Fruiting	
duration	
relation to transpiration	Succulence
accretion rate	
temperature effects	

Source: Moss et al. (1974).

being the grain yield. The stability indices of 17 cultures belonging to *Triticum aestivum*, *T. durum* and Triticale have also been estimated. Among *T. aestivum*, C 306 exhibited better stability and was followed by HD 2009 (Sinha et al. 1986). In contrast, Moti had the poorest stability (Fig. 1). Thus, at the field level, stability index could be equated with drought resistance. However, it must be recognised that such genotypes are not able to take advantage of a good environment from the point of view of water availability.

Efforts have also been made by biochemists and molecular biologists to define drought resistance. Bewley (1981) reviewed literature on protein synthesis in relation to drought in two mosses which were categorised as drought resistant and susceptible. Quick recovery in protein synthesis because of conservation of messenger RNA was possibly associated with drought resistance. He candidly stated that these criteria could not be extended to crop plants.



GROUP	NO	CULTIVAR	G
I	7	MG 191-24-1	D
	15	DTS141	T
	16	DTS205-4-1	T
	17	DTS 701	T
II	2	MOTI	A
	6	HD 2163	A
	8	MG 120-1	D
	9	MG 180-9	D
	11	MALVIKA	D
	12	RAJ 911	D
III	3	C 306	A
	4	NP 824	A
	5	HD 2009	A
IV	1	KALYANSONA	A
	10	MG 413-2	D
	13	DTS 138	T
	14	DTS 47-1	T

Fig. 1. Stability by grain yield and drought susceptibility index and cluster analysis.

More recently, the interest in molecular aspects of drought resistance has been generated by Le Rudulier et al. (1984), by discovering genes, called Osm (osmotic tolerance) for osmoregulation. The latter was considered the cardinal point in drought resistance of crop plants, though the survival of *E. coli* mutants was tested in a medium containing sodium chloride. Therefore, for a molecular biologist, drought resistance is osmoregulation, irrespective of the source of stress, such as lack of water, salinity, alkalinity or temperature.

It would thus be realised that scientists belonging to different disciplines have different perceptions of drought resistance and therefore their definitions would vary accordingly.

Molecular biologist	: Drought resistance as survival of individual cells or unicellular organisms such as *E. coli*, by adaptation to osmoregulation.
Biochemist	: The tolerance of import antbiochemical reactions such as protein synthesis, conservation of messenger RNA etc. to water deficit in an organism.
Physiologist	: Maintenance of growth during water stress and its accelerated resumption on termination of water stress.

Agronomist : Stability in yield performance of a crop or a variety in a water deficit environment.

It is this perception of an individual that becomes the basis of search for a criterion of drought resistance. However, these perceptions refer to different time scales in the life of a plant and crop which culminate in producing an economic yield. Thus, an integration of events in different time scales is essential for assessing drought resistance in an agronomic sense, which is the ultimate objective of agricultural programmes. It might be useful, therefore, to define drought resistance as *the mechanism/s causing minimum loss of yield in a water deficit environment relative to the maximum yield in a water constraint free management of the crop.*

This definition of drought resistance includes the concepts of relative amount of water and of relative yield. Therefore, an understanding of the basis of yield is essential to describe the performance of a genotype, in a water limiting and water sufficient environment. A recent example, given by Passioura (1976, 1983) would emphasise this point clearly. The effects of equal amounts of water availability, either distributed throughout the life cycle of wheat or provided in the beginning alone, are shown in Fig. 2. It is obvious that the same amount of water could produce altogether different results.

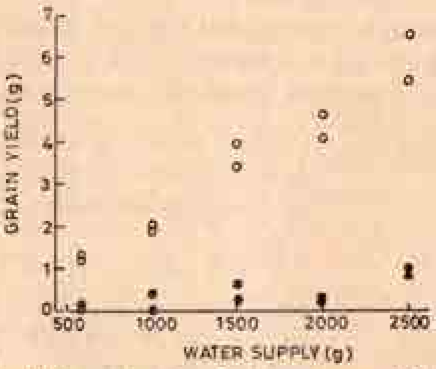


Fig. 2. Grain yield as a function of total water supply for individual wheat plants grown in pots. (from Passioura, 1983).

BASIS OF YIELD

Although each crop has its own characteristics, every crop passes through different growth phases starting from sowing to maturity, to culminate in economic yield. One can show that it is a sigmoid curve for the whole plant or a crop canopy. Indeed, it is differentiation along with growth, which results in the development of economically important structures such as spikes, influorescence, tubers etc. in different crops. Growth, basically, results in accumulation of dry matter while differentiation and subsequent development lead to economic yield. It is obvious that any amount of growth or dry matter production would not help in producing grain yield unless the yield components differentiated and developed appropriately. In a sense, there is a dynamic relationship between 'source' and 'sink'. It is their complementation during the differentiation of 'sink' such as panicle, spike, tubers etc. and subsequently their development which determines yield (Sinha and Khanna 1975).

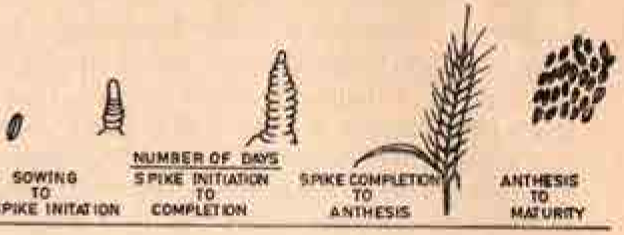
It would be useful to illustrate this with some specific examples, such as wheat, pigeonpea and Sorghum. Wheat has been extensively studied in many parts of the world (Asana 1976; Evans, Wardlaw and Fischer 1975; Fischer 1983, 1984) and the following phases of growth can be clearly distinguished (Sinha et al. 1982):

1) germination to spike initiation,
2) spike initiation to terminal spikelet formation;
3) terminal spikelet formation to spike emergence; and
4) spike emergence to grain development and maturity.

These four phases at Delhi location take about 26, 25, 40 and 45 days respectively if a crop is sown in mid-November and receives adequate irrigation (Fig. 3). The duration of these phases changes at different latitudes leading to changes in crop duration and yield (Sinha et al. 1985). The process of yield realisation actually starts after ear or spike initiation. How does the growth achieved earlier or leaf area at a particular stage determine the yield ? From the past studies, the following main conclusions can be drawn :

1) Approximately 60 to 70 per cent of the total dry matter is produced before anthesis.

2) After anthesis, only flag leaf, peduncle and ear photosynthesis contribute to assimilation.



CULTIVAR TREATMENT	NUMBER OF DAYS			
	SOWING TO SPIKE INITATION	SPIKE INITIATION TO COMPLETION	SPIKE COMPLETION TO ANTHESIS	ANTHESIS TO MATURITY
C 306 IRRIGATED	25	30	32	50
C 306 UNIRRIGATED	25	25	30	50
K-SONA IRRIGATED	24	25	33	53
K-SONA UNIRRIGATED	23	17	33	48

Fig. 3. Phenology of wheat, with and without irrigation at Delhi (Sinha et al. 1982).

3) Only 15 to 25 per cent of pre-anthesis assimilates are mobilised for grain development.

4) Pre-anthesis assimilates are mobilised as amino nitrogen from different plant parts.

5) 80 to 85 per cent of the total nitrogen is assimilated before anthesis, and is present in leaves and stem.

Thus, current assimilation or photosynthesis and mobilisation of previously accumulated nitrogen are important for grain development. There is now additional evidence to show that:

1) When grains develop, they trigger senescence of the flag leaf, presumably by enhancing the level of ABA, or ABA like substances (Morgan 1980). The main feature of this is the mobilisation of protein nitrogen from the flag leaf.

2) Protein, mostly present as RuBP carboxylase in leaves, is mobilised (Dalling et al. 1976; Peoples et al. 1980; Sinha and Rajagopal 1980).

3) There is disruption of chloroplast membranes.

The above processes lead to impairment of photosynthesis and hence carbon assimilation. However, these processes are delayed if the number of developing grains is less. Thus, present evidence suggests that eventually the 'sink' disrupts the 'source' or shortens the leaf area duration. It is likely that some balance is maintained between the 'sink' demand and the 'source'.

Analysis of Yield in Pigeonpea and Other Pulses

The growth of pigeonpea or other pulses can be divided into the following phases :

1) Germination to flower initiation
2) Flower initiation to 50 per cent flowering
3) Flowering to pod development.

In pigeonpea and chickpea, the initial growth rates are very slow and in many instances the plant produces only 1/3 of its final dry matter by the time flowering occurs (Fig. 4). Subsequently, a period of very high growth rate commences during which vegetative growth and flower production is profuse. Thus,

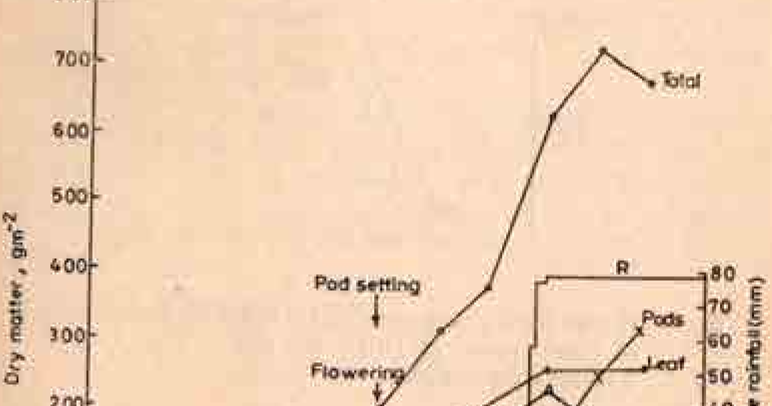


Fig. 4a. Growth, phenology and dry matter partitioning in *Cicer arietinum* at Delhi. (R. Khanna-Chopra, K.R. Koundal and S.K. Sinha).

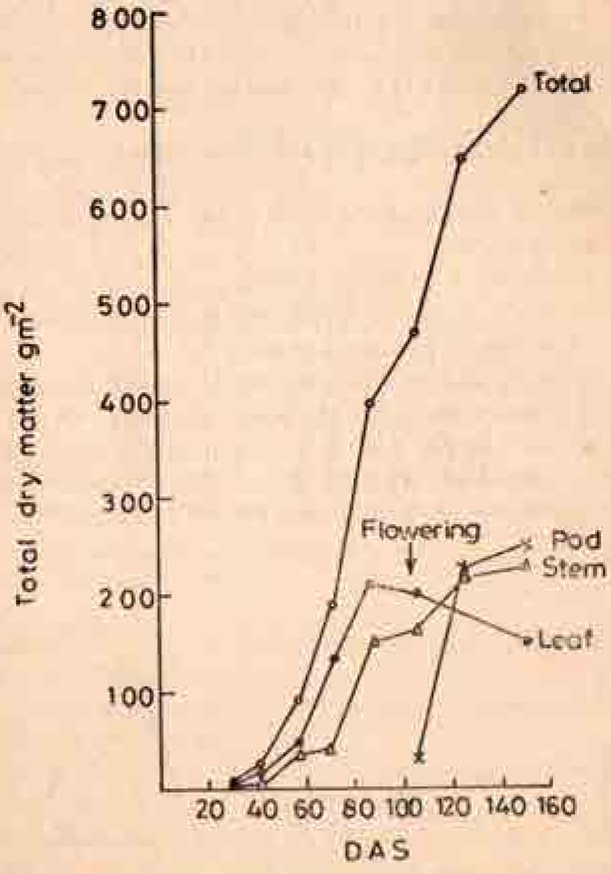


Fig. 4b. Growth and dry matter partitioning in a determinate cultivar of *Cajanus cajan* at Delhi. (R. Khanna-Chopra, K.R. Koundal and S.K. Sinha).

the plant acquires almost two-thirds or more of its dry matter by the time early pod development starts. This stage coincides with the disintegration or inactivation of root nodules, which deprives the plant of its source of nitrogen availability. There is considerable evidence to show that there is no mobilisation of assimilates (carbon or nitrogen) between different branch nodes (Lindoo and Nooden 1977). Consequently each node, consisting of a leaf (trifoliate or multifoliate) and developing fruits, functions as a unit. With the commencement of fruit development, the leaf subtending the developing fruits starts loosing nitrogen accompanied by a loss of RuBP carboxylase (Grover et al. 1985; Grover and Sinha 1985). Using several biochemical and immunoassay techniques, it has been demonstrated that RuBP carboxylase protein itself is mobilised resulting in the impairment of photosynthesis. Excision of fruits delays senescence. There is evidence that the developing fruits have a dosage effect (Nooden 1980). Again, it is proposed that some signal from the developing seeds triggers mobilisation of this important protein.

Since there is an insignificant or no intraplant and intranodal mobilisation, a large amount of dry matter accumulated prior to fruit development remains unutilised. Most of the leaves are shed and the stem contains a high percentage of nitrogen, even at the time of harvest (Sinha et al. 1983). However, the leaf area at a particular node correlates strongly with seed yield (Savithri et al. 1978 and the latter is the cause of leaf senescence at the node. Thus on a whole plant basis the yield is determined by the fruiting nodes, while a large vegetative structure though essential for plant is not utilised for yield. Needless to say, the growth of these vegetative structures does require a certain amount of water.

In most other pulses such as mungbean, chickpea, cowpea and soybean similar observations have been recorded. All these results lead to the important conclusion that a physiologically active leaf is essential for development of fruits at each flowering node.

Analysis of Yield in Sorghums

Eastin (1972) described the phenological stages in Sorghum as follows:

GS_1 (vegetative)—planting to panicle initiation (P I)
GS_2 (Influorescence development)—P I to bloom.
GS_3 (Grain fill)—bloom to kernel dark layer.

The duration of these stages differs among cultivars, depending upon their sensitivity to photoperiod, temperature and interaction of these two factors. Most of the traditional varieties of Sorghum were sensitive to these factors and took a considerably longer time in GS_1 and GS_2. By the time they flower, the rains ceased (Fig. 5). Therefore, grain development occurred when the soil moisture was depleted. Under such conditions, the pre-anthesis assimilates constituted a significant 'source' for grain development. However, in recent years many hybrids have been released which complete their life cycle within 90-95 days from sowing. Such hybrids complete GS_1 in 26 days, GS_2 in 30-34 days and GS_3 in 30-35 days. One of the major advantages of these hybrids is their higher growth rate in early stages because of faster rate of leaf area development. In fact, at a plant population density of 180,000 plants per hectare, they develop a full crop canopy within 30-35 days of sowing. At most locations the duration of rainfall is 80-90 days. A higher growth rate in the early stages coupled with adequate water holding capacity of the soil, these hybrids complete their life-cycle without frequent exposure to a water deficit. However, the water stress of a crop depends upon the pattern of rainfall. If this happens after anthesis, the yield is severely reduced, but water stress in GS_1 does not influence yield adversely because of compensation. The magnitude of effect depends upon the degree of stress and this has often not been quantified.

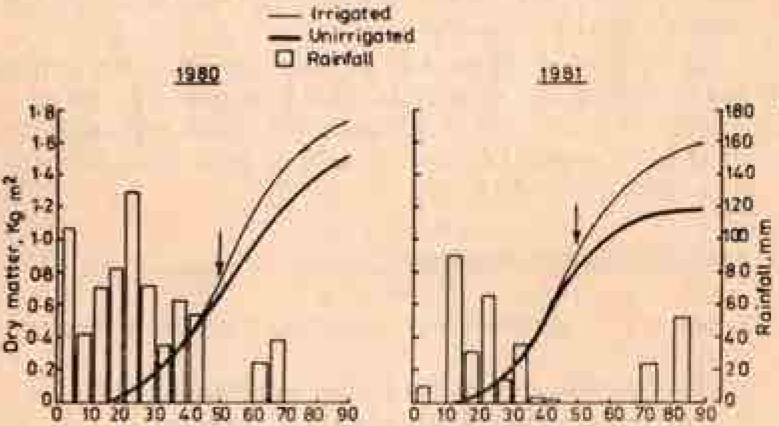


Fig. 5. Dry matter production in Sorghum CSH-6: Response to irrigation in relation to rainfall pattern.

In conclusion, the varieties or hybrids which apparently are resistant to water stress, are those which complete their life cycle in 90±5 days but have a higher growth in the beginning. Long duration (150 days or more) varieties also show stress resistance because they mobilise preanthesis assimilates for grain development. Thus, the phenology of the plant is important in determining its yield and adaptability.

Such examples could be multiplied to explain the basis of yield and yield differences of different crops.

Effects of Drought

Inadequate availability of water in quantity and distribution leads to water deficit, and has profound effects on various plant processes. These processes have different time scales in their responses to water deficit or drought (Table 2). Change in leaf water potential, turgor pressure and stomatal resistance are influenced within seconds or minutes while cell growth, accumulation of proline and betaine, degradation of protein and polysaccharides are effected in hours. Leaf expansion, shoot growth and root growth might take days while reproductive biology and grain yield are influenced in days or months. Plant physiologists and biochemists who seek a criterion of drought resistance which often responds in minutes or hours, have the unenviable task of relating the criterion to final grain yield which is a cumulative effect of a number of processes occurring over a period of days or months. Therefore, it is not surprising that many criteria which appeared promising when proposed were not subsequently useful.

Table 2. Plant water status (Low †) influencing plant characteristics and processes in time scale

Yield	*Days to months*
Flower and fruit development	days
Leaf senescence and shedding	days
Root growth	days
Leaf growth	hours to days
Leaf movement	hours—minutes
Cellular metabolism	hours—minutes
Changes in hydraulic resistance	hours—minutes
Stomatal movement	hours—minutes
Turgor pressure	minutes—seconds

When a crop grows under field conditions, it experiences the effects of water deficit gradually. However, in most instances where a drought condition was applied to plants in pots, the development of stress was very fast. For example, in the experiments of Fischer (1973) and Asana & Saini (1962), the plants were brought to −20 to −25 bars within four days or to permanent wilting in seven days. Under field conditions, leaf water potential drops at a rate of −0.40 to −0.1 bars per da y. Thus, many of the adaptive adjustments which are possible under field conditions, where decrease in water potential is slow, cannot be expected to occur in pots. Furthermore, during the growth of the plant, the source and sink relationships undergo change and adjustment. In a seedling or during the vegetative stage, roots constitute in addition to the young emerging leaves a major 'sink'. The latter become a source subsequently. It was observed by Aggarwal and Sinha (1983) that the dry weight of roots either increased or remained unaffected when maize seedlings were water stressed. On the release of water stress, the roots lost dry weight, suggesting that they became a source to the reviving shoot. However, once the reproductive stage commences (spike emergence in wheat, cob development in maize or fruit development in pulses) then the developing grains become a major 'sink'. Roots no longer remain the major recipients of assimilates mobilised from leaves due to water stress. This change in the 'source' and 'sink' relationship will presumably express itself in resistance to water stress if it were based largely on delayed senescence of leaves or some other morphological score such as leaf rolling or stomatal resistance. As long as roots remain the major 'sink', they would grow and explore more water from the soil, and hence increase water availability to the plant. The same would not happen if flowering or grain development had commenced. On the basis of the present available information, one can visualise a change in hormonal status of the plant depending upon the 'sink'. The growing roots serve as a source of cytokinins (Hsiao 1973), whereas the developing grains possibly trigger synthesis of ABA or ABA like substances, leading to a faster senescence of leaves on the whole plant. The synthesis of the amount of ABA or ABA like substances could be dependent upon the number or weight of the grains, the size of the 'sink'. It has been demonstrated by Nooden (1980) that the larger the number of developing pods, the faster is the senescence in soybean.

This explains why the 'apparent' drought resistance should, or would, change from vegetative to reproductive stage. A recent study by Armenta-Soto et al. (1983) brings this out clearly (Table 3). All the high yielding varieties of rice changed their score from medium resistance to high susceptibility from vegetative to reproductive stages. The varieties which did not flower, or were poor yielders, did not change their drought resistance score. If this interpretation is correct, then it should be possible to prove it further by using different genetic materials or manipulative techniques. The A and B lines in Sorghum are said to differ only in their fertility. When the plants of 2077A and 2077B were exposed to stress in seedling stage and subsequently given water, they showed no difference either in survival or recovery. The same treatment, however, at the time of grain development resulted in faster senescence of leaves in 2077B and other B lines, but not in 2077A or other A lines (Khanna-Chopra and Sinha, unpublished). In mungbean and cowpeas, plants with developing pods showed faster senescence under water stress than when the pods were excised (Paharia and Sinha, unpublished; Reddy and Sinha, unpublished). These examples indicate that a plant uses its resources for grain/seed development when its survival is threatened due to drought. This

Table 3. Root characteristics and drought score of the eight parental varieties

No.	*Variety/line*	*Origin*	*Variety group*[a]	*Maximum root length (cm)*	*Root thick-ness (mm)*	*Root number*	*Field drought reaction*[b]	
							Veg.	*Repro.*
1	IR8	IRRI	IS	74.9	0.80	77	5	7-8
2	IR20	IRRI	IS	62.3	0.67	63	7	8-9
3	Moroberekan	Guinea	U	84.0	1.48	32	3	3-5
4	OS4	Nigeria	U	88.3	1.06	27	3	3-5
5	20A	Liberia	U	87.2	1.45	35	3	NF
6	IR480-5-9	IRRI	IS	88.4	1.05	48	5	NF
7	IR841-67-1	IRRI	IS	70.2	0.74	44	5	9
8	MGL-2	India	TL	85.2	0.87	51	3	NF

[a] IS—Improved semi-dwarf lowland; U—Upland; TL—Traditional lowland.

[b] The decimal score for vegetative and reproductive phases (1-resistance to 9-susceptible) is based on Loresto and Chang, 1981. NF means plants did not flower during the 140-day cut-off date.

Source: J. Armenta-Soto, T.T. Chang, G.C. Loresto and J.C. O 'Toole.

is possibly an evolutionary obligation. Nonetheless, the development of grains/seeds would depend upon the available resource within the plant, a major portion of which is current assimilation and the remaining that of pre-anthesis assimilation. These considerations now could be used for analysing yield under drought.

Analysis of Yield under Drought

Often relationships between ET (Evapotranspiration) and dry matter and ET and yield have been described (Slabbers 1980). Most of these studies show a linear relationship. Therefore, we must expect that a decrease in water availability would result in decreased dry matter and yield. If we accept this generalisation, then a reduction of ET from optimum to half should result in producing half the maximum dry matter and yield. However, in wheat a fully irrigated crop used 43 cm water and produced 1437 g m^{-2} dry matter and 458 g m^{-2} yield (Table 4). As against this, when water use was reduced to 24 cm, the total dry matter production and yield were 991 and 388 g m^{-2}, respectively (Aggarwal and Sinha 1984). We should, therefore, assume that within certain limits (which at present are not well defined), a reduction in water availability could lead to improvement in water use efficiency. Such observations have been made for other crops too. We now know that the water use efficiency (WUE) of C_3 and C_4 plants based on laboratory or water culture experiments does not conform to those obtained in field experiments (Aggarwal & Sinha 1983). In fact, water use efficiency of a crop varies at different stages of plant growth. Therefore, a large amount of data obtained on seedlings in pots may not be applicable to field conditions. We can use a couple of examples to illustrate this point. A water use efficiency has been reported, of 4 g dry matter kg^{-1} water, for the whole life cycle in wheat and gram at Delhi location (Aggarwal and Sinha 1983). Assuming that the soil profile up to 1.5 metre depth can be tapped by plants, the total available water could be approximately 20 cm. This is equal to 200 kg. water m^{-2}, and should be adequate to produce 800 g m^{-2} dry matter. If it rains, then each 1 cm of rainfall would contribute 40 g m^{-2} of dry matter. Thus, with 25 cm of water (20 cm from soil+5 cm rain) a total of

Table 4. Water use, DM production, grain yield and WUE in wheat per crop season (data are the mean of two years and values are means ± 1 s.e.m)

Treatment	*Water used* ($kg\ m^{-2}$)	*DM produced* ($g\ m^{-2}$)	*Grain yield* ($g\ m^{-2}$)	*WUE* ($g\ DM\ kg^{-1}$ *water used*)
C 306, irrigated	430 ± 14	1437 ± 35	429	3.34 ± 0.10
C 306, non-irrigated	244 ± 10	991 ± 90	350	4.05 ± 0.33
Kalyansona, irrigated	410 ± 19	1578 ± 46	568	3.85 ± 0.20
Kalyansona, non-irrigated	228 ± 7	1073 ± 81	348	4.70 ± 0.82

Source : Aggarwal and Sinha 1983.

1,000 g dry matter m^{-2} could be produced if other inputs were available. Assuming a 40 per cent harvest index, the grain yield could be 400 g m^{-2} or 40 q ha^{-1}. Grain yield up to such high levels have, in fact, been obtained under dryland conditions by De et al. (1984). Needless to emphasise, water availability throughout plant growth is essential otherwise though dry matter is produced the harvest index is reduced, particularly if the amount of available water after anthesis is not adequate (Passioura 1983). We have also observed that current assimilation, dependent upon post anthesis water availability, is an important determinant of yield (Figs. 6 and 7). Thus, the pattern of crop growth should ensure water availability in the post-anthesis period.

Ideotype Concept for Dryland

Extensive studies at the Indian Agricultural Research Institute, New Delhi, led Asana (1968) to suggest an ideotype of wheat for dryland agriculture. The main features of this ideotype were as follows:

1) Non-tillering or single culm.
2) Large number, approximately 60 grains per ear.
3) Small but horizontal leaves. From the proposed diagrams, they appear about 10 cm^2 (flag leaf)
4) Slow senescence of ear and flag leaf.

The above characteristics were identified based on several experiments and the conclusions were primarily arrived at through statistical correlations. The conclusions have, however, several physiological and biochemical contradictions. Though

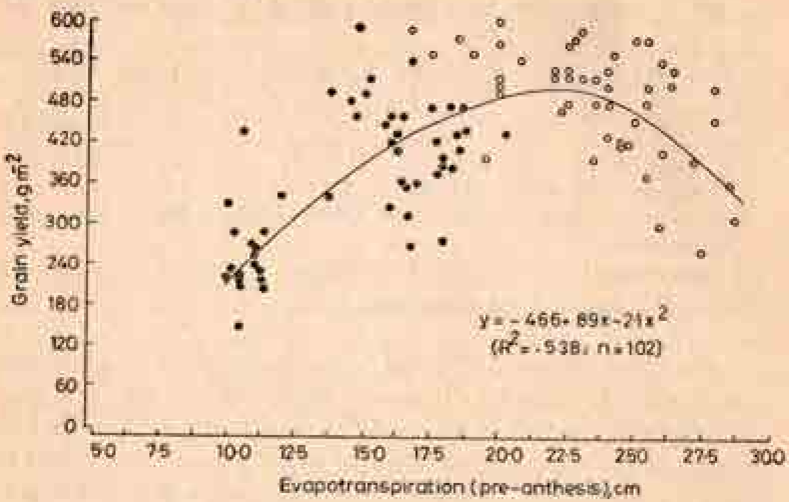


Fig. 6. Relation between post-anthesis evapotranspiration and grain yield in wheat (P.K. Aggarwal, A.K. Singh, G.S. Chaturvedi and S.K. Sinha).

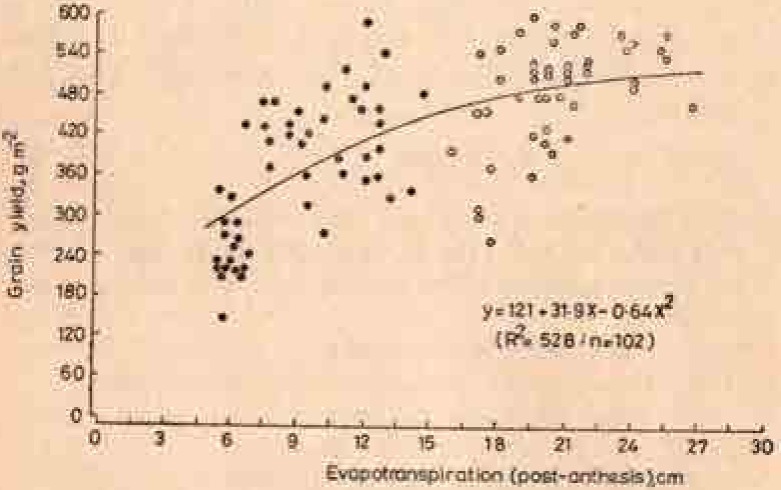


Fig. 7. Relation between pre-anthesis evapotranspiration and grain yield in wheat (P.K. Aggarwal, A.K. Singh, G.S. Chaturvedi and S.K. Sinha).

it is true that the number of grains in a mother shoot correlates strongly with grain yield under conditions of water stress yet this statistical correlation would be observed irrespective of the number of grains. The number of grains would itself be physiologically determined by the availability of photoassimilate dependent on the area of flag leaf and the rate of photosynthesis. A practical situation may be examined. Wheat var. Kalyansona, was grown at different moisture levels with the leaves having a water potential ranging from —12 to —30 bars at anthesis. There was a sharp decline in leaf area with reduction in water potential. This was accompanied by a similar decrease in dry matter m^{-2}. The fully irrigated plants had a leaf water potential of —12 bars and the flag leaf area was 60 cm^2, but it decreased to 25 cm^2 at —17 bars (Fig. 8). Assuming that the plants maintained the maximum rate of photosynthesis of 30 mg CO_2 d m^{-2} hr^{-1}, it would result in 107 mg dry matter per day per flag leaf for 11 hour photosynthesis. For the stressed plants, it would be 45 mg dry matter per day per flag leaf for 11 hour photosynthesis. If these rates are maintained for 30 days, a maximum of 3,210 mg and 1,350 mg assimilates by flag leaves of control and stressed plants respectively could be expected. It is further assumed

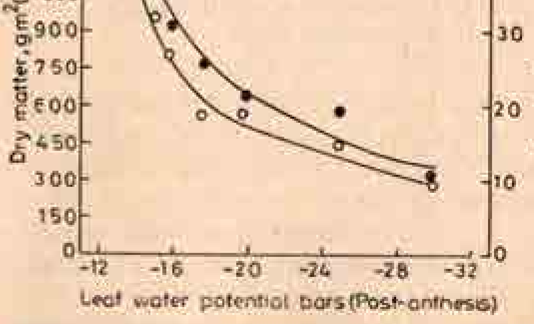


Fig. 8. Effect of gradual development of water stress (field conditions) on dry matter and flag leaf area in relation to leaf water potential at post-anthesis.

that all this is utilised (not excluding even respiratory losses) for grain development. Then, the control and stressed plants can, at most, produce 80 and 34 grains of 40 mg each, respectively (Table 5). However, if we consider the fact that as a result of water stress, there could be a reduction in the rate of photosynthesis and senescence would be hastened, then development of even 34 grains would be impaired. Therefore, the plant might mobilise its preanthesis reserves which could support up to 25 to 30 per cent of grain weight depending upon the preanthesis growth. It is thus clear that there are physical and biological constrains for realising the productivity of the ideotype suggested by Professor R.D. Asana. His introduction of the ideotype concept for selection has been a valuable step even though the ideotype suggested by him is not physiologically and biochemically suitable.

Table 5. Photoassimilation potential of flag leaves of control (non-stressed) and water stressed plants in wheat

	Control	*Stressed*
Plant† at anthesis	—12 bars	—17 bars
Flag leaf area	60 cm^2	25 cm^2
Maximum photosynthesis rate dm^{-2} hr^{-1}	30 mg CO_2	30 mg CO_2
Dry matter production $leaf^{-1}$ per day (11 hrs)	107 mg	45 mg
Duration of activity	30 days	30 days
Maximum potential for assimilation as dry matter	3210 mg	1350 mg
Maximum potential for number of grains of 40 mg each	80	34

Assumptions:
a) Maximum photosynthesis for 30 days.
b) All assimilates mobilised to grains.
c) No respiratory losses.

This brings us to the conclusion that statistical relationships, howsoever strong, do not necessarily represent the functional relationships. The ideotypes based essentially on statistical correlations may not present achievable objectives. Considering that water is a limiting factor, the amount of available water should constitute the basis of an ideotype and the latter should include the functional aspects of the plant.

In north India, it is estimated that water availability in fully charged soil profile after monsoon rains is about 20 cm. Therefore, on the basis of our present sudies on water use efficiency under field conditions, this much water is adequate to produce 800 g dry matter m^{-}. The winter rains would add further to this dry matter. For 5 cm rain, another 200 gm^{-2} could be produced. Therefore, the yield components and phenology of the plant should conform to these requirements. The crop should be able to produce 800 g dm m^{-2} if there was no rain but should have the possibility of responding to additional water. This will not be possible for a uniculm plant, but a tillering variety would respond to this situation. Of this, at least 40 per cent dry matter should be produced after anthesis. Therefore, about 40 per cent of the total available water should be available at anthesis. In other words approximately 8 cm water should at least be present in the soil profile to ensure post-anthesis photoassimilation. This means that the growth of the plant should be slow at early stages but by anthesis it should contribute approximately 500 gm^{-2} of dry matter. Having reached anthesis, it would be desirable if the spike has a potential of 35 to 40 grains. There should be 250 to 300 spike bearing shoots per m^{2}. Such an ideotype would have to be adequately supported by nutrient supply. For example, a crop producing 1000 g m^{-2} dry matter and 400 g m^{-2} grain would need approximately 110 kg N ha^{-1}. If such, an amount of nitrogen was not provided, the tillering and spike characters would not be expressed despite water availability. Thus our proposed ideotype of wheat would have the following traits :

1) Tillering type
2) Slow early growth, reaching approximately 500 g m^{-2} by anthesis.
3) Adequate leaf area at anthesis to produce 300 g m^{-2} or more dry matter after anthesis
4) 250-300 shoots m^{-2}
5) Potential of 35-40 gm of 40 mg each per spike
6) Medium duration and semi-tall to ensure adequate pre-anthesis conservation of assimilates.

Indeed some of these characteristics do exist in some genotypes such as C 306 and HD 2009.

Thus depending upon the estimated water availability and a particular crop, a location specific ideotype could be proposed. In many instances it may be necessary to estimate the final yields based on water availability to assess whether the upper limit was achieved.

Single Trait and Drought Resistance

Several efforts have been made to identify a single character which could serve as the basis of selection for drought resistance. Among these, chlorophyll stability, proline accumulation, betaine accumulation, occurrence of specific fatty acids, and now osmoregulation are noteworthy. Positive correlation of these individual characters to drought resistance (possibly in agronomic sense) were shown by some workers but negated by others. Proline accumulation as an index of drought resistance has been extensively debated (Singh et al. 1972; Sinha and Rajagopal 1975, 1978; Hanson 1980). That proline could provide protection to enzymes against desiccation or high temperature now seems to be beyond doubt (Sinha and Rajagopal 1975; Paleg et al. 1981; Nash et al. 1982). However, a correlation between proline accumulation and drought resistance estimated on the basis of yield, is difficult to establish because of a number of intervening biochemical, physiological and differentiation steps. Proline accumulation may offer short-term advantages at the cellular level but it may not be a practically useable selection criterion. The influence of environmental factors, growth stages and a relatively low heritability further support this contention (Lewin and Sparrow 1975; Aspinall and Paleg 1981). The evidence in support of using betaine accumulation as a criterion for drought resistance is very limited, and may again have importance in cellular functioning rather than the whole plant system. Accumulation of ABA as a criterion of drought resistance has also not been established (Quarrie 1981).

Recently osmoregulation both in microbes and higher plants has been advocated as a mechanism causing drought tolerance (Le Rudulier et al. 1984; Morgan 1984). In *E. coli* this evaluation was based in response to salinity stress, and osmoregulation was mostly due to proline accumulation. Salinity stress cannot be equated with water stress for a variety of reasons. Furthermore, in higher plants, such as wheat and barley, the osmoregulation is achieved by accumulation of sugars and inorganic ions (Munns et al. 1979). Proline contributes very little to this phenomenon. If osmoregulation is achieved by accumulation of organic molecules, then partition of assimilates between growth and osmoregulation would become an important factor in determining yield. This could assume even greater significance if water stress developed at the time of grain development. Therefore, it is not surprising that osmoregulating cultures of wheat had a maximum yield of 1 to 1.5 tons/ha (Morgan 1984). This once again shows that a combination of high yield and drought resistance is an incompatible objective.

The above discussion leads to the conclusion that it may not be realistic to look for a single trait as a selection criterion for drought resistance.

Integration

In this review an effort has been made to define drought and drought resistance, analysis of yield of crops and the effects of water deficit on growth and yield. It would be appreciated that several plant processes which occur in time scales ranging from seconds to minutes, hours, days and months culminate in crop yield under field conditions in a competitive environment. This relationship is diagrammatically shown in Fig. 9. It should be clear from this, that while the importance of short-term responses can not be denied, their correlation with yield is difficult to expect. It is for this reason that many individual tests have not been found of wider application in selection for drought resistance. It is obvious that a more complete view of plant growth, development and yield components in relation to water availability will have to be taken for a particular crop. This can be summarised as follows:

1) Reduced water availability reduces growth and dry matter production.

2) Stress at flowering/anthesis has a severe influence, particularly on senescence.

3) Larger the sink size, faster is the leaf senescence. Therefore, the sink potential is not realised.

4) These effects are possibly accentuated because of increasing canopy temperature.

5) Intraplant competition for assimilates, particularly between roots and grains 'sink', impair the former. This in turn

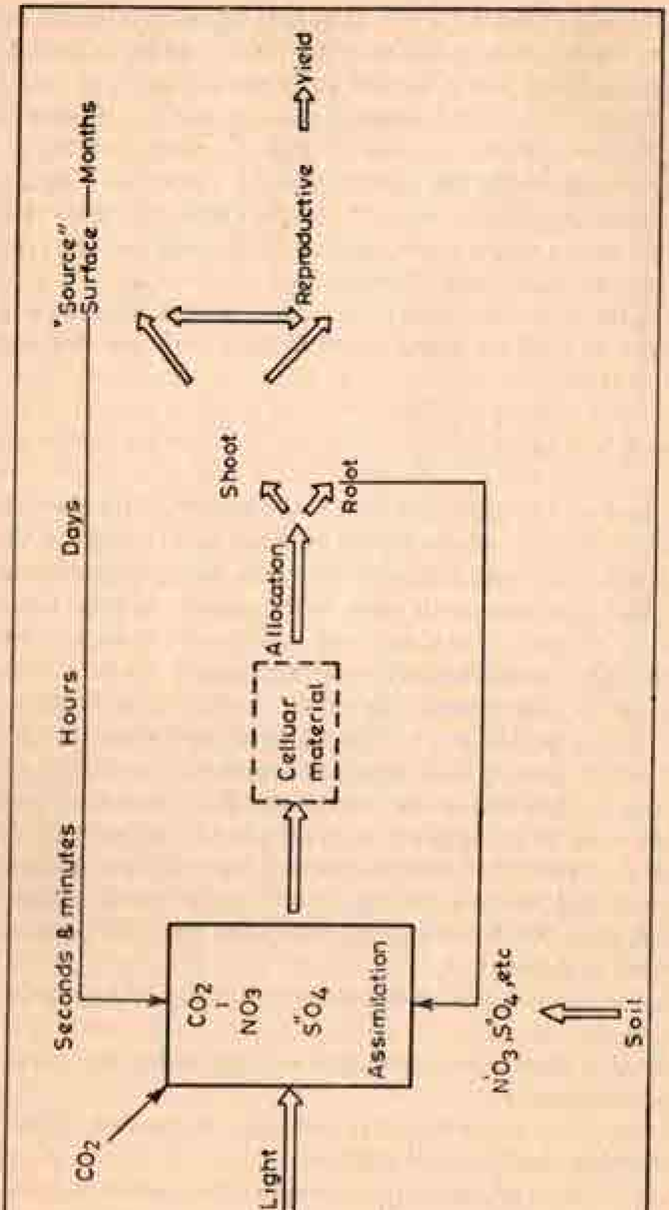


Fig. 9. Integration of processes leading to yield in terms of time.

further reduces water collection ability of roots.

In view of the above, the following approaches are suggested:

1) In a situation of intermittent rainfall, the genotypes with shorter duration be selected. They, however, should have faster initial growth rates. Such genotypes should have the ability to utilise nitrogen enabling a high percentage of it in leaf tissues. Such genotypes will have the capacity to recover when faced with water deficit and complete their life cycle soon after the cessation of rains. The hybrid CSH-6 of Sorghum is an example of such genotypes.

2) When the crop is grown on a receding soil moisture as wheat in *rabi*, the genotype should have a slower aerial growth combined with delayed differentiation. This plant behaviour ensures better root development and ensures a reasonable number of tillers. By anthesis the crop should attain 500 to 600 gm^{-2} dry matter, and leave 8-10 cm water in soil profile for maintaining adequate photoassimilation in postanthesis phase. Each spike in wheat, should have a potential of 1.0 to 1.2 g of grain weight. This means that the genotypes should have tillering capacity along with approximately 40 grains in each spike.

These two approaches can be adopted under limited water availability instead of irrigated or completely rainfed conditions. By providing a uniform population in early stages of growth, the performance of genotypes can be appropriately judged. This is possible during *kharif* because the crop is usually sown after an adequate rainfall. However, in *rabi* it would be advisable to grow a crop after a presowing irrigation to ensure germination and appropriate competition.

Having emphasised the complete approach in relation to environment, particularly the water availability, it may be mentioned that the following criteria might prove useful in selecting physiologically superior genotypes to conform to the above mentioned approach.

1) Seedling vigour in *kharif* and slow aerial seedling growth in *rabi*.

2) Canopy temperature, when crop canopy is formed, lower than the ambient temperature is desirable.

3) Physiological impairment of photosynthesis at anthesis to judge the capacity to mobilise preanthesis reserves.

4) Assessment of total dry matter production in relation to soil moisture depletion.

5) Medium capacity of yield components.

Acknowledgements

I am grateful to Dr. (Mrs) Renu Khanna-Chopra and Dr. P.K. Aggarwal for help in the preparation of this article. Thanks are also due to all those who very kindly responded to the questionnaire.

REFERENCES

Aggarwal, P.K. and S.K. Sinha (1983). Water stress and water use efficiency in field grown wheat : A comparison of its efficiency with that of C_4 plants. *Agricultural Meteorology* 29 : 159-167.

Aggarwal, P.K. and S.K. Sinha (1983). Dynamics of root and shoot growth during water stress and recovery in maize and cucumber seedlings. *Plant Physiol. Biochem.* 10 : 95-106.

Aggarwal, P.K. and S.K. Sinha (1984). Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield stability in a drought environment. *Ann. Bot.* 53 : 329-340.

Arnon, I. (1980). Breeding for higher yields. In : *Physiological aspects of crop productivity.* Proc 15th Colloquium of the International Potash Institute, Wageningen, pp. 77-81.

Armenta-Soto, J., T.T. Chang, G.C. Loresto and J.C. O'Toole (1983). Genetic analysis of root characters in rice. *SABRAO Jour.* 15 : 103-116.

Asana, R.D. (1968). Growth habits of crops of non-irrigated areas. Important characteristics of plant types. *Indian Farming* 18 : 25-27.

Asana, R.D. (1976). Physiological approaches to breeding of drought-resistant crops. Indian Council of Agricultural Research Technical Bulletin (Agriculture) no 52, New Delhi, pp. 48.

Asana, R.D. and A.D. Saini (1962). Studies in physiological analysis of yield V. Grain development in relation to temperature, soil moisture and changes with age in sugar content of the stem and in the photosynthetic surface. *Indian J. Plant Physiol.* 5 : 128-171.

Aspinall, D. and L.G. Paleg (1981). Proline accumulation : Physiological aspects. In: *Physiology and biochemistry of drought resistance in plants.* Eds. L.G. Paleg and D. Aspinall, Academic Press, Sydney, pp. 206-239.

Bewley, J.D. (1981). Protein Synthesis. In: Ibid., pp. 261-282.

Dalling M.J., G. Boland and J.H. Wilson (1976). Relation between acid proteinase activity and redistribution of nitrogen during grain development in wheat. *Aust. J. Plant Physiol.* 3 : 721-730.

De, R., G. Saran, B.B. Turkhede, R.B. Lal, R.K. Singh and G. Giri (1984). Response of wheat cultivars to date of sowing under dryland conditions. *J. Agric. Sci.* 101 : 727-733.

Eastin, J.D. (1972). Photosynthesis and translocation in relation to plant development. Eds. N.G.P. Rao and L.R. House In : *Sorghum in seventies.* Oxford & IBH Publishing Co., New Delhi.

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

Evans, L.T., I.F. Wardlaw and R.A. Fischer (1975). Wheat. In : *Crop physiology*, Ed. L.T. Evans, Cambridge University Press.

Finley, K.W. and G.N. Wilkinson (1963). The analysis of adaptation in plant breeding programme. *Aust. J. Agri. Res.* 14 : 742-754.

Fischer, R.A. (1973). The effect of water stress at various stages of development on yield processes in wheat. In: Plant responses to climatic factors. Ed. R.O. Slatyer, UNESCO, Paris, pp. 574.

Fischer, R.A. (1983). Wheat. In : *Potential productivity of field crops under different environments*, IRRI, Los Banos, Laguna, Philippines.

Fischer, R.A. (1984). Physiological limitations to producing wheat in semi-tropical and tropical environments and possible selection criteria. Paper presented at Wheat Workshop, CIMMYT, Sept., 1984.

Gotoh, K., T.T. Chang, J.C. O'Toole, R. Riley and B.R. Murty (1979). Crop adaptation. In : *Plant breeding perspectives.*

Eds. J. Sneep and A.J.T. Hendriksen, Centre for Agricultural Publication and Documentation, Wageningen, pp. 234-261.

Grover, A., K.R. Koundal and S.K. Sinha (1985). Senescence of attached leaves : Regulation by developing pods. *Physiol. Plant* 63 : 87-92.

Grover, A. and S.K. Sinha (1985). Senescence of attached leaves in *Cicer arietinum* : Regulation by developing pods. Proc. Indian Acad. Sci. (Plant Sci.) 95 : 333-340.

Hanson, A.D. (1980). Interpreting the metabolic responses of plants to water stress. *Hort. Science* 15 : 623-629.

Hsiao, T.C. (1973). Plant responses to water stress. *Ann. Rev. Plant Physiol.* 24 : 519-570.

Le Rudulier, D., A.R. Strom, A.M. Dandekar, L.T. Smith and R.C. Valentive (1984). *Molecular Biology of Osmoregulation Science* 224 : 1064-1068.

Lewin, L.G. and D.H. Sparrow (1975). The genetics and physiology of resistance to stress. Barley genetics. *Proc. IIIrd International Barley Genetics Symposium.* Garching, 1975, pp. 486-501.

Lindoo, S.J. and L.D. Nooden (1977). Studies on the behaviour of the senescence signal in Anoka Soybeans. *Plant Physiol.* 59 : 1136-1140.

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

Morgan, J.M. (1984). Osmoregulation and water stress in higher plants. *Ann. Rev. Plant. Physiol.* 35 : 292-319.

Moss, D.N., J.T. Wolley and J.F. Stone (1974). Plant modification for more efficient water use : The challenge. *Agricultural Meteorology* 14 : 311-320.

Munns, R., C.J. Brady and E.W.R. Barlow (1979). Solute accumulation in the apex and leaves of wheat during water stress. *Aust. J. Plant Physiol.* 6 : 379-389.

Nash, D., L.G. Paleg and J.T. Wiskich (1982). Effect of proline, betaine and some other solutes on the heat stability of mitochondrial enzymes. *Aust. J. Plant Physiol.* 9 : 47-57.

Nooden, L.D. (1980). Senescence in the whole plant. 219-258.

In : *Senescence in plants*. Ed. K.V. Thimann, CRC Press, Florida.

Paleg, L.G., T.J. Douglas, A. Van Daal and D.B. Kaech, (1981). Proline, betaine and other organic solutes protect enzymes from heat inactivation. *Aust. J. Plant Physiol.* 8 : 107-114.

Passioura, J.B. (1976). Physiology of grain yield in wheat on stored water. *Aust. J. Plant Physiol.* 3 : 559-565.

Passioura, J.B. (1983). Root and drought resistance. *Agricultural Water Management* 7 : 265-280.

Peoples, M.B., V.C. Beilharz, S.P. Waters, R.J. Simpson and M.J. Dalling (1980). Nitrogen redistribution during grain growth in wheat (*Triticum aestivum*). *Planta*. 149 : 241-251.

Quarrie, S.A. (1981). Genetics variability and heritability of drought induced abscisic acid accumulation in spring wheat. *Plant Cell and Environment* 4 : 147-151.

Savithri, K.S., P.S. Ganapathy and S.K. Sinha (1978). Fruit and seed development in mung bean *Phaseolus aureus* (Roxb). *J. Agri-Sci.* 90 : 551-556.

Singh, T.N., D Aspinall and L.G. Paleg (1972). Proline accumulation and varietal adaptability to drought in barley: a potential metabolic measure of drought resistance. *Nature* (*New Biology*) 236 : 188-190.

Sinha, S.K. and R. Khanna (1975). Physiological, biochemical and genetic basis of heterosis. *Advan. Agron.* 27 : 123-174.

Sinha, S.K. and V. Rajagopal (1975). Proline slow down the loss of nitrate reductase in moisture stressed plants. *Plant Physiol.* (Suppl). 56 : 225.

Sinha, S.K. and V. Rajagopal (1975). Effect of moisture stress on nitrate reductase activity and accumulation of proline in Sorghum. *Proc. Symp. on crop plant responses to environmental stress.* Vivekananda Laboratory for Hill Agriculture (India), 1-9.

Sinha, S.K. and V. Rajagopal (1978). Effect of moisture stress on proline accumulation in Sorghum and wheat. In : Nitrogen Assimilation and Crop Productivity. Eds. S.P. Sen, Y.P. Abrol and S.K. Sinha, pp. 158-163.

Sinha, S.K. and V. Rajagopal (1980). Photosynthetic characteristics and nitrate reductase activity during development of flag leaf of wheat. *Photosynthetica*. 14 : 189-192.

Sinha, S.K., P.K. Aggarwal and R. Khanna-Chopra (1985). Irrigation in India: Physiological and phenological approach to water management in grain crops. Irrigation Science Vol. 3 : (129-212) Academic Press, New York.

Sinha, S.K., P.K. Aggarwal, G.S. Chaturvedi, A.K. Singh and K. Kailasnathan (1986). Performance of wheat varieties in a variable water environment I. Grain Yield Stability. Field Crops Research (in press).

Sinha, S.K., R. Khanna-Chopra, P.K. Aggarwal, G.S. Chaturvedi and K.R. Koundal (1982). Effect of drought on shoot growth : Significance of metabolism to growth and yield. In : *Drought resistance in crops with emphasis on rice*. IRRI, Los Banos, Laguna, Philippines, pp. 153-169.

Sinha, S.K., B. Lal, K.R. Koundal and R. Khanna-Chopra (1983). Nitrogen fixation does not limit yield in pulses. *Curr. Sci.* 52 : 916-918.

Slabbers, P. J. (1980). Crop response to water under irrigated conditions. *Land reclamation and water management*. Publication No. 21, ILRI, Wageningen.

Breeding Approaches for Drought Resistance in Crop Plants

R.S. PARODA

Introduction

Man's intervention in the evolution of plants, to adapt them to suit his needs, constitutes the practice of plant breeding. Historically regarded as an art and still too empirical to be accepted universally as a science, it has recently been described as a technology (Riley 1978). Whether art, science or technology, it certainly draws on a wide range of disciplines and embodies all those principles of organisation and management that determine success in any production-oriented programme.

Perhaps the biggest contribution that the plant breeder has made to increased production during the past 50 years has been in helping to alleviate the effects of natural hazards such as lodging, pests and diseases on crop production. While most of this progress has been through the manipulation of biotic stresses, much is still to be achieved under non-biotic stresses such as drought, salinity, temperature, etc. This argument is strengthened by the fact that in spite of the spectacular achievements made possible by the 'Green Revolution', the productivity level of most crop plants, including wheat and rice, has remained both low and static under stress conditions. Concerted efforts are needed through an approach of interdisciplinary research, since not much has been done to define criteria for stress assessment and evolving breeding approaches for incorporating stress tolerance in crop plants.

Genetic improvement of a plant's drought resistance by selection for yield under stress is a possible but prolonged and problematic procedure. The physiological and genetical aspects of the improvement of drought resistance in crop plants have been comprehensively reviewed recently (Mussell and Staples 1979; Turner and Kramer 1980; Blum 1981; Paleg and Aspinall 1981; Christiansen and Lewis 1982; Kramer and Raper 1983). The present state of knowledge allows for several conclusions to be drawn. Yield performance of a genotype under stress is a reflection of both its response to stress and its potential yield level. This conclusion led many plant breeders to believe that the genetic improvement of yield potential will also result in improved yields under stress. Using this concept, while some numerical empirical improvements in yield under sub-optimal environments have been realised, the concept loses meaning when the yield has plateaued. A direct tackling of sub-potential yield levels through breeding is, therefore, essential, and the question immediately raised is whether drought resistance exists and can be measured. The positive answer is deliberated in many of these cited reviews and an effort has been made in this paper to discuss the breeding approaches for drought resistance in crop plants.

Drought Defined

Drought is defined in both the Concise Oxford Dictionary and Webster's New World Dictionary as "prolonged dry weather". The definition, however, is not precise as both "prolonged" and "dry", like drought, are relative terms. For a period of dry weather to affect a plant community, the rainfall deficit must lead to a soil water deficit and ultimately to a plant water deficit. The degree to which a rainfall deficit is translated into a soil water deficit depends on the rate of evaporation during the rain free period, and on the physical and chemical characteristics of the soil. The degree to which a particular soil water deficit influences the plant again, depends on the degree of aridity of the atmosphere. However, it also depends on a number of plant characteristics which influence water uptake, the rate of transpiration and the response of the plant to the water deficit so generated. It is the degree to which the plant can withstand the rainfall deficit that constitutes its drought tolerance.

Hence, drought tolerance to an agronomist would mean 'yield', whereas to an ecologist it would mean 'survival'. Therefore, to define drought resistance without defining the environmental conditions and specific requirements in terms of 'plant type' would not be of much use. Blum et al. (1981) has stated that the total drought resistance of genotype cannot yet be defined physiologically and most probably it does not exist as a unique plant trait. According to Passioura (1981), drought resistance is a nebulous term that appears to become more nebulous the more closely we look at it. Drought resistance, by its simplest definition, is the sum of drought avoidance and drought tolerance (Levitt 1972). Avoidance, called drought tolerance with high tissue water potentials by May and Milthorpe (1962), consists of mechanisms to reduce water loss from plant and of mechanisms to maintain water uptake. Drought tolerance refers to the ability of the plant to withstand low tissue water potentials.

Understanding the Extent of Stress

A drought in the world's wet tropics would constitute a flood in the arid zones. Similarly, a period of two weeks without significant rain may represent drought to a lowland rice farmer in the Philippines, but would be proclaimed as abnormal rains by a nomadic grazier in the Sahel or for that matter in the Thar desert in India. It is, therefore, essential to define the extent of drought stress in the context of existing agro-climatic conditions of the area/region for which one is particularly concerned. There is no point in initiating breeding programmes for drought stress without clearly understanding the extent of stress and possible strategies which could help in achieving the desired objectives. Oswal (personal communication) has tried to define the extent of stress at different locations in Haryana keeping in view the rainfall probability values based on data available for the last 50 years. He has also tried to superimpose the curves of different crop growth periods with a view to see which crop could be more successful if drought is to be avoided (Fig. 1), or which crop would best withstand drought. In deep soils, a plant with a deep root system may have an advantage, whereas in shallow soils the requirements for the root system would differ as demonstrated by Passioura (1981). Similarly, for rainfed wheat

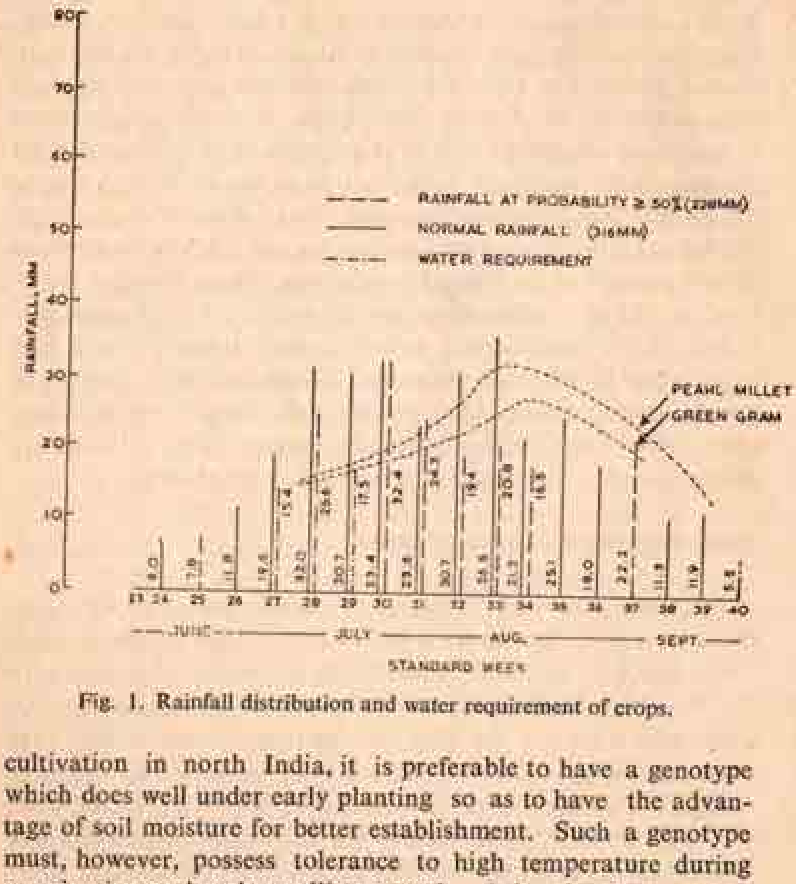


Fig. 1. Rainfall distribution and water requirement of crops.

cultivation in north India, it is preferable to have a genotype which does well under early planting so as to have the advantage of soil moisture for better establishment. Such a genotype must, however, possess tolerance to high temperature during germination and early seedling growth. It is, therefore, necessary to understand the environment more precisely in terms of timing and the length of water stress likely to be encountered before initiating any breeding programme for drought resistance in crop plants. Jordan and Miller (1980) provided such an analysis by giving three patterns of drought encountered in the Sorghum growing region of the U.S.A. which provides the basis for determining the requirements of breeding material likely to perform well under different conditions.

Mechanism of Drought Resistance

Three primary types of drought resistance mechanisms in crop plants have been identified (May and Milthorpe 1962; Levitt 1972; Turner 1979). These are:

a) *Drought escape*: The ability of a plant to complete its life cycle before a serious plant water deficit develops.

b) *Drought tolerance at high tissue water potential*: The ability of a plant to endure periods of rainfall deficit while maintaining a high tissue water potential. Many reviewers have simply referred to this as drought avoidance, although it is to be understood that plants with these mechanisms do not avoid drought but avoid tissue dehydration.

c) *Drought tolerance at low tissue water potential*: The ability of a plant to endure rainfall deficits at low tissue water potential.

The above classification is chosen because of its simplicity and because it uses drought as a meteorological term, thereby avoiding the confusion arising from equating "drought" with "plant water deficit". For a further amplified and subdivided system of defining drought resistance the reader is referred to Levitt (1972). There are several mechanisms that enable plants to

Table I. Mechanisms of drought resistance

- Drought escape
  - (a) Rapid phenological development
  - (b) Developmental plasticity
- Drought tolerance with high tissue water potential
  - (a) Maintenance of water uptake
    - (i) Increased rooting
    - (ii) Increased hydraulic conductance
  - (b) Reduction of water loss
    - (i) Reduction in epidermal conductance
    - (ii) Reduction in absorbed radiation
    - (iii) Reduction in evaporative surface
- Drought tolerance with low tissue water potential
  - (a) Maintenance of turgor
    - (i) Solute accumulation
    - (ii) Increase in elasticity
  - (b) Desiccation tolerance
    - (i) Protoplasmic resistance

Source: Jones et al. (1981).

resist drought and these have been summarised in Table 1 by Jones et al. (1981).

Parameters of Drought Resistance

Three parameters of drought resistance i.e. morphological, physiological and biochemical, are considered to be important. Turner (1982) has defined three mechanisms of drought tolerance: phenological, morphological and physiological (Table 2). Also, different parameters which give an account of possible attributes responsible for increased tolerance to water stress are detailed in Table 3. There is no intention of reviewing the knowledge relating to mechanisms of drought resistance, since this aspect has been extensively covered by other contributors to this volume. However, the parameters which have been found to be important and for which genetic variation exists are: dehydration avoidance (maintenance of relatively higher leaf water potential under conditions of soil moisture stress); osmotic adjustment: tolerance of plants due to the organ growth rate; plant recovery

Table 2. Effects of mechanisms of adaptation to drought on productivity and on reversibility on relief of stress : ease in screening

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

Source : Turner (1982).

upon rehydration; tolerance of the photosynthetic system or its components; tolerance of enzyme activities; tolerance in translocation; stability of the cellular membranes; proline accumulation; root growth attributes such as density, depth, hydraulic resistance; plant developmental or morphological attributes, such as leaf size, leaf area per plant, leaf orientation or leaf movement; tiller survival; epicuticular wax content, organ pubescence; awns and kernel weight.

Table 3 Morphological, physiological and biochemical parameters

Morphological
- Earliness
- Reduced leaf area
- Leaf rolling
- Wax content
- Colour of leaves
- Root system
- Awns
- Hairs
- Increased grain weight

Physiological
- Photosynthesis—efficient system like C_4
- Reduced transpiration
- Stomatal closure (CAM mechanism-*Agave*)
- Osmotic adjustment
- Reduced xylem vessel in roots
- Reduced respiration losses
- Desiccation tolerance (ex. *Acacia arabica*)
- Canopy temperature

Biochemical
- Proline accumulation
- Betaine accumulation
- Protein synthesis
- Nitrate—reductase activity
- C+C/A+U ratio in RNA

The volume of information concerning drought parameters is, however, of limited value to actual breeding work mainly because of two reasons. First, while the existence of genetic variation for a given drought-resistance attribute can be indicated by using the standard, accurate but slow physiological methodology, this methodology is impossible for use in routine screening work. The physiological methodology has been developed with a major concern for accuracy. Routine screening methodology demands ease and speed of operation even at the expense of accuracy, if necessary. While physiological work requires accurate and absolute terms, selection work involves the probabilities and frequencies of population breakdown, often in relative terms. The breeder's main interest is in efficiently reducing population size, even with a margin of error, normally unacceptable by a physiologist. This is because the breeder compensates for the marginal loss of accuracy by repeated testing in subsequent generations. The margin of acceptable error to the breeder would depend on the method used as well as on the genetic structure of the tested populations. Second, there is a serious lack of information on the relationships between given physiological drought adaptive traits and economic yield within defined stress and non-stress environments. It is extremely difficult today to formulate a plant 'ideotype' in terms of the physiological responses required for yield buffering in defined or undefined drought environments. This is where the importance of plant modelling work becomes evident. Recent evidence (Blum 1979; Sammons et al. 1980; Nass and Sterling 1981) suggests that no single drought-adaptive trait is predictive of plant response to stress and that multiple physiological selection criteria are required.

Also, at present, our knowledge about the following is incomplete:

a) Which attributes are most reliable as indices of drought resistance.

b) Whether genotypes good for these attributes will also be good for yield under stress.

c) Whether usable genetic variation exists for these attributes.

d) Whether quick and efficient techniques exist for screening large number of genotypes for such attributes.

e) Whether these attributes are less influenced by environmental interactions so that these could be used in breeding programmes effectively.

Because of these constraints in understanding, an improvement over the presently used empirical approach would be to apply physiological and morphological selection criteria for identifying high yielding families. This approach will, no doubt, be a transitional programme and would change as new knowledge accumulates. It will have the advantage, however, that progress will be possible concurrent with enquiry. In recent years, attributes such as an efficient root system (Hurd 1976; Chang et al. 1974; Passioura 1981; Armenta-Soto et al. 1983); leaf rolling (Parker 1968; O'Toole et al. 1979; Chang et al. 1974); cool canopy temperature (Blum 1983; Blum and Ebercon 1981); osmotic adjustment (Turner and Jones 1980; Cutler et al. 1980; Morgan 1980); awns (Sunesan and Ramage 1962, Grundbacher 1963), waxiness or increased pubescence (O'Toole et al. 1979; Ehleringer 1980; Quarrie and Jones 1977; Turner 1981; Blum 1975; and grain weight (Asana and Saini 1962; Saghir et al. 1968; Paroda and Luthra 1981) have been found to be quite reliable and useful criteria.

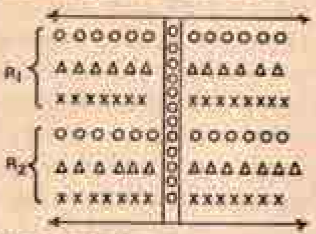
Screening Methods to Study Drought Resistance Mechanisms

Before further progress can be made in utilising morphologically and physiologically based adaptations to drought, it is necessary to develop suitable screening methods (Blum 1979; O'Toole and Chang 1979). The major problem with many methods developed for the screening of these parameters, is that they are too slow and laborious for use in screening large plant populations. Morphological and physiological mechanisms, such as a reduction in leaf area, radiation interception, and an increase in stomatal resistance, that enable a plant to avoid water deficit, are major factors for reducing photosynthesis and productivity. Drought resistance mechanisms such as increase in root density and depth and osmotic adjustment also may reduce productivity, but their effects are indirect and more difficult to quantify. Their contribution is likely to be less than the direct effects of a reduction in leaf area, changes in radiation interception, and stomatal closure. Blum (1979) has argued that a knowledge of the influence of drought resistance characters on yield is not essential. Rather, if a particular physiological or morphological character can be identified and shown to improve the drought resistance of the crop and if the character and yield are independently inherited (the drought resistance character and yield are not negatively correlated), incorporation of the character into a high yielding line should improve the crop's yield under drought. Hence, it is obviously necessary to first evaluate genotypes for stable and high yield under drought stress conditions so that these could be used as agronomic base material for incorporating other desired attributes that are expected to further improve the drought tolerance ability. Some of the effective screening techniques for identifying drought tolerant plants are given in Table 4. Though each technique has some limitations yet the first two (screening through multilocation testing and through drought plots) are perhaps the most convenient and reliable. Field testing under different stress environments followed by testing for stability of yield performance as per Eberhart and Russell (1966) has proved to be very useful and appears to be the best alternative presently available with the breeders. Turner (1981) has reviewed the techniques for evaluation of different attributes. It is observed that efficient techniques are available for studying the root pattern, canopy temperature, waxiness, and osmotic adjustment. Genotypes could be effectively evaluated for these attributes, and the promising ones could be used as donors for improving agronomically superior lines for drought tolerance.

Table 4. Screening techniques for drought tolerance in crop plants

SCREENING TECHNIQUES

- MULTILOCATION TESTING – SIMPLE AND CONVENIENT
- DROUGHT PLOTS (WITH SHELTER SCREENS)
- A LINE SOURCE SPRINKLER SYSTEM



- USE OF SLOPES AND DRAINS IN THE FIELDS
- GREEN HOUSE SCREENING IN POTS/TUBES
- TESTING THROUGH HYDROPONICS/AEROPONICS (BY CREATING VARYING LEVELS OF WATER STRESSES)

Breeding Approaches

To define only one breeding approach for drought resistance would obviously be an over-simplification of an otherwise complicated process. Hence, different breeding approaches will have to be used under different situations for which different drought resistance mechanisms (escape, avoidance and resistance) will need to be exploited.

a) BREEDING FOR ESCAPE MECHANISM

One of the simplest mechanisms by which plants deal with drought is drought escape. This, as the name implies, is accomplished by rapid phenological development or by developmental plasticity. Drought escape is perhaps the most dramatic in the 'ephemeral' plants of desert regions which complete life cycles in a very short span. However, drought escape also plays a significant role in crop species both through yield and their early maturity and developmental plasticity. Invariably, earliness, which is otherwise a highly heritable character, is negatively correlated with high yield. For this reason whenever breeding efforts were directed towards earliness, yield had to be sacrificed to a certain extent. However, escape has proved to be a very useful mechanism for coping with drought stress and breeders have capitalised on it quite extensively. It has recently been shown that through the adoption of biparental approach, undesirable linkages in the repulsion phase can be broken and it is possible to obtain recombinants that are both early and high yielding (Yunus and Paroda 1982). The same holds good for attributes related to developmental plasticity such as tiller numbers and their association with grain yield. In some crops, developmental plasticity is exhibited by varying degrees of determinacy of growth habit (Quisenberry and Roark 1976). Fortunately, screening and selection for drought escape through maturity or developmental plasticity is relatively simple compared to screening and selection for other drought resistance characteristics. Also, the genetic architecture of attributes such as earliness, tillering and determinate growth habit is better understood. This knowledge can be effectively used in breeding for drought escape mechanisms by employing breeding methods such as pedigree method and biparental approach, especially when negative linkages are to be broken.

b) BREEDING FOR DROUGHT AVOIDANCE

There seems to be some controversy as to which component of drought resistance, avoidance or tolerance, is of more importance in a crop. Although drought avoidance might permit a longer period of crop growth with reduced water use or increased water uptake, drought avoidance mechanisms often operate at the expense of photosynthesis. They reduce top growth at the expense of increased root development (Boyer and McPherson 1975). It is suggested that tolerance would be more desirable since the crop could produce more yield at lower water potentials. Levitt (1972), however, stated that, in general, drought avoidance is more important than drought tolerance in higher plants. Fisher and Turner (1978) suggested that mechanisms favouring drought survival and those favouring productivity are naturally opposed. In reality, a mixture of both avoidance and tolerance mechanisms is required. Even the best drought avoiding species requires tolerance, since some reduction in plant water potential is unavoidable during severe stress.

Among avoidance mechanisms, attributes related to both water saving and water spending devices are important. The fundamental importance of root system in the drought avoidance of plants has been well established. Species and genotypic differences in a root system, size and efficiency, in particular, have been widely researched (Hurd 1964; Raper and Barber 1970; Sullivan and Ross 1979). The high labour requirement for root system analysis has limited the amount of work done in this area, although there is a continuing search for simple and effective screening techniques. Armenta-Soto et al. (1983) have recently studied root system genetics using an aeroponic culture in rice and found that long roots and high root number are primarily controlled by dominant alleles and these characters are highly heritable. Hence, efforts could be made to breed for this trait. There has been some controversy as to whether an extensive root system or a more restricted system, which conserves water for late season use, is preferable. Hurd's results support the former for sandy and deep soil conditions prevailing at Swift Current, Canada, whereas Passioura has suggested that the latter type may be superior under shallow soil depths prevailing in Australia. Hence, the breeding approach for this trait would differ depending upon the conditions encountered.

The purpose here is not to repeat the importance of different attributes, both morphological and physiological, that can be used for avoidance either through water saving or through water spending mechanisms. However, it is now clearly understood that attributes such as rooting pattern, waxiness, awns, high kernel weight, leaf rolling, leaf orientation play a considerable role towards drought avoidance and are under genetic control. The exact extent of their role is yet to be evaluated. For this the approach of using isogenic lines will be desirable. Nevertheless, to capitalise on whatever advantage these attributes may provide to an otherwise agronomically superior genotype under stress conditions, it will be appropriate to use the following breeding approach:

1) Identification of promising and stable genotypes for yield performance under stress conditions by using multilocation tests.

2) Identification of source materials that possess desired physiological and morphological attributes related to drought avoidance mechanism.

3) Attempting crosses to incorporate the desired attributes one by one in the high yielding stable genotypes by using such breeding approaches as pedigree method, back-cross method, etc.

4) Multiple cross approach with a view to assembling different desired attributes simultaneously after the source genotypes have been identified. Breeding method such as recurrent selection could be used for this purpose (Fig. 2).

The steps of the above approach have been summarised in Table 5. Blum (1983) has used a similar approach for wheat in Israel (Fig. 3). The assumption of his programme is that improvement in drought resistance can be enhanced beyond the empirical approach by applying multiple selection criteria imposed on high yielding families. Such an approach in no way adversely affects the on-going empirical breeding approach and hence can be used effectively.

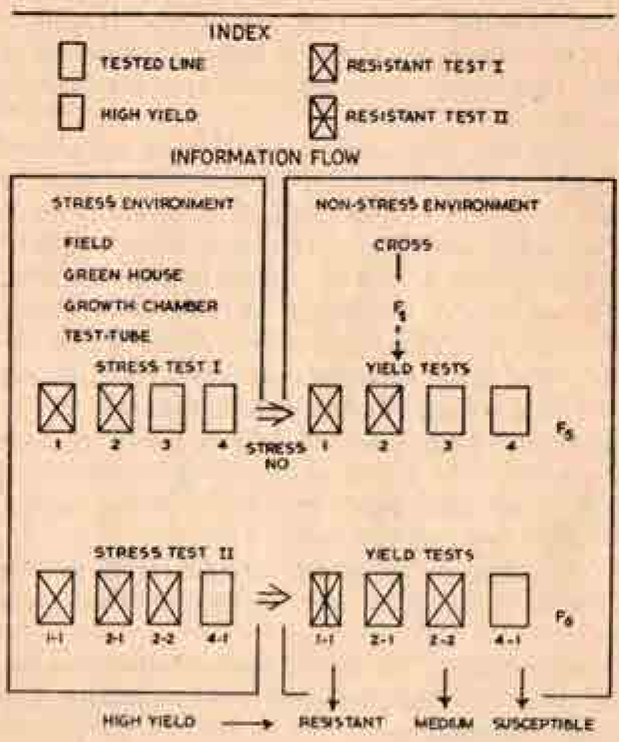


Fig. 2. A schematic outline of a pedigree selection programme under non-stress (right) and stress (left) conditions.

Table 5. Proposed scheme for breeding drought resistant genotypes

Step I

1. Multilocation testing under stress conditions.
2. Identification of stable genotypes.
3. Crosses involving stable genotypes in stress and agronomically superior cultivars
4. Selection (Pedigree of SSD) in F_2 generation under non-stress conditions for yield performance.
5. Testing of F_4 selected lines under stress conditions as well as non-stress conditions (for seed multilocation).
6. Same as 5 using F_5 selected lines.
7. Multilocation tests and release.

Step II

1. Crosses using selected F_6 lines under stress and identified genetic sources for desired morphological and physiological traits.
2. Same as 4-7 of Step I.

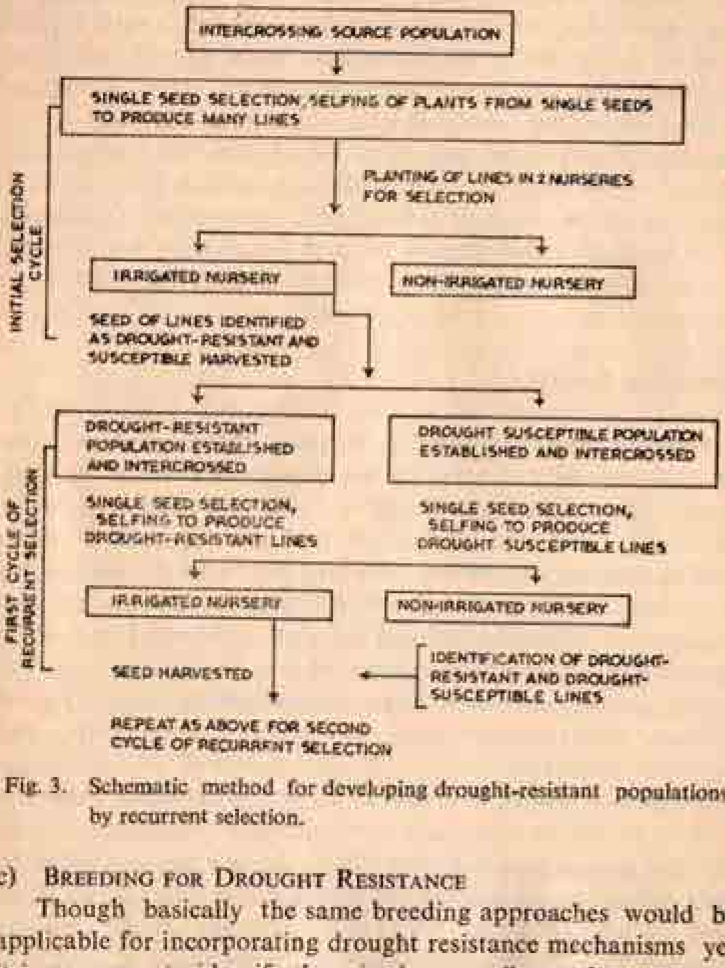


Fig. 3. Schematic method for developing drought-resistant populations by recurrent selection.

c) Breeding for Drought Resistance

Though basically the same breeding approaches would be applicable for incorporating drought resistance mechanisms yet it is necessary to identify the criteria or attributes that would be helpful in this regard. Many attributes such as dehydration tolerance (Keim and Kronstad 1981; Sojka et al. 1981 in wheat, Boyer et al. 1980 in soybean; O'Toole and Chang 1979 in rice), tolerance to post-anthesis stress (Boyer 1976; Austin et al. 1980) stability of the cellular membranes (Blum and Ebercon 1981; Blum 1983), osmotic adjustment (Turner and Jones 1980; Turner 1982; Cutler et al. 1980; Morgan 1980) and stomatal resistance (Turner 1974; Blum 1974; Jones 1977; Ludlow 1980) have been found to be responsible for drought resistance in crop plants. Whereas some of these can be used effectively for screening a large number of genotypes in the field, most cannot be used as effectively till better and more reliable screening techniques are established by physiologists. One would be required to use the identified sources for these attributes in the breeding programmes and then see whether the end product selected on the basis of higher yield performance under drought stress conditions, also possesses these attributes. Obviously, to be successful, this area of research necessitates an effective inter-disciplinary approach which seems to have been lacking in the past.

Concluding Remarks

It is evident from the foregoing discussion that much needs to be done in the field of breeding for drought resistance in crop plants. Several parameters appear to be related to drought in one or the other crop species and they also appear to be under genetic control. However, none appears to be the most reliable parameter in itself. A combination of some attributes (biochemical, physiological and morphological) could provide a better index for resistance to water stress. There is an apparent need to intensify inter-disciplinary research efforts involving plant breeders, crop physiologists, biochemists, agronomists, soil physicists and meteorologists. Till some reliable parameters are established, it will be desirable to incorporate attributes that are related to either drought escape, drought avoidance and/or drought resistance. We still do not know enough about the exact principles, procedures and parameters which make a plant more drought resistant. Meanwhile, breeders should continue their selection programmes for drought resistance, even if it is to be defined as experimental since the resulting information could prove to be extremely valuable for future research and development in this important area which has somehow remained unattended in the past.

REFERENCES

Asana, R.D. and A.D. Saini (1962). Studies in physiological analysis of yield V. Grain development in wheat in relation to temperatures, soil moisture and changes with age in the sugar content of the stem and in the photosynthetic surface. *Indian J. Plant Physiol.* 5 : 128-171.

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

Armenta-Soto, J., T.T. Chang, G.C. Loresto and J.C. O'Toole (1983). Genetic analysis of root characters in rice. *SABRAO Journal* 15 : 103-116.

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

Boyer, J.S. and H.C. McPherson (1975). Physiology of water deficits in cereal crops. *Adv. Agron.* 27 : 1-23.

Blum, A. (1975). Effect of the Bm gene on epicuticular wax and the water relations of *Sorghum bicolor* L. (Moench). *Israel J. Bot.* 24 : 50-51.

Boyer, J.S. (1976). Photosynthesis at low water potentials. *Phil. Trans R. Soc. London* B 273 : 501-512.

Blum, A. (1979). Genetic improvement of drought resistance in crop plants : a case for sorghum. In : *Adaptation of plants to water and high temperature stresses.* Eds. H. Mussell and R.C. Staples, Wiley Interscience, New York, pp. 429-445.

Boyer, J.S., R.R. Johnson and S.G. Sonpe (1980). Afternoon water deficits and grain yields in old and new soybean cultivars. *Agron. J.* 72 : 981-986.

Blum, A. and A. Ebercon (1981). Cell membrane stability as a measure of drought and heat tolerance in wheat. *Crop Sci.* 21 : 43-47.

Blum, A., C. Gozlan and J. Mayer (1981). The manifestation of dehydration avoidance in wheat breeding germplasm. *Crop Sci.* 21 : 495-499.

Blum, A. (1981). Evidence for genetic variability in drought resistance and its implication in plant breeding. *Symp. Principles and methods in crop improvement for drought resistance : With emphasis on rice.* IRRI, Los Banos, Philippines, pp. 30.

Blum, A. (1983). Genetic and physiological relationships in plant breeding for drought resistance. In : *Agricultural* *water management*. Eds. J.F. Stone, W.O. Willis, Elsevier Science Publishers B.V., Amsterdam, pp. 195-205.

Chang, T.T., G.C. Loresto and O. Tagumpay (1974). Screening rice germplasm for drought resistance. *SABRAO Journal* 6 : 9-16.

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

Christiansen, M.N. and C.F. Lewis (1982). *Breeding plants for less favourable environments.* Wiley Interscience, New York, pp. 459.

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

Ehleringer, J. (1980). Leaf morphology and reflectance in relation to water and temperature stress. In : *Adaptation of plants to water and high temperature stress.* Eds. N.C. Turner and P.J. Kramer, Wiley Inter-science, New York.

Fisher, R.A. and N.C. Turner (1978). Plant productivity in the arid and semi-arid zones. *Ann. Rev. Plant Physiol.* 29 : 277-317.

Grundbacher, F.J. (1963). The physiological function of the cereal awn. *Biol. Rev. Cambridge Phil. Soc.* 29 : 366-381.

Hurd, E.A. (1964). Root study of three wheat varieties and their resistance to drought damage by soil cracking. *Can. J. Plant Sci.* 44 : 240-248.

Hurd, E.A. (1974). Phenotype and drought tolerance in wheat. *Agri. Meteor.* 14 : 39-55.

Hurd, E.A. (1976). Plant breeding for drought resistance. Water deficits and plant growth. Ed. T.T. Kozlowski, Vol. IV, Academic Press, New York, pp. 317-353.

Jones, H.G. (1977). Aspects of water relations of spring wheat (*Triticum aestivum* L.) in response to induced drought. *J. Agric. Sci.* 88 : 267-282.

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

Jones, M.M., N.C. Turner and C.B. Osmond (1981). Mechanism of drought resistance. In : *Physiology and biochemistry* *of drought resistance in plants.* Eds. L.G. Paleg and D. Aspinall, Academic Press, New York, pp. 15-37.

Keim, D.L. and W.E. Kronstad (1981). Drought response of winter wheat cultivars grown under field stress conditions. *Crop Sci.* 21 : 11-15.

Karmer, P. J. and C.D. Raper Jr. (1983). Crop reactions to water and temperature stresses in humid temperate climate. In : *Proc. Cong.* Duke University, Durham. NC West View Press Boulder Co. (In Press).

Levitt, J. (1972). *Responses of plants to environmental stresses.* Academic Press, New York.

Ludlow, M.M. (1980). Adaptive significance of stomatal responses to water stress. *Adaptation of plants to water and high temperature stress.* op. cit., pp. 123-138.

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

Mussell, H. and R.C. Staples (1979). *Stress physiology in crop plants.* Wiley Interscience, New York, pp. 510.

Morgan, J.M. (1980). Osmotic adjustment in the spikelets and leaves of wheat. *J. Exp. Bot.* 31 : 655-665.

Nass, H.G. and J.D. E. Sterling (1981). Comparison of tests characterizing varieties of barley and wheat for moisture stress resistance. *Can. J. Plant Sci.* 61 : 283-292.

O'Toole, J.C., R.T. Cruz and J.N. Seiber (1979). Leaf rolling and transpiration. *Plant Sci. Letters* 16 : 111-114.

O'Toole, J.C. and T.T. Chang (1979). Drought resistance in cereals-rice : a case study. In : *Stress physiology in crop plants.* op. cit., pp. 373-405.

Parker, J. (1968) In : *Waetr deficits and plant growth.* Eds. T.T. Kozlowski, Vol. I, Academic Press, New York, pp. 195-234.

Paleg, L.C. and D.D. Aspinall (1981). *The physiology and biochemistry of drought resistance in plants.* Academic Press, New York, pp. 492.

Passioura, J.B. (1981). Water collection by roots. In : *The physiology and biochemistry of drought resistance in plants.* Eds L.G. Paleg, and D. Aspinall, Academic Press, New York, pp. 39-53.

Paroda, R.S. and O.P. Luthra (1981). Breeding for resistance to water stress in wheat. *Wheat and wheat improvement*, pp. 123-139.

Quisenberry, J.E. and B. Roark (1976). Influence of determinate growth habit on yield and irrigation water use efficiency in upland cotton. *Crop Sci.* 16 : 762-764.

Quarrie, S.A. and, H.G. Jones (1977). Effects of abscisic acid and water stress on development and morphology of wheat. *J. Exp. Bot.* 28 : 192-203.

Raper, C.D, and S.A. Barber. (1970). Rooting system of soybeans. I. Differences in root morphology among varieties. *Agron. J.* 62 : 581-584.

Riley, R. (1978). Plant breeding—an integrating technology. In : *Technology for increased food production*. Eds. J.C. Holmes, W.M. Tahir, F.A.O. Rome, pp. 267-272.

Sunesan, C.A. and R.T. Ramage (1962). Competition between near isogenic genotypes. *Crop Sci.* 2 : 249-250.

Saghir, A.R., A.R. Khan and W.W. Worzella (1968). The effect of plant parts on grain yield, kerner weight and plant height of wheat and barley. *Agron. J.* 60 : 95-97.

Sullivan, C.Y. and W.M. Ross (1979). Selecting for drought and heat resistance in grain sorghum. In : *Stress physiology in crop plants*, op. cit.

Sammons, D.J., D.B. Peters and T. Hymowitz (1980). Screening soybeans for tolerance to moisture stress : a field procedure. *Field Crops Res.* 3 : 321-335.

Sojka, R.E., L.H. Stozy and R.A. Fisher (1981). Seasonal drought response of selected wheat cultivars. *Agron. J.* 73 : 833-844.

Turner, N.C. (1974). Stomatal response to light and water under field conditions. In : *Mechanisms of regulation of plant growth*. Eds. R.L. Bieleski, A.R. Fergrision and M.M. Cresswell, Bull. 12, Royal Society of New Zealand, Wellington, pp. 423-432.

Turner, N.C. (1979). Drought resistance and adaptation to water deficits in crop plants. In : *Stress physiology in crop plants*, op. cit., pp. 343-372.

Turner, N.C. and J.P. Kramer (1980). *Adaptation of plants to water and high temperature stresses*. Wiley Interscience, New York, pp. 482.

Turner, N.C. and M.M. Jones (1980). Turgor maintenance by osmotic adjustment : a review and evaluation. In : *Adaptation of plants to water and high temperature stress.* op. cit., pp. 87-103.

Turner, N.C. (1981). Designing crops for dryland Australia. Can the deserts help us ? *J. Aust. Inst. Agri. Sci.* 47 : 29-34.

Turner, N.C. (1982). The role of shoot characteristics in the response of millet to drought. In : *Drought resistance in crops with emphasis on rice.* IRRI, pp. 115-134.

Yunus, M. and R.S. Paroda (1982). Impact of biparental mating on correlation coefficients in bread wheat. *Theor. Appl. Genet.* 62 : 337-343.

Screening Techniques for Drought Resistance in Rice

T.T. CHANG AND GENOVEVA C. LORESTO

Introduction

Drought is one of the primary factors responsible for depressing rice yield in chronic areas and in destabilising rice production in drought-prone areas. It is a production constraint common to all rainfed rice cultures: wetland, upland, and deepwater (O'Toole and Chang 1979). Breeding for drought resistance, a major component of the International Rice Research Institute's (IRRI) Genetic Evaluation and Utilization (GEU) Program since the early 1970s, aims at countering the adverse effects of drought in unfavoured rice production areas.

Rice germplasm has such remarkably rich diversity that a continuous spectrum of genotypes differing in the various physiological mechanisms can be found and is available for genetic manipulation (Chang et al. 1982a). However, effective evaluation methods are essential for unravelling the specific mechanism(s) involved and for devising efficient selection criteria in a breeding program. Moreover, the broad spread in growth duration among rice cultivars makes it impractical to obtain uniform evaluation of a large number of cultivars when they differ in physiological responses that are specific to certain growth stages. Methods that can accommodate large numbers are essential to breeding program.

The research being conducted at the IRRI on methodology for large-scale evaluation of drought resistance, is summarised in this chapter.

Screening Techniques

The screening techniques are related to the underlying physiological mechanisms for coping with drought stress—escape, avoidance, tolerance and recovery. These terms were defined by Sullivan et al. (1971); Chang et al. (1974); and Loresto et al. (1976).

Mass Screening

After a two year intensive study on a set of test varieties (Chang et al. 1972), a field screening method for evaluating field reactions of a large number of cultivars to drought (Chang et al. 1974; Loresto et al. 1976) was devised. Seeds of test varieties are sown in 5 m rows in granulated soil early in the year and watered well until 40 days after seeding (DAS). Then, irrigation water, applied either by surface flooding or sprinkling, is withheld for about 20 days until the plants show distinct signs of internal water stress. The symptoms range from gentle leaf rolling (and unrolling at night) to leaf-tip drying and the death of the lower leaves. Cultivars differ in the onset of leaf rolling, plasticity in rolling and unrolling, tightness of rolling, drying of leaf tips, death of lower leaves and development of new leaves. To record the visible developmental changes sequentially, a decimal scoring system has been devised. Two sets of visual scoring are used to accommodate the marked differences between traditional upland varieties and semi-dwarf lowland varieties in the mentioned changes (Loresto and Chang 1981). The stress treatment and continuous scoring usually extend over a period of 15-20 days until the soil moisture content has reached 13 per cent and is no longer differentiated by soil tensiometers. IRRI agronomists stop recording when the soil moisture tension at 20 cm depth reached 8-10 bars (De Datta and Seshu 1982). This process provides information on the responses to vegetative-phase stress.

The field is rewatered after the data have been recorded. The recovery of the stressed plants is recorded on the basis of (1) rate and degree of leaf unrolling, (2) reappearance of greenness, and (3) growth of new leaves and tillers. Again, the semi-dwarf and the lowland varieties differed in their ability to recover as compared to the traditional upland varieties (Chang et al. 1972, 1974).

Two weeks later, the plants are again subjected to stress to gain information on reproductive-phase stress responses. The susceptible varieties cease to enter reproductive phase. Other criteria used are : (1) delay in heading, compared with continuous irrigation, (2) leaf rolling and drying, (3) degree of panicle exsertion and (4) spikelet fertility. Notes are also taken on a decimal scale (Loresto and Chang 1981). Cultivars with maturities of 100 days or less, usually exsert panicles before the reproductive stage stress sets in, often escaping severe stress. Early showers in April may also delay or upset the reproductive phase test. Highly resistant cultivars at the reproductive stage are rather few (IRRI 1978; Chang et al. 1979, 1982b). However, a large number of cultivars and breeding lines (Table 1) are resistant at the vegetative stage (Chang et al. 1982b; De Datta and Seshu 1982).

Crop physiologists (IRRI) have carried out similar tests in a specially constructed greenhouse in 1 m deep soil tanks. Their findings (IRRI 1974, 1975; O'Toole and Maguling 1981) are similar to the field results. The greenhouse tests can only accommodate 1,000-3,000 accessions a year, while the field tests can screen up to 10,000 in a dry season (Chang et al. 1982b; De Datta and Seshu 1982).

Varietal differences in leaf rolling and unrolling have been shown to be correlated with the internal water status of the leaf tissue (Fig. 1) by IRRI crop physiologists. Varieties rated resistant in the field tests retain a higher leaf water potential of about —15 bars (Fig. 2) during the day than the susceptible semi-dwarfs and also regain the original level sooner than the susceptible entries in the late afternoon or early evening (IRRI 1977, 1978; O'Toole and Moya 1978; O'Toole and Cruz 1980). Our earlier studies on the root systems of different cultivars (Fig. 3) have shown that leaf-rolling behaviour is related to root length and thickness (Loresto and Chang 1971; Chang et al. 1972, 1974; IRRI 1975, 1977). Studies on rice roots inside soil boxes, by IRRI plant physiologists, have verified the positive correlation between our field screening scores (IRRI 1975, 1976) and the extent of root growth inside the soil boxes (Parao et al. 1976).

Table 1. Summary of field scores on drought resistance of 44,379 varieties and lines, IRRI plant breeding department and international rice germplasm centre, 1973-84 dry seasons

Groups	*Entries (no.)*	*Entries (no.) with given vegetative score*								
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Germplasm bank accessions[a]	25,333	96	807	2334	5103	8825	6458	1632	68	10
Dryland breeding lines	10,009	394	543	1397	2457	3416	1527	261	14	0
Wetland breeding lines	5,260	0	14	138	471	1635	1963	882	145	12
Breeding lines from other countries	2,155	93	250	316	451	542	379	87	11	6
Entries in international nurseries	479	1	1	11	40	141	166	80	4	35
Oryza glaberrima strains	1,143	16	291	109	124	322	195	68	7	11
		Entries (no.) with given reproductive score								
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
Germplasm bank accessions	7,567	12	24	249	191	738	341	2008	763	3241
Dryland breeding lines	2,879	0	1	24	16	152	151	1114	633	788
Wetland breeding lines	2,073	0	0	1	2	49	52	676	348	945
Breeding lines from other countries	596	0	0	24	21	54	53	137	26	281
Entries in international nurseries	151	0	1	2	3	8	7	60	10	60
Oryza glaberrima strains	635	0	2	132	51	49	26	100	6	269

[a] 21,000 accessions have field drought scores and recovery data in the GB file. About 4,000 accessions were either duplicates or were retested 2 to 3 times.

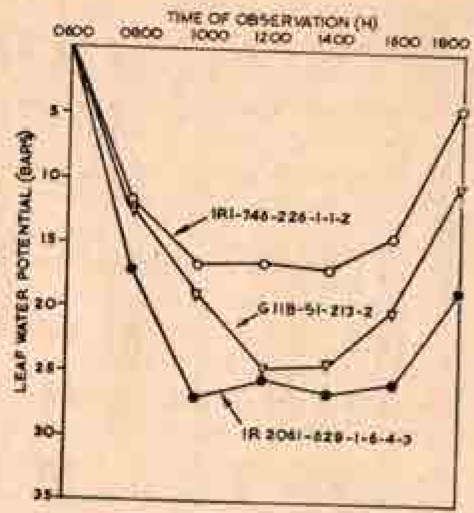


Fig. 1. Leaf water potential values through the day, of three rices, 28 March. Low-land drought screening, IRRI farm, dry season.

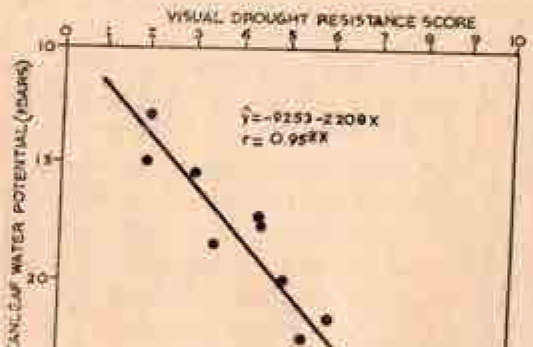


Fig. 2. Relationship between visual drought resistant score of rice varieties and the mean leaf water potential over the day. Low-land field screening, IRRI, 1977 dry season.

Leaf rolling decreases transpiration from rice leaves (O'Toole et al. 1979). Along with stomatal closure, it may also contribute to the maintenance of high leaf water potential at dawn (O'Toole and Maguling 1981). Gentle leaf rolling in response

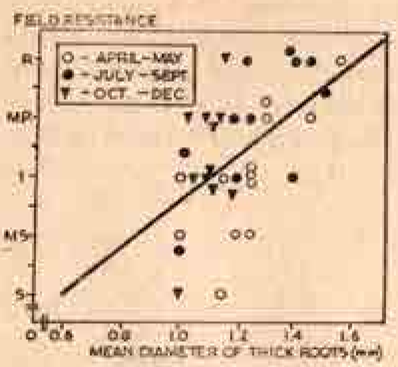


Fig. 3 Relationship between field resistance to drought (Y) and the mean diameter of thick roots (X) obtained from 35 varieties and lines in three plantings. Estimated regression line
$Y = -1.39 + 4.01\ X.$
$r = 0.5397^{**}.$

to decreasing leaf water potential is more characteristic of the traditional upland varieties which have longer leaf blades than the semi-dwarfs (Chang et al. 1974; Loresto et al. 1976). At the same leaf-rolling index, semi-dwarfs, such as IR 36 and IR 20, have lower leaf water potentials than upland varieties, such as IAC 25 and Azucena (IRRI 1984).

Line-source Sprinkler Technique

In recent years, IRRI crop physiologists have used the line-source irrigation method in the dry season to assess reproductive-stage stress reactions through comparison of grain yields in varieties of identical maturity in well-watered and stress situations (IRRI 1980, 1981; Puckridge and O'Toole 1981). The technique permits frequent sampling of leaf tissues and soil cores to obtain supplementary information on the internal water status of the plant tissues in relation to soil moisture supply and evapo-transpirational demands. It is difficult, however, to time the irrigation cycles in the stress treatment correctly because the irrigation treatments also differentially affect reproductive processes of the varieties.

The system consisted of a single line of closely spaced (6.1 m) sprinklers located across the centre of the plot and parallel to the crop-row direction. The sprinklers produce linearly decreasing amounts of applied water with distance from the line (Fig. 4). The sprinklers are pre-calibrated to determine the amount of water delivered at a given pressure and length of operating time (Puckridge and O'Toole 1981).

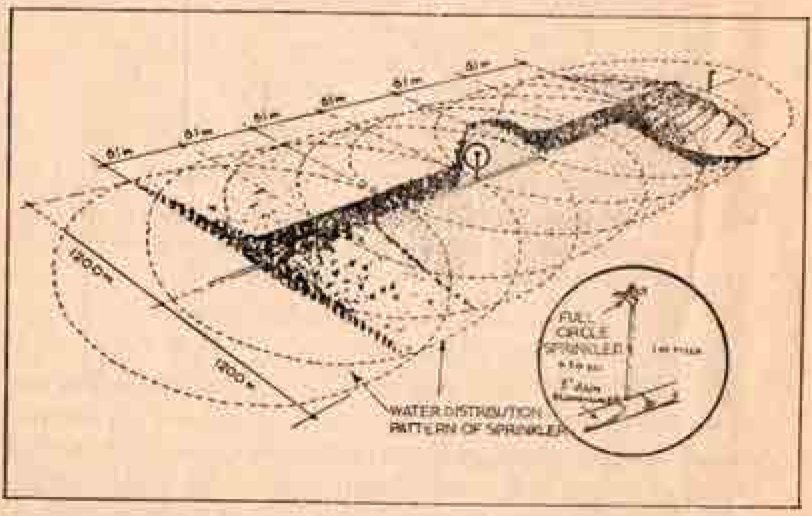


Fig. 4. Schematic representation of the line source sprinkler and crop response to the variable water supply, IRRI, 1979.

Under the system, six levels of irrigation can be simulated in an upland field of silty loam clay with level 6 as the wettest. The degree of panicle exsertion was sensitive to changes in leaf water potential and was correlated with spikelet sterility. Spikelet sterility (73 per cent) was the highest in the driest treatment (level 1) compared with 20 per cent in level 6. Spikelets of unexserted panicles were all sterile (O'Toole and Namuco 1983; Cruz and O'Toole 1984). The degree of panicle exsertion in plants subjected to water stress during flowering serves as a useful criterion for visual selection for reproductive-phase drought resistance (Chang et al. 1974; O'Toole and Namuco 1983). The system also allows an evaluation of root system and water-use efficiency of rice cultivars (IRRI 1980). A neutron probe showed that *kinandang patong* has a higher water-use efficiency than IR36 and IR20, reflecting the upland variety's more extensive root system.

It has been observed that under stressed conditions the root length and density of each cultivar was related to the leaf water potential and water extraction pattern of the cultivar (IRRI 1980; Chang et al. 1982b). The high leaf water potential of *kinandang patong* was related to its higher soil moisture extraction rate below the 60 cm depth at —25 to —40 bars. The two wetland semi-dwarfs, having very high root length densities in the upper profile, have higher water extraction rates at 60 cm depth (Chang et al. 1982b).

Toposequence

Long rows of plants are grown along a gently sloping field to evaluate the ability of different genotypes to extract soil moisture at varying distances from the water table (IRRI 1976). The technique is a forerunner of the line-source method. Because toposequence can only be carried out in the wet season, it is subject to the vicissitudes of nature and to soil erosion during torrential rains. Less than 100 varieties can be evaluated because the technique requires a field of uniform grade and fertility.

Tolerance Tests

When the root systems of different cultivars are confined to a constant volume of soil inside a large container, the ability of rice plants to withstand desiccation may be determined after the soil moisture tension has reached 16 bars or higher. Large clay pots were used to carry out desiccation tests. Seedlings of *Mimosa pudica* L. were planted along with rice plants as indicators. When the leaves of *Mimosa* plants failed to respond to physical stimulation after prolonged water stress, the rice varieties in different pots were evaluated for degree of leaf rolling, death of leaves and loss of chlorophyll (green colour). The soil moisture was replenished after 48 hours and degree of recovery was recorded. Normal colour usually returned to the leaves of cultivars with high resistance or tolerance to desiccation, 12 hours after watering. Semi-dwarfs such as TN1, IR8, and IR20 were lightly damaged and recovered fully. The reactions of traditional upland varieties ranged from significant damage and light recovery in Azucena and E425 to death of all plants in upland M1-48, Rikuto Norin 21 and Dinalaga (IRRI 1971; Chang et al. 1972).

Studies by IRRI agronomists have shown marked differences in response to severe desiccation among rice cultivars grown and stress-treated in large steel drums. Three semi-dwarfs produced more grain than an African upland variety (IRRI 1974; De Datta et al. 1975). Seedlings of many deepwater rice cultivars and lowland varieties surpassed those of the traditional upland varieties in withstanding desiccation (De Datta and O'Toole 1977; O'Toole et al. 1978).

Screening for Deep-root System

Root systems have been studied by a variety of techniques: root boxes, mylar tubes, extraction from the soil either whole or in cores, and the aeroponic technique. In the root-box technique used by the plant physiologists, the root-to-shoot ratio and the vertical distribution of roots have been compared among different varieties. The percentages of thick roots by weight and by root-to-shoot weight were also obtained. Traditional upland varieties such as OS4 have a high root-to-shoot ratio (mg/g), while the drought-susceptible variety, IR20, has a lower root. As is reflected in Fig. 3, high root-to-shoot ratios were correlated to field resistance to drought (IRRI 1975, 1980; Yoshida and Hasegawa, 1982). Deep and thick roots also enhanced the plant's ability to extract water and nitrogen from the soil strata (IRRI 1981; O'Toole 1982; Yoshida and Hasegawa 1982). Similar results were obtained with soil cores mechanically sampled from different depths. The core samples estimate root density as well as vertical and lateral root distribution. Varieties differ in their distribution patterns and density ratio, below 30 cm depth (Fig. 5). The core-sampling method, however, is laborious and time consuming (IRRI 1978).

A simple method of evaluating the root system under rainfed-wetland conditions was developed to measure the pulling force required to uproot rice seedlings 3-4 weeks after emergence (IRRI 1977). Among six varieties, the differences in the required pulling force were significant. The important characters influencing root-pulling force were related to root length, root

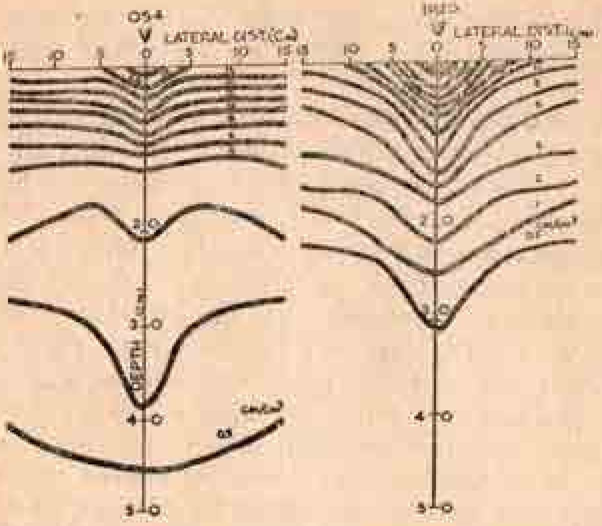


Fig. 5. Iso-root density diagram of rice varieties OS4 and IR20 grown in the field, IRRI, 1977.

weight, root number and root branching. Pulling force was negatively correlated with field drought score: resistant varieties were harder to pull than susceptible ones (O'Toole and Soemartono 1981).

The entire root system of juvenile and adult plants from the field under both dryland and wetland conditions was dug up and studied. Earlier evaluation of root characters of adult plants grown under upland field conditions showed that drought scores were associated with predominantly thick roots, dense formation of roots at the crown and deep roots (IRRI 1971). The results were the same in roots of 21-and-60-day old plants grown in a simulated upland condition in mylar tubes. The traditional upland varieties, OS4, E425, Dinalaga, Rikuto Norin 21 and Palawan, have deep and thick roots, while the semi-dwarf Taichung Native 1 and IR20 have shallow and thin roots although the roots are more numerous (Chang et al. 1974; IRRI 1975). The findings were verified by those obtained by IRRI physiologists in root boxes and in the field (IRRI 1975; Yoshida and Hasegawa, 1982). However, the above techniques are laborious, time consuming and inefficient in extracting the intact roots from the soil mass. Frequently, many rootlets are either broken during sampling or lost during removal of soil particles from the roots.

A rapid and systematic method of screening root characters using the aeroponic culture technique was adopted (Carter 1942). 11-day-old rice plants were transplanted into holders on the lid of circular drums with 97 plants to a drum. Water and plant nutrients were provided in mist form from a nozzle situated at the bottom of the 1 m deep drum. After 45 days, most of the plants had developed roots that extended to the bottom of the drum. The plants were then taken out. The shoots and the roots that remained intact were counted and measured (Armenta-Soto et al. 1981). This approach gives a comprehensive assay of the root characters (Fig. 6) and their relationship to the shoot characters and brings out marked varietal differences. This method also enables the study of inheritance of root characters in wide crosses (Armenta-Soto et al. 1983).

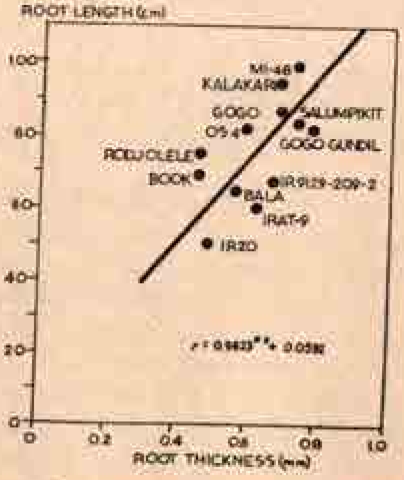


Fig. 6. Relationship between root length and root thickness in dryland, bulu, and semi-dwarf varieties. IRRI, 1981.

The technique demonstrates an advantage over root boxes or field sampling in screening a fairly large number of rice cultivars and breeding lines. The data obtained are reproducible and similar to that obtained in root boxes, field and greenhouse studies. Among the thick and deep-rooted upland varieties. Moroberekan showed a more stable growth performance, while IR20 was more stable among the shallow and thin-rooted cultivars. These two varieties, being resistant and susceptible to field drought respectively, are used as check varieties in root-characteristic evaluation (Loresto et al. 1984).

The drawback of the technique is the absence of information on root penetration, an important factor under field conditions where soil impedance prevails; the total root length in the tank may not give a true picture of rooting depth. Penetration strength is related to the ability of the rice plant to extract water and nutrients in the subsoil below the hard pan, especially in rainfed-wetland culture (Chang et al. 1982b). However, the data (Table 2) showed a high correlation between long and thick roots and field resistance to drought at both vegetative and reproductive growth stages (IRRI 1983; Loresto et al. 1984).

Table 2. Correlation coefficients between root characters and field resistance to drought at vegetative and reproductive stages of growth

	Correlation coefficient			
	Root length	*Root diameter*	*Root number*	*Root-shoot ratio*
Vegetative field reaction score*	-0.16^{ns}	-0.46^{*}	0.27^{ns}	-0.36^{ns}
Reproductive field reaction score[a]	0.54^{**}	-0.78^{**}	0.53^{**}	-0.77^{**}

[a] 1 = resistant —9 = susceptible.
*significant at 5% level of probability.
**significant at 1% level of probability.
ns—non-significant.

The drought-avoidance mechanism of field drought resistance in rice is largely manifested by deep and thick roots. In earlier studies, significant varietal differences in this mechanism were detected among two-week-old seedlings grown under two water regimes (IRRI 1971; Loresto and Chang 1971). Deep and thick roots have been used as a selection criterion in screening for drought avoidance in the early generations of breeding populations.

Seeds of F_3 or F_4 generations from bulk populations were grown in a dry aerobic seedbed during the dry season. After 21-30 days, the seedlings were gently pulled and washed. Seedlings with deep and thick root systems were selected and transplanted. The plants were grown in an intermittently irrigated culture. The F_3 and F_4 plants with improved characteristics (intermediate height, well-exserted panicles, moderately long to long panicles, and heavy grains) were bulked and grown during the wet season under upland culture without repeated selection for deep and thick roots. The F_5 and F_6 plants were further selected for root system in the next dry season, and were subsequently screened for such diseases as blast and sheath blight. Selected progenies were then screened for field resistance to drought.

It was found that when the F_2 to F_4 plants are bulked and selection for deep and thick roots is delayed until the F_5 or F_6, recovery of phenotypes with deep and thick roots and intermediate height is more probable than when the selection is carried out in the earlier generations (IRRI 1984).

Supplementary Evaluation Methods

CONSTANT WATER TABLE BOX

Plant physiologists at IRRI used a constant water table to simulate field drought conditions. The water table was kept at 45 cm below the soil surface with an open siphon. The soil water potential at 15 cm depth started to change at 40 DAS from —0.25 bar to —0.35 bar at flowering. At a depth of 30 cm, the soil water potential was kept at —0.25 bar until harvest. At 45 cm below the surface, the soil water potential was assumed to be zero. At flowering time, the soil surface was dry and the soil water potential approached the permanent wilting point (about —15 bar or lower). The roots were subjected to different degrees of water stress according to their distance from the soil surface.

Ten varieties have been evaluated for drought resistance on the basis of panicle number, panicle sterility, and grain weight. Traditional upland varieties were scored as resistant or moderately resistant. Semi-dwarfs such as IR1529-680-3 and IR20 were screened as susceptible because there was no panicle exsertion. Such findings agreed with those obtained under field screening (IRRI 1975).

LEAF AND ROOT CHARACTERS AFFECTING EVAPOTRANSPIRATION

Physiologists at IRRI have explored varietal differences in selected leaf traits that affect evapotranspiration. Leaf resistance to water-vapor transport comprises stomatal resistance and cuticular resistance. A diffusion porometer and moisture stress induction with polyethylene-glycol revealed a greater rise in stomatal resistance in the upland varieties than in the semi-dwarfs. Leaf injury levels at 50°C, and under moisture stress, were also observed to be lower in the upland varieties (IRRI 1973, 1975).

Leaf-diffusive resistance rises with soil moisture tension and the onset of the reproductive stage of growth. During the reproductive phase, most semi-dwarfs were more resistant at 10-11 bars of stress than the traditional upland varieties (IRRI 1976).

Cuticular transpiration is a major source of water loss from the plant when the stomata are closed during stress. Some traditional drought-resistant upland varieties such as Azmil, Rikuto Norin 21, and MI-48 have high cuticular resistance values while some others such as Palawan, E425, and OS4 have low values (Yoshida and de los Reyes 1976). Cuticular resistance was observed as associated with the formation of epicuticular wax, which serves as a barrier to water vapour flux. Epicuticular wax varied by as much as 500 per cent among rice varieties and showed no consistent relationship with drought resistance or site elevation at the variety's original habitat (IRRI 1977; O'Toole et al. 1979; O'Toole and Cruz 1983).

Root sections of young seedlings of different varieties varied in the diameter of main xylem vessels in the seminal roots. Dryland varieties generally have seminal roots with larger vessels than the semi-dwarf check, IR20. Nodal roots of 15-day-old seedlings showed a similar comparison (IRRI 1983). Larger vessels decrease root axial resistance to upward water transport (Passioura 1982).

CROP CANOPY TEMPERATURE

Crop physiologists at IRRI used an infrared thermometer to evaluate the canopy temperatures at the reproductive stage of 11 genotypes grown under various drought conditions. The measurements were compared with leaf water potential and root system development under a line-source sprinkler system.

There was an inverse curvilinear relationship between canopy temperature and midday leaf water potential as soil moisture progressively declined from the wettest plot to the driest. As leaf water potential ranged from —0.8 to —1.9 MPa (Megapascal), canopy temperatures ranged from 28.5 to 35°C in the wettest plot and decreased further to —3.1 MPa as canopy temperature increased to 37.5°C in the driest plot.

Canopy temperature at 50 per cent flowering was linearly related to relative spikelet sterility (r=0.79 m). There was a 0.20 per cent increase in relative sterility for every degree increase in canopy temperature. Relative spikelet sterility (stress/control) partially eliminated the high temperature effects on sterility observed even in the high-irrigation treatment.

The ability of a cultivar to satisfy evapotranspiration demand and maintain low canopy temperature and high plant water status could be attributed to its rooting behavior. Comparison of cultivars IR52 and IR36 showed that IR52 had 2°C cooler canopy temperature and higher leaf water potential than IR36. The root length density of IR52 was 24 per cent greater than that of IR36 in the upper 30 cm of soil where about 93 per cent of the total water extraction occurred (IRRI 1983).

Relative Yield Reduction under Stress

The complex end-product, grain yield, is the final manifestation of a genotype's ability to withstand drought and to recover from it after the stress is removed. The yield comparison between stressed and unstressed plants would ideally be the best indicator of varietal performance. On the other hand, such comparisons involve large investment in land and other inputs and can only accommodate a small number of varieties.

IRRI scientists have made such comparisons to: (1) arrive at an integrated interpretation of various physiologic mechanisms that interact at different growth phases, and (2) explain yield performance under different environments. Examples of such approaches may be found in Fig. 7 and the following references (Chang et al. 1974; IRRI 1977, 1979, 1980, 1981, 1982, 1983).

Different levels of panicle fertility and grain weight, obtained from various treatments, can also serve as useful criteria in varietal comparisons (IRRI 1973; Chang et al. 1974).

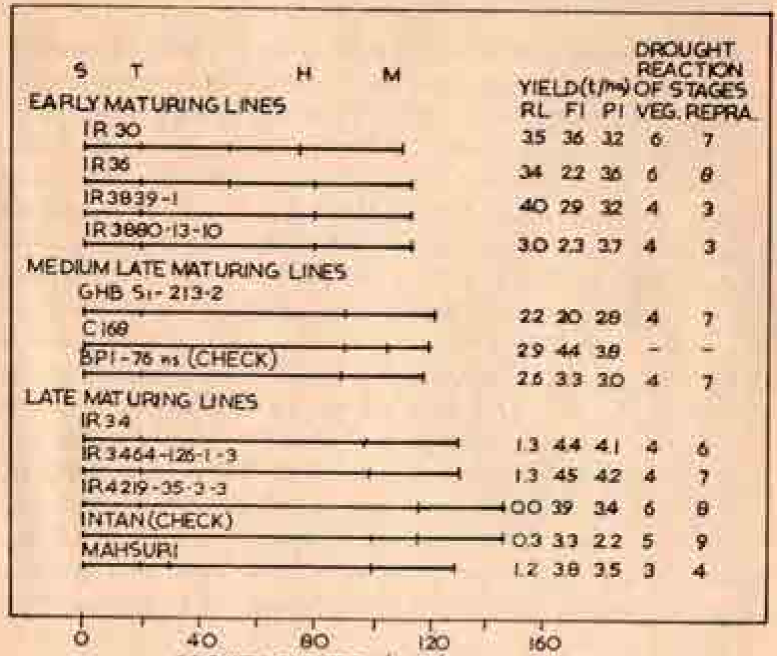


Fig. 7. Rainfall distribution, stress days, growth duration, drought reactions, and yields of 12 rices tested at Talavera, Nueva Ecija Province, Philippines, 1977 wet season. S = seedling, T = transplanting, H = heading, M = maturity, RL = rainfed-lowland, FI = fully irrigated, PI = partially irrigated.

Osmotic Regulation

Osmotic adjustment occurs in response to various environmental stresses and is manifested as the net increase in intracellular solutes (Steponkus et al. 1982). Lowering of the osmotic potential by osmotic adjustment enables the plant to maintain turgor at lower water potentials (IRRI 1980). Osmotic adjustment may postpone tissue death. Plants that can adjust osmotically will suffer less leaf tissue death than others that cannot adjust osmotically at greater plant water deficit. They, therefore, have a better chance of recovery when water becomes available.

Osmotic potential values of several rice cultivars, grown in irrigated conditions, changed from season to season; they ranged from —9.3 to —11.3 bars during the wet season and from —12.4 to —14 bars during the dry season. Osmotic adjustment in rice appeared limited to the range of 5 to 8 bars, much like that in other crop species. It results in leaf elongation (perhaps the most sensitive crop response to water deficit), continuing at more negative leaf water potential. Little difference was noted among upland rice cultivars (Steponkus et al. 1982; O'Toole 1982).

Conclusion

The complexity of the interacting factors leading to drought has defied a simplistic and linear analysis of the process or a prediction of events to follow. Under different types of rice culture (irrigated wetland, rainfed wetland, upland, and deepwater), the hydrologic, physiographic, edaphic, and climatic factors of variability further interact with the rice genotypes, agronomic practices, biotic factors, and specific growth stages of the rice plant at which water deficit occurs or is relieved. Such a complex system of interacting factors and the difficulties in dealing with the variable phenomena in a hydrophytic (semiaquatic) crop species have been pointed out (O'Toole and Chang 1979). Both location and growth stage specificity were indicated.

Our experience in the past decade has indicated that the mechanism of escape, largely represented by early maturity, is the simplest form of resistance one deals with. In fact, ancestral forms of *O. sativa* evolved during the Neothermal Period (about 10,000—15,000 years ago) as early maturing rices (Chang 1976).

Under dryland culture, the deep and thick roots of traditional upland varieties, coupled with thrifty shoot growth, enable the rice plants to complete their life cycle by drawing residual moisture from the lower soil horizons. The same avoidance mechanism operates under rainfed-wetland culture where the rainy season is short and the soil substrate permits root penetration. On the other hand, rice genotypes possessing thick and deep roots are frequently deficient in tissue tolerance or ability to recover (Chang et al. 1972, 1974; De Datta et al. 1975; O'Toole 1982). For combining both avoidance mechanism and recovery ability, we need to compromise on one of them.

Traditional lowland varieties and many semi-dwarf varieties often are tolerant to tissue desiccation. Tolerance compensates for the lack of a deep and extensive root system, though the mechanism by which it does so remains unclear. Osmotic regulation may not be a promising component of tolerance in upland varieties.

The ability of plant tissues, to recover quickly after rehydration, was overlooked by most plant physiologists in the past. During crop seasons of erratic rainfall distribution, this becomes a predominant factor in determining final grain yield (Chang et al. 1974; IRRI 1976, 1978). The semi-dwarfs are generally superior in recovery ability, whereas the upland varieties have poor recovery. However, tolerance and recovery are not necessarily correlated (IRRI 1971; Chang et al. 1972, 1974).

The foregoing generalised interpretations have led not only to a greater appreciation of the complexities underlying drought stress but also to the realisation that no single drought screening method can be applied to all situations found in farmer's fields. Moreover, screening during the wet season is subjected to the vagaries of weather, while testing in the dry season does not reveal agronomic promise in the wet season. Only in areas, such as the Llanos areas of Brazil and northcentral India, where drought frequently occurs, could the breeders depend on multi-season and multilocation testing to identify drought-resistant genotypes.

Repeated field drought tests have shown that a relatively high percentage of resistant progenies from wide crosses was obtained from those cross combinations that had at least one drought-resistant parent (Chang et al. 1982b). Establishing the heritable nature of drought resistance is essential to progress in rice breeding.

The choice of a specific screening technique or a combination of techniques, by the rice breeders and their colleagues, in crop improvement should first involve a careful study of the broad array of environmental factors which will affect the genotypes of rice to be grown. Most of the available techniques could best serve as indirect selection criteria in the quest for managing drought resistance. A resourceful breeder is one who will pragmatically adopt the appropriate techniques to suit his breeding objectives.

The preceding survey also suggests the need for further research to augment the knowledge of drought resistance of the genetically diverse rice cultigens grown under ecologically divergent cultural systems. Further understanding of the drought phenomena will also improve yield stability and efficiency in the use of water and plant nutrients.

International and inter-institutional collaboration is needed to further improve the screening techniques for location-specific applicability. It is encouraging that most of the techniques apply to both upland and shallow, rainfed-lowland cultures (Chang et al. 1979, 1982b) and the decimal scoring system has been widely adopted by the rice researchers in such studies.

REFERENCES

Armenta-Soto, J.L. P.L. Steponkus and J.C. O'Toole (1981). Aeroponic technique for root system studies of rice (*Oryza sativa* L.). *Int. Rice Res. Newslett.* 7 (1) : 22.

Armenta-Soto, J.L., T.T. Chang, G.C. Loresto and J.C. O'Toole (1983). Genetic analysis of root characters in rice (*Oryza sativa* L.). *SABRAO J.* 15: 103-116.

Carter, W.A. (1942). A method of growing plant in water vapor to facilitate examination of roots. *Phytopathology* 32: 623-625.

Chang, T.T. (1976). The rice cultures. *Philos. Trans. Roy. Soc.* London B 275: 143-157.

Chang, T.T., G.C. Loresto and O. Tagumpay (1972). Agronomic and growth characteristics of upland and lowland varieties. In: *Rice breeding*, IRRI, Los Banos, Philippines, pp. 645-661.

Chang, T.T., G.C. Loresto and C. Tagumpay (1974). Screening rice germplasm for drought resistance. *SABRAO J.* 6 : 9-16.

Chang, T.T., Boriboon Somrith and J.C. O'Toole (1979). Potential for improving drought resistance in rainfed lowland rice. In : *Rainfed lowland rice*, IRRI, Los Banos, Philippines, pp. 149-164.

Chang, T.T., C.R. Adair and T.R. Johnston (1982a). The conservation and use of rice genetic resources. *Adv. Agron.* 35: 37-91.

Chang, T.T., G.C. Loresto, J.C. O'Toole and J.L. Armenta-Soto (1982b). Strategy and methodology of breeding rice for drought-prone areas. In : *Drought resistance in crops with emphasis on rice*. IRRI, Los Banos, Philippines, pp. 217-244.

Cruz, R.T. and J.C. O'Toole. 1984). Dryland response to an irrigation gradient at flowering stage. *Agron. J.* 76: 178-183.

De Datta, S.K. and J.C. O'Toole (1977). Screening deepwater rices for drought tolerance. *Proc. Deepwater Rice Workshop*, 1976, IRRI, Los Banos, Philippines, pp. 83-92.

De Datta, S.K. and D.V. Seshu (1982). Evaluating rices for drought tolerance using field screening and multilocation testing. In : *Drought resistance in crops with emphasis on rice*, op. cit., pp. 245-263.

De Datta, S.K., T.T. Chang and S. Yoshida (1975). Drought tolerance in upland rice. In : *Major research in upland rice*. IRRI, Los Banos, Philippines, pp. 101-116.

IRRI (1971). Annual report for 1970. IRRI, Los Banos, Philippines, p. 265.

IRRI (1973). Annual report for 1972. Ibid., p. 246.

IRRI (1974). Annual report for 1973. Ibid., p. 266.

IRRI (1975). Annual report for 1974. Ibid., p. 384.

IRRI (1976). Annual report for 1975. Ibid., p. 479.

IRRI (1977). Annual report for 1976. Ibid., p. 418.

IRRI (1978). Annual report for 1977. Ibid., p. 548.

IRRI (1980). Annual report for 1979. Ibid., p. 538.

IRRI (1981). Annual report for 1980. Ibid., p. 467.

IRRI (1983). Annual report for 1982. Ibid., p. 532.

IRRI (1984). Annual report for 1983. Ibid., p. 494.

Loresto, G.C. and T.T. Chang (1971). Root development of rice varieties under different soil moisture conditions. *Proc. Second Annual Scientific Meeting*, May 4-6, Crop Sci. Soc. of the Philippines, Los Banos, Philippines, pp. 412-416.

Loresto, G.C. and T.T. Chang (1981). Decimal scoring systems for drought reaction and recovery ability in rice screening nurseries. *Int. Rice Res. Newslett.* 6 (2): 9-10.

Loresto, G.C., T.T. Chang and O. Tagumpay (1976). Field evaluation and breeding for drought resistance. *Phil. J. Crop Sci.* 1 (1): 36-39.

Loresto, G.C., W.X. Zhang, D. Chaudhary and T.T. Chang (1984). Aeroponic technique for screening the drought avoidance mechanism of rice genotypes by the root characters. In : *Serie de Estudos Agronomicos*, Vol. 1984, Ed. Garcia de Orta, Instituto de Investigacao Cientifica Tropical, Libson, Portugal (in press).

O'Toole, J.C. (1982). Adaptation of rice to drought-prone environments. In : *Drought resistance in crops with emphasis on rice*. op. cit , pp. 195-213.

O'Toole, J.C. and T.T. Chang (1979). Drought resistance in cereals—Rice: a case study. In : *Stress physiology of crop plants*. op. cit., pp. 373-405.

O'Toole, J.C. and R.T. Cruz (1980). Response of leaf water potential, stomatal resistance and leaf rolling to water stress. *Plant Physiol.* 63: 428-432.

O'Toole, J.C. and R T. Cruz (1983). Genotypic variation in epicuticular wax of rice. *Crop Sci.* 23: 392-394.

O'Toole, J.C. and M.A. Maguling (1981). Greenhouse selection for drought resistance in rice. *Crop Sci.* 21: 325-327.

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

O'Toole, J.C. and O.S. Namuco (1983). Role of panicle exsertion in water stress induced sterility. *Crop. Sci.* 23: 1093-1097.

O'Toole, J.C. and Soemartono (1981). Evaluation of a simple technique for characterizing rice root systems in relation to drought resistance. *Euphytica* 30: 283-290.

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

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

Parao, F.T., E. Paningbatan and S. Yoshida (1976). Drought resistance of rice varieties in relation to their root growth. *Phil. J. Crop Sci.* 1 (1): 53-55.

Passioura, J.B. (1982). The role of root system characteristics in the drought resistance of crop plants. In : *Drought resistance in crops with emphasis on rice.* op. cit., pp. 71-82.

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

Steponkus, P.L., K.M. Shahan and J.W. Cutler (1982). Osmotic adjustment in rice. In : *Drought resistance in crops with emphasis on rice.* op. cit., pp. 181-194.

Sullivan, C.Y., F. Yoshikawa, J.D. Eastin, W.M. Ross, M.D. Clegg, J.W. Maranville and A.L. Hollister (1971). Sorghum drought and heat resistance. In: *Research in physiology of yield and management of sorghum in relation to genetic improvement.* Annual Report No. 5, University of Nebraska, Crop Research Division of ARS/USDA and the Rockefeller Foundation, pp. 9-23.

Yoshida, S. and E. de los Reyes (1976). Leaf cuticular resistance of rice varieties. *Soil Sci. Plant Nutr.* 22 (1): 95-98.

Yoshida, S. and S. Hasegawa (1982). The rice root system: Its development and function. In : *Drought resistance in crops with emphasis on rice.* op. cit., pp. 97-114.

Index

The Authors

Dr. I.P. Abrol
Director
Central Soil Salinity Research Institute
Karnal 132 001
Haryana

Dr. T.T. Chang
International Rice Research Institute
P.O. Box 933
Manila
Philippines

Dr. R.S. Paroda
Director
National Bureau of Plant Genetic Resources
Pusa Complex
New Delhi 110 012

Prof. R.S. Rana
Professor of Eminence
Central Soil Salinity Research Institute
Karnal 132 001
Haryana

Dr. S.K. Sinha
Professor of Eminence
Water Technology Centre
Indian Agricultural Research Institute
New Delhi 110 012