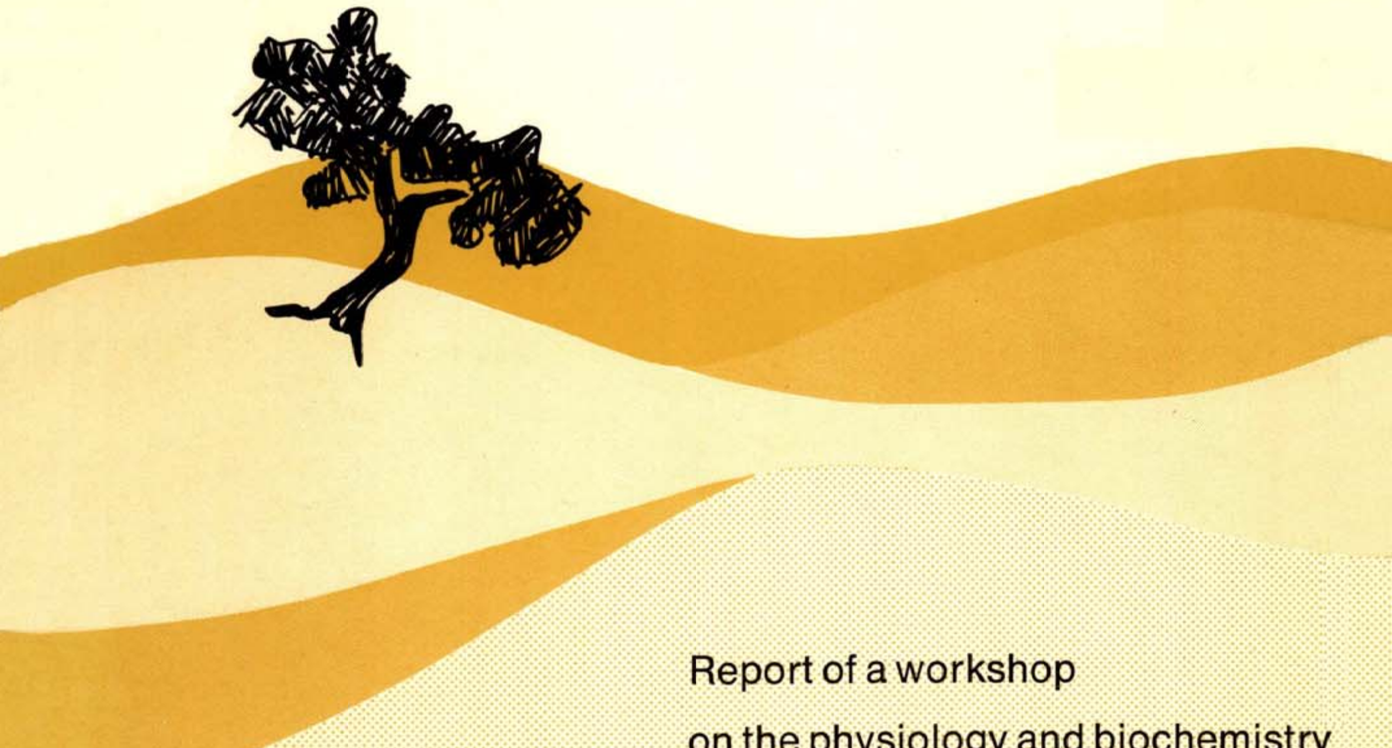
IDRC-026e

FOOD CROP RESEARCH FOR THE SEMI-ARID TROPICS



Report of a workshop
on the physiology and biochemistry
of drought resistance and
its application to breeding
productive plant varieties
University of Saskatchewan,
Saskatoon, Canada,
22-24 March 1973

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Abstract

A workshop was convened by IDRC at the University of Saskatchewan, Saskatoon, to consider the long-term fundamental research needed to develop a more productive agriculture for the semi-arid tropics, which include large parts of Africa and Central and South America, most of India, and part of Australia. Six research topics were suggested as priorities: hormonal interactions, root/shoot translocation, morphology, growth-stage response to specific environmental characteristics, stress resistance of different tissues, and simulation modelling. The International Crop Research Institute for the Semi-Arid Tropics in Hyderabad, India, which concentrates on the food crops sorghum, pennisetum millet, chickpea, and pigeon pea, is likely to act as the focal point for this research, which should be done under differing environmental conditions.

Résumé

Sous l'égide du CRDI, un colloque fut tenu à l'Université de la Saskatchewan, à Saskatoon, sur les recherches fondamentales à long terme nécessaires à l'amélioration de la productivité de l'agriculture dans les régions tropicales semi-arides; ces dernières englobent des zones étendues de l'Afrique, de l'Amérique centrale et du sud, la quasi-totalité de l'Inde, et une partie de l'Australie. Les priorités suggérées correspondent à six domaines de recherche: intéractions hormonales, translocation racine/tige, morphologie, réponse du stade de la croissance aux caractéristiques écologiques spécifiques, résistance des différents tissus aux traumatismes, et modèles de simulation. C'est l'Institut International de Recherches sur les Cultures dans les Régions Tropicales Semi-arides, à Haïdarabad, en Inde (qui s'occupe essentiellement de cultures vivrières: sorgho, mil chandelle, poischiche, et pois cajan) qui sera vraisemblablement l'élément moteur de ces recherches qui devraient être entreprises dans les conditions de divers environnements.

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Food Crop Research for the Semi-Arid Tropics

Report of a workshop on the physiology and biochemistry of drought resistance and its application to breeding productive plant varieties, University of Saskatchewan, Saskatoon, Canada, 22-24 March 1973

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Foreword

Though millions of people live on subsistence farming in areas prone to drought — areas like the Sahelian zone, so tragically stricken in the last few years — comparatively little research has been done on the crops that can be grown there. The tremendous improvements in agriculture that will be needed if there is to be any chance of warding off famine and overcoming malnutrition in these regions can only be achieved by an international effort. IDRC, in its Agriculture, Food and Nutrition Sciences program, is paying particular attention to the problems of the semi-arid tropics, and, in association with other donor agencies, is supporting a new international agricultural research institute — ICRISAT, the International Crops Research Institute for the Semi-Arid Tropics — that will seek to improve the crops of the semi-arid tropics in cooperation with other research institutes in other parts of the world.

Breeding improved crop varieties must ultimately be based upon a fundamental understanding of how plants survive drought conditions. To suggest promising directions for this long-term research, IDRC called together a small group of experts, who met informally at the University of Saskatchewan, under the leadership of Dr Graham Simpson.

Their discussions are recorded here, together with their recommendations, at least one of which has already led to a research project funded by IDRC. This report, after being circulated to all the participants for final comment, is being published and widely distributed in the hope that other funding agencies and research institutions will take up some of the challenges it contains.

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Introduction

The International Development Research Centre (IDRC) has devoted a major portion of its agricultural budget to research in the semi-arid tropics. In these regions, evapotranspiration exceeds rainfall for 5-10 months of the year, and the rainfall is often erratic. The regions include large parts of Africa and Central and South America, most of India, and part of Australia. Similar conditions are also found outside the tropics in the Middle East and parts of Central Asia. The major problem of the crops of rain-fed agriculture in these regions is stress, arising directly from water shortage and from compounding effects such as high temperatures in the aerial parts of the plant. Many millions of the people living in these regions are subsistence farmers, whose only agricultural input is their own labour, and who develop virtually no surpluses to generate cash. Many of these people and their families are malnourished.

The steps necessary to generate a more productive agriculture, and so to bring the benefits of the green revolution to these people, are: (1) improvement of the crop varieties grown, so that they will yield better under adverse conditions; (2) improvement of the methodology of the agricultural systems; (3) adoption by the farmers of the improved varieties and agricultural methods, with adequate support from governmental and other agencies. Surpluses can then be developed that will pay for more agronomic inputs, thereby initiating a continued improvement in the standard of living.

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) was established in 1972 in Hyderabad, India, to tackle major problems of crop and farming systems improvement in these regions. The effective implementation of the three steps listed above cannot be done at any single centre, but requires a network of activity throughout the semi-arid tropics, with the closest possible links between the farmer and the local research terminal. IDRC has an abiding interest in all aspects of this network, but especially in seeing that the links between scientist and small farmer are made as effective as local circumstances permit.

This workshop was assembled by IDRC to examine some of the more fundamental and long-range problems of basic research during the next 15 or 20 years that could be of practical value in breeding improved crops for semi-arid regions. The participants were asked to consider drought stress and to suggest:

(1) what specific problems need to be tackled;
(2) how these problems should be handled;
(3) the staff required;
(4) the time scales involved.

A workshop was chosen to facilitate a free exchange of tentative findings, suggestions, and scientific information. The discussions focussed on the practical needs of, and the limitations in, developing countries. Methods or varieties requiring expensive agronomic inputs, which therefore could be totally unsuitable in some parts of the third world, were not considered.

Environment — General And Specific

Unpredictable rainfall, together with scanty reserves of soil moisture, present serious obstacles to agricultural development in the semi-arid tropics. After all forseeable irrigation resources have been developed, over 60% of these land areas will still have to rely upon precipitation alone. Reliable though infrequent rainfall is a lesser problem, as crop varieties can be developed whose maturity length takes advantage of the water when it is there.

In addition to rainfall, altitude and temperature may also be important. Though widespread frost is not usual in the regions of interest, cold weather may be serious at the start of the growing season. Productivity may also be reduced if flowering and ripening have to take place at higher than optimum temperatures. The whole range of precipitation and temperature conditions had to be considered in the discussions of general problems. Specific stress patterns, whether they be due to water, temperature, or other factors, can be defined only for specific locations, and probably only for

specific crops. Growers worry about a particular crop in a particular place, and the varieties they grow there reflect particular environmental conditions.

Varietal breeding needs a well-defined environment. Controlled experiments in sophisticated growth chambers are useful in exploratory research, but new crop varieties must yield under actual conditions from year to year if they are to benefit farmers of the semi-arid regions. The climatic data recorded by many meteorological services are often average figures that do not reveal transient extremes. Small transient stresses, however, particularly those occurring at sensitive growth stages such as anthesis, can be especially serious and may cause marked reductions in yield. The microclimate in the particular location of the field experiment must be known in detail: photosynthetically active and total radiation, precipitation, soil moisture tension, evapotranspiration, winds, and extremes of hot and cold, as well as the probability of occurrence and the ways they interact. These data can now be recorded by inexpensive instruments and should be regarded as essential to all the other research topics discussed. Conversely, research projects should indicate what environmental data are needed for particular stages of plant growth.

It was impossible to discuss environmental conditions without, at the same time, considering their effects, that is, particular stresses on particular crops. Unfavourable conditions cause different stresses in different species at different times in the life cycle; if favourable conditions occur at an unsuitable time for existing crops, new crops could perhaps be developed to match them. To be able to manipulate all the variables, it is necessary to know more about stress in general.

Water Stress and Its Relationship to Other Stresses

Difficult climatic conditions do not necessarily create stresses within all plants. One species may be under stress while another is not; a particular measured value may have serious implications for wheat and be of no consequence for the creosote bush.

Resistances to stresses of different types may be related and common factors of stress-control systems could be sought for particular growth stages of a plant. For example, a frost-hardy plant may also be drought-resistant; thus, frost-hardiness, which is critical in wheat during ear development, could well be compared with water-stress resistance in different varieties of wheat at similar stages of development. Stresses of different types produce similar effects. In barley, for example, different stresses produce similar changes in the relative levels of endogenous growth regulators and in transpiration. Conditioning of tobacco to a nutritional stress produces resistance to an aeration stress. There is evidence that if a plant acquires greater efficiency for water use, it also develops tolerance to other environmental stresses. This interrelationship suggests that crops could be hardened to drought by subjecting them to other types of stress, which experimentally may be more easily applied.

The yield of a crop is the integrated result of all the influences acting upon it since germination. It is thus important to know what stresses a plant has experienced throughout its life. In some varieties, early season growth and storage of photosynthate can compensate for damage to the photosynthetic system in late season droughts; these varieties may then produce the same yield as varieties that actively photosynthesize for a longer duration. By competition experiments with limited amounts of water, plants can be evaluated as to their ability to adapt to stress. Plants and varieties that do not adapt easily to stress grow actively when conditions are good, but poor conditions bring disaster; conversely, varieties that are highly adaptable to stress are able to grow more slowly as stress develops. Whether adaptable varieties, in fact, store some hardiness factor is not known, and though such parameters as plant water potential may have been estimated in such experiments, they have not been widely measured.

The range of plant water potential experienced by a plant throughout its growth period may give an integrated measure of the effects of radiation, precipitation, and other factors contributing to stress. This water potential range could then be related to productivity, and could be used to describe crop and environment together — the range of water potential expe-

rienced by a particular crop in a particular region over a period of years. Caution is needed, however, in extrapolating from one species to another or even from one variety to another.

The value of plant water potential measurements must be considered in the context of secondary changes, however. Hormone levels, for example, affect stomatal closure and transpiration ratios, which in turn will alter patterns of growth. There is a debate in the literature on the value of transpiration ratio (water used per unit of dry matter produced) as a measure of plant water use. The original plotting of transpiration ratio directly against evapotranspiration produced an unacceptable scatter of data points. Plotting the same data as dry matter production against water used per unit evapotranspiration minimizes statistical errors and produces a smooth curve for each species. The results show that for the same species grown in widely different conditions around the world, vegetative growth is proportional to the amount of transpiration that actually occurs. This could be used as a selection criterion for growth efficiency, but the results have not been related to productivity, and again, information is needed on actual plant water potentials. The close relationship between growth and transpiration may obtain in moderate stress conditions. Under severe stress, however, there are distinct differences in dehydration hardiness between species and cultivars, that are not indicated and that are important for yield.

Little is known about hardening responses or about stress control mechanisms. A plant may avoid water stress by keeping its water potential constant; it may resist water stress by functioning over a wide range of water potential. The plant's metabolic response under stress is a related factor, which also requires much research. A rapid drop in nitrate reductase activity, for example, is a good indication that irrigation may be needed. There is some indication in the literature that stress leads to accumulation of sugars, which may be due to a greater reduction in growth than in photosynthesis, or possibly to increased breakdown of polysaccharides. Stress also hinders the transfer of assimilates into the vascular system, but, even in the absence of stress, too little is known about the metabolism of assimilates, their storage, and the transport of sugars from the chloroplasts to the veins in the leaf.

One stress may also create another; thus, stomatal closure decreases transpiration cooling and increases leaf temperatures. Stress interrelationships are complicated and it is difficult to separate cause and effect. Repeated attempts by participants to define stress and its relationship to particular crops and environments clearly indicate the need for much more research in this area.

Choice of Crops

Many plant species are adapted to semi-arid conditions and several are farmed successfully, except for sorghum, however, not much research has been done on any of the food crops at present considered suitable for the semi-arid tropics. To increase the chances of making substantial improvements to harvests, attention must be focussed on only a few; too wide a view would entail a serious risk of achieving nothing. Therefore an attempt was made to choose suitable crops for further study and to relate stress to them.

Various criteria were established. The paramount consideration is that a plant must be productive. Sheer survival may make a plant successful in natural selection, but the plant will nevertheless be useless as a food crop if it does not ensure a harvest.

Each crop must also be considered against the total agriculture of a region — the range of crops available, possible cropping systems, local farming practices, the regional economy, educational levels, tradition, customs, and diets. Only then can one consider whether an existing crop should be improved or another introduced. New crops have sometimes brought about radical changes in diets and economies, but local populations have also rejected new crops despite their technical or dietary advantages. When distribution facilities are poor, Western-type monocultures must also be suspect. Local pictures of dietary needs and balances change completely when intercropping or multiple cropping are considered, so that dietary deficiencies resulting from one crop can be made up from another.

Food crops were concentrated on; oil crops were considered less important though some may also be protein sources; fibre crops and others were not discussed. The crops of prime concern to ICRISAT are the sorghums (*Sorghum* spp.), pennisetum millet (*Pennisetum typhoides*), pigeon pea (*Cajanus cajan*), and chickpea (*Cicer arietinum*), sorghum being the most important. On these four crops alone much work is needed in many geographic areas. It is dangerous to extrapolate results from one species to another, as growth mechanisms may be different; yet it will be necessary to generalize, for example, within the monocotyledons or within the legumes, if the immense amount of work needed is to be reduced to a manageable size.

Though importance to human well-being must be the prime concern of any research program, research needs results on which to build if it is to thrive. Fundamental research should not be concentrated completely on one species, which may eventually prove to have been an unfortunate choice for experimentation. At least two initial species are needed for insurance and also to test the generality of principles established with one. But the first choice is very important, as success will encourage the undertaking of related projects.

The crops listed above are, in fact, already grown in semi-arid regions, and are all important in human nutrition. The consensus was that the initial choice of crop for study depended upon IDRC or other funding agencies, who would take into account need, economics, diseases, and other factors outside the scope of the workshop. Nevertheless, sorghum was favoured, presently the most important crop in the semi-arid tropics and a crop on which some work has been done. Chickpea should probably then be the second crop for study, with subsidiary work on others as necessary to test principles.

Components of Yield

Certain stages in a crop's development are most important for an economic yield. If these stages are sensitive to stress, prevention of stress at certain times may be crucial. Knowledge of all the factors contributing to yield in a particular species would help both in fundamental investigations of stress and in breeding programs.

Pollination is obviously essential for a seed crop, but is not for some root crops. To take a more complicated example, yield in sorghum depends, among other things, on two related factors: grain number and grain size. Grain number is decided early in the season at a time when there may be stiff competition between the fast-growing vegetative parts and the panicle, which bears the flowers. Water stress at that time may result in fewer grains per head. If the water stress continues into the grain-filling period, the yield will be low. If, on the other hand, grain-filling occurs without stress, a large grain size may partially compensate for a smaller grain number. In sorghum, most improvements in yield have resulted from increases in grain number rather than grain size. Interaction between grains may influence the final yield and has been investigated in wheat by experiments in which some set grains are removed from the head.

Procedures are now available to determine the length of grain-filling period in sorghum and maize. Hence it is possible to field-check the degree of association between yield and deviation of grain-filling period for a range of genotypes in different environments. With such information, along with yield component data, something can then be deduced regarding the relative importance of length of the grain production period and the efficiency of grain dry matter accumulation in specific environments. Such knowledge would help in deciding whether to concentrate research on morphological and physiological factors relating primarily to the length of grain filling, or on efficiency of grain formation, or on both, as they dictate or limit grain yield in some given environment.

However, the factors indentified and selected for in plant breeding may be important only with respect to the genetic makeup of a particular variety. In other genotypes, they may have no marked effects on yield.

Plant Breeding Problems

Not only is the physiology of stress in plants poorly understood, but there is also a gulf between understanding stress and using that understanding to obtain high yields in food crops under stress conditions. As yield is an integrated consequence of all factors throughout the growth period, plant breeders, lacking clear guidance from plant physiologists, can at present only use a high yield in field experiments as a criterion for selection.

A systematic program for breeding better-yielding varieties must be carried out on a large scale and over a period as long as 20-30 years. It involves four main steps: (1) the factors on which yield depends must be identified, often in the face of differing interpretations of the data and no proper understanding of causal relationships; (2) the genetic variability of these factors must then be determined, and for this the breeder needs suitable methods; (3) the heritability of each factor must next be ascertained, so that selection can be continued through several generations; (4) finally, the factors that are confirmed as important for yield must be combined into new varieties.

Drought avoidance and desiccation tolerance traits depend upon many genes; screening techniques may therefore be very hard to find. For a problem as complex as drought behaviour, large numbers of segregating progenies will be involved, and from these, promising single plants will have to be selected (or at best a very few plants). Even then the job may be too large to complete in a reasonable time, unless rapid screening techniques can be developed. What is needed is some sort of "handle" for the breeder to grasp when large segregating populations are screened — preferably some morphological marker of resistance, but failing that, some property that can be measured rapidly. Though one test could have its dangers, such as overlooking photosynthetic material stored early in growth, the geneticists would welcome even rough methods of excluding the 95% of the progenies with the worst potential, so that they could concentrate in much more detail on the most promising 5%. One test may not in fact be possible as different effects will be important at different stages of growth; on the other hand, if a series of tests takes as long as field tests of yield, little will be gained.

The hazards of breeding from too narrow a gene base are widely recognized. Within a broad gene base, a wider variety of characteristics is available; hence, the chances of finding alternative desirable properties are greater, and the necessity of breeding one "super" variety eliminated. Growing the same variety over a large area could lead to catastrophic outbreaks of new diseases or pests.

In view of the very long time scale likely to be involved in building drought-resistance characteristics into lines, it may be more rewarding to adopt a more traditional approach to improving world yields rapidly. Significant progress in breeding better-yielding varieties may come easily in first adapting a crop to a specific environment. If cross-pollinated plants were available, or if self-pollinated crops could be made to cross-pollinate, then large populations with a broad range of variability could be used instead of populations derived from a few deliberate crosses. A few lines could be selected as parents on the basis of yield over 5 years, then a selection pressure applied by withholding irrigation to shift the mean characteristics of the population gradually in the desired direction, in this case high yield in drought conditions. This experiment could be performed in many different locations around the world, backed up by suitable physical or biochemical measurements. Mutually exclusive characteristics might be selected in different places, and for this reason several separate populations would have to be maintained in each location. This procedure has been successfully applied to improving the oil production of sunflowers, where a single assay of oil content was performed on seeds of 80,000 plants a year.

Drought resistance is a much more complicated problem than selection for oil content, as no single criterion of drought resistance can at present be determined by a simple analysis. The problem of how to aid the plant breeder in his task was discussed repeatedly. To create variability, he has to make many crosses, but as a result it is even more difficult to identify the individual plants that are promising. Few aids to plant breeding could be suggested, however. The breakthroughs leading to a new order of yield in crop production in the semi-arid tropics will most likely come from a long-term team effort of breeders and physiologists where both are involved directly in the experiments, evaluation, and decision-making at every step of the process.

Hormonal Mechanisms Related to Stress

Many hormones have now been identified that are active in the control of plant growth. Little is known, however, about specific hormonal interactions and the mechanisms of hormonal plant growth regulation. As one hormone can influence the synthesis or destruction of another, it is difficult in this research to separate cause and effect. Nevertheless, some hormonal influence upon stress-control mechanisms is already apparent. In different varieties that can withstand different amounts of water stress, different levels of endogenous abscisic acid and cytokinins are found, and perhaps some endogenous hormone levels could be a measure of plant water use. To aid selection and breeding, hormone applications might also be used to manipulate varietal properties, confer hardiness, or simulate stress.

The following two examples of hormonal effects on water-stress reactions indicate how little is known about the way they work.

(1) Abscisic acid closes the stomata. In well-watered dwarf beans, an evaporation stress causes rapid wilting but increases the level of abscisic acid in the leaf. The resulting stomatal closure enables the plant to regain turgor, and it is then conditioned to water stress. The abscisic acid produced in this way is partly converted to its glucose ester and an equilibrium between these two substances is established. In this way, abscisic acid may be slowly released again, maintaining an abnormally high level in the tissues and consequently keeping the stomata closed. These effects are not limited to this species; they also occur with wheat, cotton, pea, Brussels sprout, and tomato seedlings. Simultaneous stomatal closure and increases in abscisic acid level have also been demonstrated when dwarf bean, wheat, and tomato seedlings are subjected to other types of physiological stress.

(2) Cytokinins are formed predominantly in the growing primordia of roots or flowering parts (but apparently not in leaves), and so are

controlled by conditions that affect new growth. They open the stomata, and are found at high levels in wilty tomato mutants, which contain little or no abscisic acid and thus cannot close stomata. Cytokinins also delay senescence and maintain protein synthesis in barley, wheat, lettuce, and other plants. A stressed plant may be considered as undergoing enhanced senescence as shown by protein synthesis and proteolysis, RNA degradation, translocation, growth, root/shoot relationships, respiration, and transpiration. Stress reduces cytokinin levels and the addition of cytokinins removes stress symptoms. Thus, stress is correlated with decreased synthesis, increased destruction, and decreased translocation of cytokinins.

Although discussion centred on abscisic acid and the cytokinins, many other plant regulators, such as the gibberellins and auxins, are also important and must be considered in relation to stress.

Artificial growth retardants, which produce such effects as thicker leaves and possibly more efficient use of water, may act by interfering with the balance of endogenous hormones. Some of the early synthetic growth retardants proved to be phytotoxic when applied to certain plants and few were equally effective in dwarfing a range of crop plants. However, new retardants are now being synthesized and recently the results of tests with a very promising group of compounds based on β-ionone have been published. Synthesis of all these growth regulators involves a complex series of chemical reactions, but nevertheless the prices are becoming low enough for them to be used in field experiments. This opens the possibility of eventually hardening entire crops by artificial means.

Morphology

Plant morphology was discussed in two contexts — the usefulness in plant breeding programs of some obvious indicator of a drought-resistance trait, and conversely, the enhancement of drought resistance by breeding in some favourable morphological characteristic. These could be different aspects of the same phenomenon; the desirable characteristic may or may not also be useful as an indicator.

Little is known about the relationship between plant water use and such factors as leaf shape, size and number, cuticle thickness, stomatal number, waxy coverings, or the number of vascular bundles. In several species, mutants are known with particular morphological features, which, however, probably result from the interaction of many genes. Some of these features, such as the production of leaf surface lipids in stress-resistant maize varieties, are connected with hardiness. This suggests that, in the absence of clear visual markers, rapid chemical or physical tests could be developed once the connection with drought resistance had been clarified.

Morphological changes could be promoted to help a plant conserve water. Experiments on wheat in special deep pots have shown that a two-part root system can assure grain production under variable conditions. One part spreads shallowly to collect subsurface water for rapid

growth, but when water becomes scarce may be useless and die. The second part has limited xylem development and goes deeper; under favourable conditions it takes up water relatively slowly, but during droughts it is available to scavenge enough water from deeper down to provide for growth. Other morphological characteristics, such as leaf-rolling when water is scarce, or roots that continue to grow after shoot growth has been stopped, could perhaps be developed to enable plants to find or conserve water, first in experimental pots, later in the field.

Translocation and Root/Shoot Relationships

Different parts of a plant may respond differently to the same stress. In wheat, for example, the flag leaf wilts under water stress and photosynthesis in it slows down, whereas in the glumes photosynthesis continues at a high rate. Some varieties of sorghum ensure grain production by translocating matter into the head even at the expense of the rest of the plant; if stress is sufficient to kill the head, however, the plant dies. In other varieties, the head or part of the head may die when stressed but the root system is kept alive and when growth is renewed, it occurs by tillering.

Defoliation, leaf shading, and isotopic tracer experiments show that in wheat, material photosynthesized in the flag leaf tends to be translocated to the head, whereas material from the other leaves is translocated downwards. In sorghum, the top four leaves are involved in head filling. As already mentioned, storage of photosynthetic material at the start of the growth season may compensate for reduced photosynthetic capacity later. Storage and translocation appear to be relatively insensitive to stress, but the processes of storing material and translocating it later for grain production involve some loss compared with immediate use of the material. For a reliable yield, therefore, it may be better to use slow-growing varieties with greater storage, so that stored material can be drawn upon at a more difficult part of the season.

The control of translocation is related to growth or cessation of growth in the parts of the plant where growth regulators are formed. Maintenance of the transport system may be dependent on hormone production. Under stress, the shoot may stop growing before the root. Continued root growth, however, is important both for scavenging water and nutrients and for producing root hormones. Very little work has been done on roots compared with shoots, and the difficulty of discussing root hormonal effects indicates the attention they should receive as research topics.

Plant Simulation Models

One area in which advances are likely to be made in the next 20 years is the use of computers to simulate plant growth. The method documents available data and evaluates their interaction, aiming at a total understanding of the relationships within the plant. The data are chosen for a specified relaxation time so that events occurring over a shorter period are automatically integrated into the model. Though many generalized models exist, to our knowledge only two advanced models have been developed so far, one for wheat, in which importance has been given to certain parameters, and one for corn, which takes all parameters into account without preference. Each gives satisfactory predictions of yield (dry matter or grain) under optimum conditions, and one is now being extended to include drought phenomena.

Even a rough model incorporating water stress could indicate where further laboratory and field research are needed, and so modelling should receive some priority. A successful model could stimulate collecting the vast amount of data needed for breeding drought-resistant varieties and quickly analyze it. The ideal would enable a plant to be "grown" through a season in a few minutes of computer time, and then "regrown" after a one-gene change. Modelling is a long way from such perfection, however, and neither of the existing advanced models is used presently by plant breeders. Although breeders have some mental model to guide their choices, much closer communication with them will be necessary if they are to take advantage of computer simulation. No model has yet been tried for sorghum or other crops of the semi-arid areas. Initially, the corn or wheat models could be used and gradually adapted as the specific data for sorghum are collected from growth chamber and other experiments.

Suggested Projects

Many of the subjects discussed impinged upon each other. Nevertheless, several long-term research projects were suggested and also several breeding techniques that might be developed from them. No order of priorities was set, as some could be carried out together or as part of much more comprehensive projects that might include large breeding programs. An additional topic, which is not a project in itself but which lies behind almost all the others, is the need to obtain microclimatological data so that the conditions of the experiments, particularly field experiments, can be closely defined.

For some of the projects, staff and time can be estimated. There was a strong feeling, however, that fewer people working over a longer period would be more effective in the long run than a massive attack on any one problem. This would be so especially if much better contact through meetings, workshops, or even international telephone calls could be maintained among the various individuals and teams working in related areas.

Fundamental Research

Hormonal Interactions in the Control of Stress Phenomena in Intact Crop Plants This work should be aimed eventually at productivity. It could concentrate, for example, on the hormonal relationships behind the development of the sorghum head, or the control of the sorghum dark layer formation. However, not much is known about when and where hormones are produced within a plant and where they act, either during normal growth or under stress. Studies are needed to identify both the sites of production and the action of specific hormones, which would necessitate an examination of the action of applied hormones and an assay of tissue extracts for endogenous growth substances. Detailed work should concentrate on the action of particular hormones on key production mechanisms such as photosynthesis or interaction between developing organs (dominance). The project would involve three scientists (biochemists and plant physiologists) supported by three technicians for a period of 5 years.

Subsidiary projects involving hormone studies could include selecting germ plasm for breeding purposes, shifting from determinate to indeterminate growth, making self-pollinating crops cross-pollinate, and evaluating hormone balances in leaves in relation to preventing senescence. Each of these subsidiary topics could take 5 years and involve one extra physiologist, depending on the location of the work in relation to the main project.

Root/Shoot Translocation of Materials A hormonal signal may be involved in the metabolic changes that accompany water stress, and this project would involve first evaluating the information from the hormone project. The aim would be to determine the nutritional aspects of root/shoot translocation, and particularly the role of nitrogen uptake and redistribution under stress and its assimilation into protein synthesis. The work would involve two scientists with support staff for at least 5 years.

Morphology of Shoot and Root This is an important aspect of crop productivity in arid areas, and topics here include water conservation either by restricting water uptake in the roots or by stomatal control in the leaves, the ability of plants to scavenge for water, and leaf characteristics such as rolling, surface waxes, hairiness, and angle. Associated with them would be the use of indeterminate types or drought evaders that are active only for an hour or so each morning. This would be a suitable project for an institute such as ICRISAT, which in any case will become involved in problems of morphology. On the other hand, not very sophisticated technology is needed and the work could be supplemented in different locations with different conditions. Three scientists — an agronomist, a physiologist, and a plant breeder — together with a large technical staff would be needed here.

Response of Growth Stages to Specific Environmental Characteristics For determinate plants, such problems as the effect of water stress during head initiation and grain development on factors such as cell division and expansion would be studied together with the variability in stress resistance. Temperature stress rather than water stress may be useful for screening purposes and the initial screening work could be done in many locations before concentrating the project in one institute. Two or three scientists, one of them a plant breeder, together with a modest amount of technical support, would make progress in these areas.

Hardening and Stress Resistance of Different Tissues Various approaches to hardening are being or could be tried including a general physiological approach, the development of a general hardening by hormone treatment of seeds, study of chloroplast resistance to stress, and comparative studies of the resistance of different tissues, such as the leaf and ear. At present, there is insufficient insight into these problems to decide how to attack them and with more information from the other studies, such as the hormone or morphology projects, they could be covered by the same staff.

Simulation Modelling Simulation modelling of plant growth has taken 6 years to reach the stage where the yield of corn or wheat can be predicted for optimal conditions. Stress conditions would have to be included in such models, which would then have to be adapted for sorghum or another semi-arid cereal as data were accumulated from controlled growth experiments. Adapting the model would require a computer simulation expert and an assistant working closely with one of the existing modelling teams. Three more scientists — a physiologist, an agronomist, and a microclimatologist — together with technical support, would be required to amass the data. The project would take at least 10 years.

Possible Breeding Techniques

Though not necessarily projects in themselves, certain breeding techniques might be developed during the fundamental research. These were simply listed and no attempt was made to assess the work involved. One major research result would be to identify ways of classifying breeding materials for their level of drought-tolerance factors.

Direct Measures of Productivity as Indices of Yield under Drought Such measures could include photosynthesis rate, including Hill reaction measurements, a screen for a suitable size of "sink" for photosynthate (potential storage capacity), and the length of the grain-filling period.

Other Direct Measures Direct measures of parameters other than productivity would include cellular stability to heat and desiccation, diffusive resistance of leaves as a measure of stomatal response, leaf temperatures, infrared reflection scanning to reveal chloroplast damage, and measurement of plant water potential.

Dry Matter Production as a Function of Transpiration In single plants, this evaluation could perhaps be developed into a method of selecting for high efficiency of water use.

Hormone Applications Though not strictly a breeder's selection technique, the application of hormones to crops would involve much more empirical work than fundamental research. Growth regulators could be applied to crops to give earlier flowering and more time for head development, or to delay growth but to give a larger ultimate yield.

Conclusion

It was recognized that the research projects proposed must not be expected to yield usable results quickly. The problems to be investigated are exceedingly complex, but without a more profound and fundamental understanding of the biochemical and physiological nature of drought-tolerant plants, the plant breeder will be restricted in his search for varieties that survive and give a significant yield under continuous or intermittent drought conditions.

Some of the projects proposed could be undertaken by scientists in Canadian universities. Others can only be pursued in research institutions located in the semi-arid tropics. It was recommended, therefore, that the report of the workshop be published by IDRC and distributed to as wide an interested audience as possible and in particular to the directors of institutions such as ICRISAT and the Arid Lands Agricultural Development program.

It is hoped that as the projects recommended get under way, another workshop can be held to review the progress made and to recommend what further future action is required.

Appendix 1

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