

DEVELOPMENTS IN AGRICULTURAL
AND MANAGED-FOREST ECOLOGY 26

agriculture in dry lands

principles and practice

I. ARNON



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Foreword

The dry lands with which this work is concerned, are the areas of meagre or undependable rainfall, in which the average precipitation is deficient in relation to water requirements. These include the arid zones, in which arable crop production is not possible without irrigation, and also their semi-arid fringes, in which rainfall, though precarious, is sufficient for certain types of crops, requiring special management techniques.

It is an interesting fact of history that in most of the dry lands in the Near East, India, North Africa, and Central Africa, very advanced agricultural civilizations developed, flourished, and eventually disappeared.

Whatever the reasons that prompted early man to choose the arid and semi-arid lands, in preference to the more favourable conditions for agriculture of the temperate regions with more reliable rainfall, it is clear that he chose an environment in which the balance between his own activities and the environment is extremely precarious.

The central problem of sustained land use in the dry regions has always been to find and maintain a balance between man's requirements and the productive capability of the land. This has rarely been achieved in the long run.

Throughout history, man has, by over-use, consistently reduced the productive capacity of dry lands. Originally, a large proportion of the more or less scanty vegetative cover consisted of palatable and nutritious grasses and shrubs. Overgrazing caused an overall reduction of the plant cover, and the large-scale replacement of useful plants by unpalatable species. The reduced cover intensified erosion by wind and rain, starting a process which is frequently irreversible. Gullies cut through alluvial valleys, water run-off increased, and water-storage reservoirs filled with silt.

Where the original plant cover of areas on the fringes of the arid regions was ploughed up for crop production, the consequences were still more disastrous. The classic, though by no means isolated, example is that of the 'dust bowl' of the Great Plains of North America.

In most dry land areas in which irrigation agriculture was developed, the consequences of cultivation were in the long run no less catastrophic; salinization and

water logging have reduced once-fertile regions to barren wastes. Economic deterioration was accompanied by political instability and the inability to withstand invasions of nomadic tribes. Wide areas were gradually abandoned, and the erstwhile cradles of civilisation became man-made deserts.

All this might be only of historical interest; unfortunately the degradation of the dry lands of the World is not only continuing, but is actually accelerating. With the explosive increase in world population, there is increasing pressure on the arid lands, which, with their semi-arid fringes, constitute fully one-third of the land area of the globe. This increased pressure applies mainly to the areas with primitive agriculture and low standards of living; but even the technologically advanced regions with a high standard of living are facing serious problems of deterioration of their natural resources.

The dry lands of a great number of countries are now usually vast empty areas. A large proportion is desert, and its contribution to food production is minimal. Other vast areas, on the fringes of the deserts, in Africa and Asia, with a rainfall that is just sufficient or even adequate to grow a single adapted crop, are still cultivated by primitive methods that have not changed since biblical days – with resultant low yields. In other vast areas, with similar climatic conditions – in the former USSR, North America and Australia – though cultivation is with the most modern equipment, the yields are often low compared with those that are common in regions of temperate climate. And yet, the combination of high insolation, favourable temperatures, and long growing periods, make possible levels of agricultural production that can exceed considerably those achieved in the temperate regions – if only an adequate supply of water can be provided.

There are however, areas, both rainfed and irrigated, that were formerly desert or seasonally dry, which produce a large variety of crops with record yields – an indication of the potential of the world's dry lands when water is no longer a limiting factor and modern technology is wisely and prudently applied. The development of other dry lands along the same lines could make substantial contributions to the economies of the countries involved and to increasing food supplies for the world as a whole.

In recent years, public awareness of the dangers inherent in the accelerating degradation of dry lands, pollution of the environment and the impending food shortage as population continues to increase explosively, has directed the attention of international and other agricultural bodies to the dire need for preserving and developing more effectively the agricultural potential of the dry lands.

World interest in this subject is evidenced by the numerous symposia and workshops and the promotion of research that has a bearing on the problems of dry lands; as a result of such research, numerous papers have been published and a huge store of important data on the dry lands and the problems of their development has become available. What appears to be lacking is the condensation of that which appears most relevant in this mass of information to the problems of agricultural production in the arid regions and their semi-arid fringes.

Twenty years ago, I attempted such a condensation in a work entitled *Crop Production in Dry Regions*, published by the since defunct Leonard Hill Books, and out of print for many years. It was felt that the current importance of the subject justified a new edition of this book. Originally, the intention was an updated version of the original. However, in the course of preparing the manuscript, it became clear that progress made in the course of the last two decades on all aspects of agricultural technology and development was so considerable, and the amount of new material published was so vast, that what was emerging was actually a new book, even if a core of material that had retained its relevance, was retained from the former work. It is for this reason that the title of the present work has been altered, even though the major topic has remained unchanged.

In a book of this nature, the author is continuously faced with the problem of deciding what general information should be included in what is destined to be a specialized account of agriculture of dry lands. Whilst the basic principles of agricultural practice are universal, an effort has been made to stress what is specific and unique to agriculture in dry regions.

A vast array of literature was perused in the preparation of the text, and a synthesis of the results of research and available information was attempted in the light of the author's own experience, after half-a-century of work in research and development in a dry region.

Only a small proportion of the literature consulted has actually been cited in the text. The references that are quoted are either in support of general principles, or are chosen as appropriate examples to illustrate these principles.

Several excellent books and reports from symposia and workshops on different aspects of agriculture in dry regions have been published since the 1970's. They are all written by experts for other experts. To the best of my knowledge, this is the only work by a generalist (an almost extinct species), that attempts to encompass the entire subject and provide an up-to-date, comprehensive, and yet concise, review of present knowledge on agriculture of the world's dry lands. Agronomists, research workers, extension workers and farmers, who live and work in the dry regions and who must cope with the complexity of the problems with which they are faced, are the primary clientele group. It is also hoped that students who are preparing for a career in these regions will find the book a useful aid in their studies.

In a way, specialists may also find interest in this work, not in their own discipline, but as a relatively easy and concise way of acquainting themselves with the state-of-the-art in associated fields. Increasing specialization, with each discipline using its own vocabulary, has created communication problems, whilst the need for multidisciplinary teams makes inter-discipline communication indispensable.

In a work of this scope, it is almost inevitable that errors of omission or commission should intrude. Quite possibly, some important aspects may have been overlooked, and there will assuredly be justification for criticism and comments. These will be welcomed by the author.

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The author is not, and could not possibly be, an authority on all special fields which this work encompasses. A number of chapters have therefore been reviewed by several colleagues, each a recognized authority in his special field, whose critical and constructive comments the author gratefully acknowledges: Dr. H. Bielora (Plant-water relationships); Prof. A. Blum (Plant breeding); Dr. Y. Dan (Soils); Dr. M. Horowitz (Weeds); Prof. U. Kafkafi (Plant nutrition); Prof. G. Loewenstein (Plant diseases); Dr. Mantell (Irrigation); Dr. Z. Plaut (Plant physiology); and Prof. E. Swirsky (Insects).

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Ramat Gan, 1992

I. Arnon

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CHAPTER 6

Plant Adaptations to Moisture Stress

Definitions and concepts

The ability of a crop to grow satisfactorily in areas subjected to water deficits has been termed drought resistance. The modification in structure and function that increases the probability that a crop will survive and reproduce in a particular environment is termed an *adaptation* (Kramer, 1980). Adaptations can be heritable or not, constitutive or facultative. *Acclimatation* is the ability to slowly adapt to a new environmental condition.

Plants have to contend with three kinds of situations in which they are submitted to moisture stress:

(a) *Transient drought*. The occasional, transient stress periods at various stages of crop development, a major characteristic of semi-arid regions.

(b) *Terminal drought*. Causing moisture stress towards the end of the growing period, which prevents normal formation and ripening of grain. This is the most common form encountered in Mediterranean climates;

(c) *Seasonal drought*. Insufficient precipitation for economic crop production characterizes the arid regions; occurs, generally in cycles, in the fringe areas of semi-arid regions and occasionally in the semi-arid regions.

Categories of drought resistance

Drought resistance has been ascribed to a number of adaptive mechanisms, but there is, as yet, no consensus on the most useful breakdown of categories of drought resistance (Turner, 1986). In many cases, the distinctions are more semantic than substantive. For our presentation, we have adopted the schema shown in Fig. 6.1 adapted from Levitt (1972) and based on three principal ways in which plants can adapt to drought:

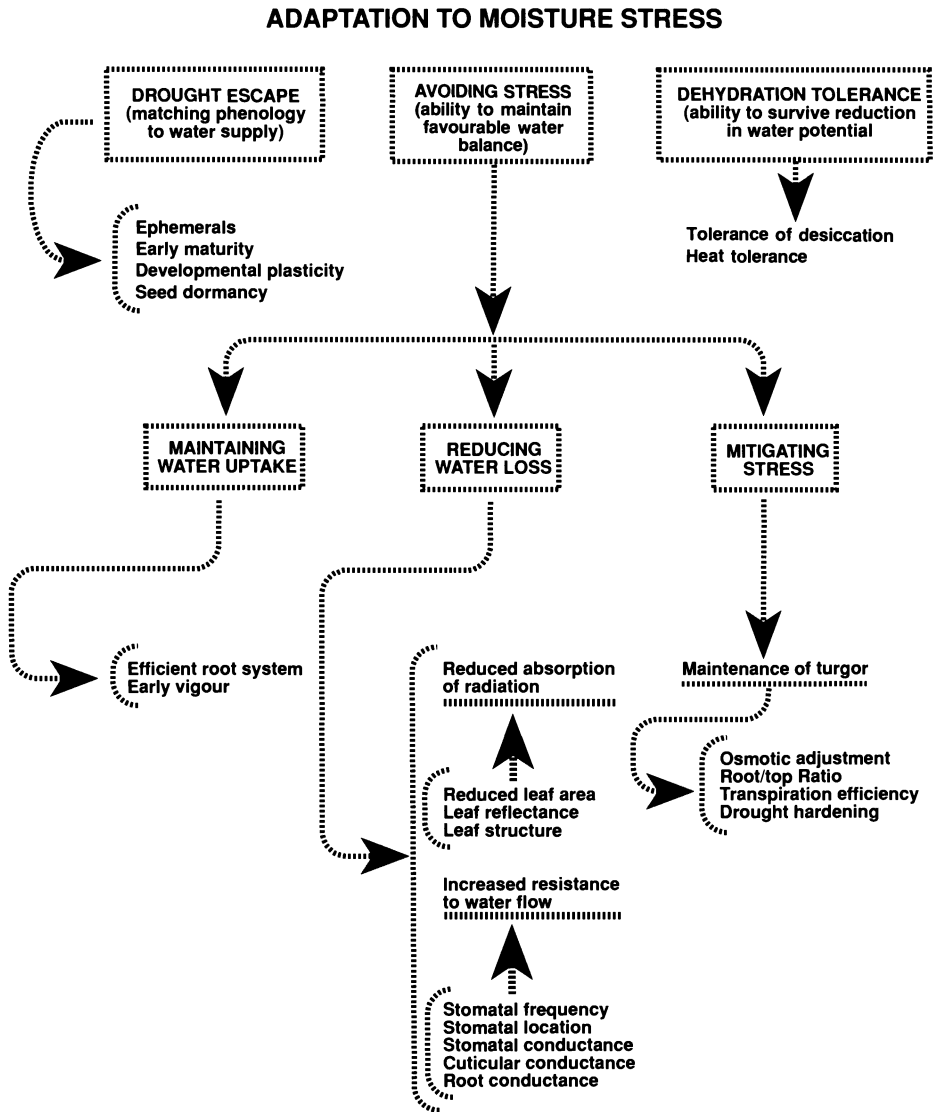


Fig. 6.1. Adaptive mechanisms to drought.

- evading the drought period (drought escape);
- maintaining a favourable internal water balance, thereby postponing the negative effects of drought (drought avoidance);
- surviving relatively long periods of drought (drought survival).

Turner (1986) stresses that not all mechanisms of drought resistance are without metabolic cost to production. He concludes that “only those mechanisms that aided in drought escape, maintenance of water uptake, and maintenance of turgor pressure

did not reduce photosynthesis, crop growth and yield". While it is relatively easy to decide whether a particular mechanism of adaptation affects a short-term process such as the instantaneous rate of photosynthesis, it is much more difficult to determine whether there are long-term consequences of a particular adaptative mechanism.

Many of the traits associated with native plants of the arid regions are concerned with survival; these are rarely, if ever useful to the plant breeder, who perforce, must consider crop productivity as his major objective. Whilst we will review all plant traits involved in drought resistance, this distinction should always be borne in mind. The feasibility of incorporating useful traits for drought resistance in crop varieties will be discussed in detail in Ch. 7.

Drought escape

Matching phenology to water supply

Ephemerals

Evading the drought period is the simplest means of adaptation of plants to desert conditions.

Many desert plants germinate at the beginning of the rainy season and have an extremely short growing period, which is confined to the rainy period. Between germination and seed maturity, as few as five (Polunin, 1960) to six (Kassas, 1966) weeks may suffice. In rainy years these ephemerals may appear in great profusion, but remain dormant during drought years, usually in the form of seeds or fruits.

Early maturity

Only very few crops have such a short growing season that they can be considered similar to the ephemerals in escaping drought. Certain cultivars of millets, that can produce mature seeds within 60 days from germination, are an exception. Even the earliest-maturing cultivars of most crops have longer growing periods and will generally experience one or more periods of moisture stress during their lifetime.

Earliness reduces the number of moisture stress periods, and early maturing cultivars usually avoid terminal stress; it is therefore an important trait. It does not, however, ensure their escaping drought completely, as do the real ephemerals. They therefore need, and usually have, actual drought resistance attributes. In a study with wheat cultivars grown under variable soil moisture regimes, Blum and Pnuel (1990) found that early cultivars tended to have better osmotic adjustment; since the drought stress occurred during the period of ear growth and development, the authors conclude that a greater capacity for osmotic adjustment apparently allowed sustained ear growth under drought stress and the maintenance of relatively larger ears in the higher-yielding cultivars.

In areas with alternate rainy and dry seasons, the ability of a cultivar to achieve maturity before the soil dries out is the main adaptation to drought of cultivated crops, and matching crop phenology to available moisture supply has always been a major breeding objective. There is genetic variability for phenology, and the inheritance is known in many cases (A. Blum, personal communication).

Fischer and Maurer (1978), working with 53 cultivars of wheat, barley and triticale, showed that each day of earliness conferred a yield advantage of almost 30 kg/ha under conditions of terminal stress.

Early maturity, however, generally reduces the potential yield of the crop by reducing the amounts of dry matter available at anthesis and the number of sites for post-anthesis grain filling. Therefore, a reduction of the growing period, as an insurance against drought, is a trade-off for yield.

The degree of earliness required is a compromise to enable the maximum possible production of dry matter before soil water is reduced to a level which will limit reproductive growth after anthesis (Fischer, 1979).

Cavaliere and Smith (1985) studied 21 commercial hybrids and one open pollinated maize cultivar that had been released over a period of 50 years. The most significant factor contributing to increased yield was the lengthening of the grain filling period, achieved without necessitating a longer growing period.

Developmental plasticity

Developmental plasticity is the mechanism whereby the duration of the growth period varies according to the extent and timing of water deficits (Ludlow and Muchow, 1990). Early maturity may be induced by water stress, which is an advantage in dry years; in more favourable years, maturity is delayed and the plant can benefit from a longer growing period. Developmental plasticity matches growth to water availability.

Therefore, whilst the development of early-maturing varieties has been beneficial where seasonal rainfall is predictable or soil moisture levels are known at the time of sowing, phenological plasticity will be more beneficial than earliness, where soil moisture supply is less predictable.

Many crops have some degree of plasticity enabling them to benefit from favourable conditions. Even in an essentially determinate crop such as wheat, e.g., if no drought occurs, and the time to reach physiological maturity is extended, the number of ear-producing tillers, the number of spikelets and florets, and the size of kernels will increase (Turner and Burch, 1983).

Bidinger et al. (1982) found that certain cultivars of pearl millet respond to drought by delayed flowering and by stimulation of secondary tillering. Sinclair et al. (1987) state that cowpeas have an advantage over other grain legumes through their ability to delay development under moisture stress so that flowering and pod formation resume when a favourable moisture regime is reestablished.

Quizenberry and Roark (1976) found that indeterminate cultivars were more pro-

ductive than determinate cultivars of upland cotton under water stress, but the advantage decreased with improved water supply.

Indeterminate growth also has disadvantages. With fresh-market crops, repeated hand-labour harvests are required, and with field crops, a significant proportion of the crop may be lost, damaged, or still be immature before an end-of-season harvest (Loomis, 1983).

Developmental plasticity can be advantageous for genotypes in both modern and subsistence agriculture where unpredictable intermittent water deficits occur (Ludlow and Muchow, 1990). However, the requirements of mechanical harvesting have led to the development of determinate cultivars such as beans, soybeans, sunflowers, thereby foregoing the lower risk advantage of indeterminate cultivars for the sake of the convenience and lower cost in labour in harvesting (Turner, 1986).

Seed dormancy

The seeds of many species that grow in regions with hot, dry seasons, are not able to germinate at high temperatures; they are thereby protected from destruction (EVENARI, 1962). In many desert plants, the process of germination can be stopped and restarted at different stages between inhibition and the appearance of the seedling rootlet and shoot. Seeds may remain soaked and return to a state of secondary dormancy without losing their viability, or they may dry out completely after wetting without losing their germinability (*ibid.*).

The presence of germination inhibitors in such seeds serves as an 'internal rain-gauge', which permits germination only after an amount of precipitation has fallen that will be sufficient to remove the inhibitor (Went, 1952).

As seeds germinate, vacuoles are formed in the cells and their drought resistance decreases very markedly before emergence (Iljin, 1957).

Avoiding stress

A favourable water balance under conditions of limited water supply can be achieved (a) by improving water uptake sufficiently, so as to replenish lost water (so-called water spenders); (b) by conserving water, i.e., restricting transpiration before or as soon as stress is experienced (water savers); or (c) by postponing dehydration and thereby enabling plants to avoid the effects of stress by maintaining turgor and cell volume.

Maintaining water uptake

Root systems

In xerophytic plants. The drier the environment, the greater the tendency to increase the root system and reduce shoot development: in annual plants of dry, tropi-

cal savannahs, roots may account for 30–40% of total dry matter, whilst the proportion may rise to 90% in perennial desert species, with the roots growing to great depths.

By contrast, annual ephemeral species, that grow during short moist periods, as and when they occur, or in depressions in which water has accumulated, have poorly developed root systems (Fitter and Hay, 1987).

In cultivated crops. Vigorous root systems are associated with drought tolerance. Blum et al. (1977) reported heterosis in the root systems of sorghum hybrids similar to that in vegetative growth and grain production. Root heterosis was expressed by faster growth rates, increased root length, and increased root volume. Gul and Allen (1976) reported that rapid emergence was associated with a faster developing root system.

In crops with a shallow root system, such as upland rice, drought resistance has been improved by genetic root extension (IRRI, 1982).

Where water remains in the root zone at maturity, greater rooting depth can contribute to increased productivity. Where the soil water at rooting depth is not replenished between crops, greater rooting depth would be of little or no advantage (Bremner et al. 1986).

Using a crop simulation model to assess the consequences of deep rooting in sorghum over a 30-year period, Jordan et al. (1983) found that the simulations indicated that deeper root systems increased yields by 20% in about one-third of the years. No effect was evidenced in wet years, when water was not limiting, or in very dry years, when there was no water in any case in the deeper soil profile.

Passioura (1983) has questioned the advisability of breeding for greater root depth, in particular for situations in which crops extract all the available soil water. He argues that the water transpired to create the greater root biomass may offset the extra water gained. Furthermore, the requirements for root growth and maintenance would be at the expense of assimilates which might have been used for above-ground growth and which eventually might contribute to yield. Passioura concludes that in situations where the roots extract all the available water from the soil every year, selection for a smaller root system, particularly in the top soil, might actually improve yield.

The benefits of saving expenditure on assimilates by reducing rooting depth would appear to be minimal, in view of the small biomass of the roots, which constitutes a very small fraction of total biomass produced by a plant.

Ludlow and Muchow (1990) suggest that more benefit could be derived by aiming for a root system with fewer surface roots and more of them deeper in the soil. They conclude from the conflicting results described above, that in situations of intermittent stress, greater root activity would improve stability by slowing the incidence of water deficits and even by reducing their incidence. In a terminal stress situation, greater root depth and density would be undesirable: by increasing the risks of de-

pleting available soil water early in the season, water stress would limit economic yield, or even prevent its formation.

Passioura (1976) describes how the dual root system of temperate cereals resolves these problems by exercising control on the rate of growth of the shoots in accordance with water availability. When the upper soil layer is wet, nodal roots develop quickly, water supply to the shoots is favourable, resulting in rapid growth; when the upper soil layer is dry, the seminal roots, which penetrate deeply, supply water to the shoots from deeper layers in the root zone; the seminal roots have relatively high resistance to flow, thereby causing a slight drop in leaf water potential, decreasing stomatal aperture and CO₂ uptake and resultant slower growth. The plants are smaller, but show no obvious signs of water stress.

The continued exploration of the soil by roots as soil water content decreases and mechanical impedance increases, is due to osmotic adjustment which prevents a decrease in turgor pressure of the root cells (Turner, 1986).

Considerable genetic variation in rooting systems has been reported in sorghum, soybeans, and wheat (Ludlow and Muchow, 1990). Root growth is also indirectly under the influence of genetic factors not related to root growth. For example, Blum and Arkin (1984) have shown that genes that control plant maturity of sorghum affect root growth rate and root length and density.

Though the root system is of considerable importance to all aspects of plant growth, development, productivity, and survival, the study of root systems has been relatively neglected; with very few exceptions, "roots are ignored in actual breeding and selection practices" ... "root systems have been the last morphological frontier" (Jensen, 1988). The main reason for this neglect is the difficulty and cost involved in investigating physiological processes in the below-ground parts of the plant.

Breeding for the improvement of the root system would benefit considerably if marker traits could be found making indirect selection possible.

An ingenious marker screening system was devised by Robertson et al. (1985): by banding a herbicide at different depths and lateral distances from the rows, visual leaf systems of herbicide damage indicate the rapidity and extent of root development.

Summarizing available information, Evans (1983) concludes that the most useful system in practice, over a wide range of environments, would probably have the following characteristics: (a) a deep root system which is also efficient in extracting water and nutrients from the surface layers; (b) does not invest a high proportion of total dry weight of the plant in its roots; and (c) has the ability to readily produce new root axes.

Hydraulic conductance. The roots may develop sufficiently to maintain water uptake adequately, but for this to benefit the whole plant, the hydraulic resistances within the plant must be low enough for the water to be available to the major metabolic centres in the shoot. This topic will be addressed in another section (cf.p. 240).

Early vigour. For cereals grown in the tropics, the yield potential is largely set during the first two to three weeks after sowing. Hence, rapid development of the young plants, with increased radiation interception, should be a favourable trait (Rawson and Hindmarsh, 1983). It would, however, be an undesirable trait for crops grown on stored moisture, as it would lead to early exhaustion of soil moisture supply (Ludlow and Muchow, 1990).

Reducing water loss

The most common way plants regulate water balance and maintain turgidity is to reduce water loss. Several mechanisms are possible, which can be grouped as (a) reducing absorption of radiation, and (b) increasing stomatal, cuticular and root resistance.

Reduced absorption of radiation

Reduced leaf area. The principal means of reducing water loss by xeromorphic plants is their ability to reduce their transpiring surface.

(1) *Shedding of leaves.* Apart from the common means of keeping the aerial parts small, a more extreme adaptation to dry conditions is the shedding of leaves, as in *Fouquieria splendens* (Shields, 1958) and species of *Euphorbia* (Kramer, 1959).

Many desert species, such as *Artemisia herba-alba*, have two kinds of leaves – large winter leaves that are shed at the end of the rainy season, and very small summer leaves which replace the large ones (Zohary, 1961).

Leaf shedding strongly affects root/leaf ratios and the carbon balance of plants. Generally, nitrogen is recovered before abscission (Schulze, 1988).

Krieg (1983) points out that the plasticity of leaf area development is a useful trait allowing plants to conserve water during the vegetative stage so that it can be used during seed formation. He, however, stresses that excessive reduction in leaf area will impose an irreversible limitation on yield, due to the close association between leaf area and seed number in most determinate crop plants.

Whilst the mechanisms for reducing leaf area described above enhance survival by conserving water, they are detrimental to productivity in cases of transient water stress, when water again becomes available. Maintaining leaf area, up to a leaf area index of about 3, is a trait contributing to yield; the lower radiation interception and reduced transpiration rates resulting from mechanisms for reducing leaf area produce the opposite effect.

Therefore, leaf area reduction is a desirable trait in terminal stress situations, because it decreases the probability of the crop running out of water before reaching maturity, and undesirable in the opposite situation, namely, transient water stress (Ludlow and Muchow, 1990).

(2) *Leaf movements.* The simplest form of reduction of leaf area is the *rolling, folding and wilting* (floppiness) of leaves at times of water stress. These leaf movements help reduce the heat load and water loss.

The rolling of leaves has been shown to reduce transpiration by almost 55% in semi-arid conditions, and by 75% in desert xerophytes (Stålfelt, 1956).

Certain genotypes of sorghum and maize, when subjected to severe stress, will roll up and look as if in very serious condition; two or three days after adequate moisture again becomes available, the plants resume growth. This useful trait for plants grown under conditions of intermittent drought has been named 'latente' (Johnson, 1980).

In crop plants, rolling, folding, and floppiness of leaves should contribute to yield stability in environments with intermittent drought, by enhancing the chance of plant survival until the next rains. These leaf movements do not occur excepting in stress conditions and are reversible, so that photosynthesis returns to normal after the stress is relieved (Turner, 1986). Therefore, no yield penalty is to be expected (Ludlow and Muchow, 1990).

Blum and Sullivan (1986) advocate delayed leaf rolling before heading, in sorghum, as a selection criterium for osmotic adjustment.

(3) *Active leaf movement.* Active leaf movement is an adaptation to both low and high light intensities. For plants growing in weak light, leaf movement follows the sun to ensure maximum illumination; in plants growing in high light intensities, leaf movement reduces the heat load on the upper leaves, and maximizes the amount of light that reaches the lower leaves (Fitter and Hay, 1987).

A special case of leaf orientation is the active leaf movement commonplace in Cucurbitaceae, Leguminosae, and others. When water supply is adequate, the leaves are oriented perpendicular to incoming radiation: thus maximum photosynthetic rates are assured, but water loss is high. When stress occurs, leaves orient parallel to incoming radiation, thereby reducing heat load and transpiration. Indirect light is still sufficient for photosynthesis (Schulze, 1988).

For example, under conditions of extreme drought and intense sunlight, bean leaves orient themselves parallel to incoming light, and follow the sun in that position. This is a reversible process, and by morning the leaves have returned to their normal position (Halterlein, 1983).

(4) *Leaf reflectance.* The reflectance of a healthy leaf increases as it loses water. In maize and soybeans, e.g., Sinclair (1968) found that reflectance was not appreciably affected in the early stages of drying, but increased markedly below 80%, at all wavelengths, and especially in the infrared bands. Cotton behaved in a similar way (Thomas et al., 1966).

Leaves of different species differ considerably in the amount of visible light they reflect. Increased reflectance alters the energy balance of the leaf (Schulze, 1988). It reduces leaf temperature, leaf-air vapour pressure difference, and hence water loss. Photosynthetic rate can be significantly increased, especially if temperatures are above the metabolic optimum (Ehleringer and Forseth, 1980).

The reflectance is caused by the presence of epicuticular wax (Ludlow and Muchow, 1990). Besides increasing reflectance, the wax also lowers epidermal conductance (Blum, 1975) and transpiration, thereby increasing WUE.

Hull et al. (1978), using a scanning electron microscope analysis of the epicuticular wax on the leaves of Lehmann Lovegrass, found that all lines had a basic type of wax, but drought-resistant lines had an additional layer of large wax plates. The authors suggested that wax morphology could serve as a selection tool for increasing drought tolerance in Lehmann Lovegrass.

The maximum yield gain under drought stress of bloomed or glaucous cereals over non-bloomed or non-glaucous was found to be – in wheat: 7% (Johnson et al., 1983); in barley: 16% (Baenziger et al., 1983); in sorghum: 15% (Jordan et al., 1983).

Ludlow and Muchow (1990) conclude from the foregoing that the yield advantage of genetically increasing the epidermal wax coating of an already bloomed or glaucous cultivar would probably be very small.

(5) *Leaf structure*. Various morphological characteristics of leaves help to reduce the transpiration rate and may affect plant performance and even survival under drought conditions: leaves with thick cuticles, waxy surfaces, sunken stomata, the presence of spines, hairiness, etc. are common and effective.

The small, thick, evergreen leaf is one of the most characteristic features of adaptation to dry habitats in Mediterranean-climate vegetation. This thick structure appears to have both beneficial and detrimental aspects. Benefits are the ability to restrict water loss and to delay the onset of drought stress. Detrimental is a simultaneous restriction of CO₂ uptake (Dunn et al., 1976).

(6) *Pubescence*. In certain species, drought stimulates the production of epidermal hairs (Shields, 1958). The mere presence of pubescence is no longer considered as an advantage in reducing transpiration (Kramer, 1959) unless it be through increasing the albedo. However, at high humidity, some desert plants are capable of absorbing water through epidermal hairs (Shields, 1958).

In cultivated plants, the evidence is not consistent. Burton et al. (1977) found that smooth-leaf lines of pearl millet had reduced transpiration (8.9–35%) as compared to near-isogenic hairy-leaf lines. The differences were partly attributed to the ability of the smooth leaves to accumulate more dew; and the authors suggested that the smooth-leaf trait was potentially useful for increasing WUE and drought tolerance. By contrast, Ghorashy et al. (1971) reported that soybean isolines with dense leaf pubescence had significantly lower transpiration rates than glabrous isolines.

(7) *Awns*. Awned cultivars of wheat predominate in the drier and warmer regions, and have been found to yield better than awnless cultivars, especially under drought conditions, though there are exceptions. Awns have chloroplasts and stomata and so can photosynthesize; it has been found that the contribution of the awns to the total dry weight of the kernels was 12% of that by the entire plant (McDonaugh and Gauch, 1959).

Blum (1985) measured carbon exchange rate (CER) and transpiration in a number

of cultivars of hexaploid and tetraploid wheats as well as six-rowed and two-rowed barleys. Awns contributed about 40–80% of total spike CER, depending on the species, but only 10–20% of spike transpiration. The transpiration rate was lower by several orders of magnitude in the awns than in flag leaves and glumes. Blum concludes that “a large amount of awns in the ear is therefore a drought-adaptive attribute in these cereals, for which tetraploid wheat exceeded hexaploid wheat and six-rowed barley exceeded two-rowed barley”.

Increased resistance to water flow

Mansfield and Davies (1981) have called the rapid response of stomata to change in air humidity “as the first line of defence” of plants, the second line of defence is the closure of stomata in response to lowered soil water potential.

Current thinking is that the mechanisms whereby stomata respond to different weather and soil moisture conditions consist of a feedback mechanism governed by the water content of the plant, and a ‘feedforward’ mechanism coupled to the water content of the atmosphere (Stanhill, 1986).

Stomatal number and location. A small number of stomata can retard the development of water deficits. Some desert plants have less than 100 stomata per cm² as compared with averages of 10 thousand per cm² in mesophytes (Killian and Lemée, 1956). In many drought-resistant species (e.g., *Retama raetam*) the stomata are located in depressions in the leaves, which is a feature that can further reduce transpiration by limiting the impingement of air currents.

In crop plants, Dobrenz et al. (1969) reported that drought-tolerant clones of blue panic grass had fewer stomata per unit leaf area than susceptible clones. Similar findings were reported for barley by Miskin and Rasmusson (1970).

Reduced stomatal conductance. Under conditions of water stress, stomatal closure may effectively reduce transpiration. Two responses need to be considered: one to air humidity, the other to soil moisture. Both responses also affect photosynthesis, and there is therefore a cost in saving water by stomatal closure (Schulze, 1988) that may eventually lead to drought-induced starvation (Levitt, 1972).

Various stomatal characteristics, such as low conductance, high sensitivity to leaf water status and saturation deficit, as well as abscisic acid accumulation, have been proposed as desirable traits to improve drought resistance in crops (Jones, 1987). All these characteristics postpone dehydration.

In contrast to the irreversible effects of reduced leaf area described in a previous section, reduced stomatal conductance, being reversible when the stress has abated, can be useful either in reducing water loss or improving productivity.

The lower conductance of the stomata improves yield stability by reducing water loss and reducing the risk of water supply exhaustion before maturity. The drought resistance of sorghum and certain varieties of maize and groundnuts has been attri-

buted, at least partly, to the ability of stomata to resume their normal functioning after a period of water stress (May and Milthorpe, 1962).

An interesting observation made in the course of trials on the effects of soil moisture regime on different wheat varieties, was that the stomata of a semi-dwarf variety remained open throughout the day, while those of the tall variety were open for only a few morning hours, remaining closed thereafter even under favourable conditions of soil moisture and transpiration (Shimshi and Ephrat, 1975).

All the mechanisms for water loss control described above, involve a trade-off between reduced water loss and reduced photosynthesis.

Ludlow and Muchow (1990) conclude that "this trade-off could be acceptable for subsistence agriculture in intermittent stress environments, if it prevents crops from dying before the next rain; and in terminal stress environments, if it prevents exhaustion of soil water before maturity. We believe, however, that the cost of these traits is high for comparable environments in modern agriculture".

Genetic variability for various stomatal characteristics has been established (Jones, 1987). Ludlow and Muchow (1990) consider the use of stomata traits as selection criteria as premature, notwithstanding their potential benefits.

Reduced cuticular conductance. When stomata are closed, the main pathway of water loss is through the leaf cuticle, and the rate of loss is determined by the saturation deficit of the air.

Plants in dry habitats usually have thicker cuticles than those growing in moist conditions. The cuticle consists of a hydrophylic framework, in which wax platelets are embedded. Under conditions of high humidity this framework absorbs water and swells, thereby separating the wax platelets and increasing the permeability of the cuticle (Van Overbeek, 1956).

The efficiency of a cuticle to reduce water loss may not necessarily be determined by its thickness, but more by the chain length of the lipids forming it (Schulze, 1988). For example, the cuticle of onion scales withold water more effectively than the thick cuticle of an orange fruit (Schonherr, 1982).

Low epidermal conductance delays leaf dehydration and therefore promotes leaf survival (Sinclair and Ludlow, 1986). Because water loss through the cuticle is significant only when the stomata are closed, low cuticular conductance has no adverse effect on photosynthesis and does not reduce yield potential. It should therefore enhance plant survival in intermittent stress environments without any cost in performance (Ludlow and Muchow, 1990).

Reduced root hydraulic conductance. Higher root resistance effectively lowers leaf water potential during periods of high evaporative demand, and plant growth and total crop water use during vegetative growth is thereby reduced. Limiting growth during the pre-anthesis period reduces the risk of complete crop failure due to early depletion of available soil water (Jordan, 1983).

Passioura (1977) suggests that decreased root hydraulic conductance could be a useful trait for plants growing on stored soil water. By restricting the water extraction by young roots, more water would remain available at later stages of growth when the plants are especially susceptible to water stress.

Richards and Passioura (1981) considered three ways of increasing flow resistance through the upper levels of the seminal root system: decreasing the number of flow axes, decreasing the diameter of main xylem vessels, and replacing these by a multiplicity of smaller vessels.

Their experiments indicated that the most promising approach was decreasing vessel diameter. It was found that xylem vessel diameter was under multigenic control and heritable. A decision was made to initiate a breeding programme for this trait in wheat for dry Australian conditions.

Richards (1987) has shown that in dry seasons, wheat lines with small xylem vessels in the roots, yielded more than those with large vessels, and the small vessels had no adverse effect in wet seasons. This trait can therefore increase yield stability. The trait is heritable, and shows genetic variability.

Mitigating stress

Certain adaptations to drought permit the plants to maintain a high internal water potential in spite of the stress. They are thereby able to maintain cell turgor and growth, avoid secondary drought-induced stress, as well as direct and indirect metabolic injury due to dehydration (Levitt, 1972).

Maintenance of turgor

Many biochemical, physiological, and morphological processes in the plant are sensitive to leaf turgor; therefore maintenance of turgor in spite of leaf water deficits is a major factor in mitigating stress (Turner and Burch, 1983).

Osmotic adjustment. Osmotic adjustment (also called osmoregulation or turgor regulation) is an adaptive process which enables a plant to lower its internal water potential in response to water stress. This is achieved by increasing synthesis and accumulation of osmotically active substances, such as sucrose, a process that lowers the osmotic potential and helps to maintain turgor of both shoots and roots. The improved turgor allows stomata to remain open at progressively lower water potentials and growth to continue, although at progressively reduced rates (Ludlow, 1987).

Osmotic adjustment can therefore be regarded as a tolerance mechanism (Radin, 1983). Begg and Turner (1976) even consider it to be the most important tolerance mechanism, though it is not present in all crops (such as soybeans and cowpeas).

Genotypes of wheat and sorghum with high osmotic adjustment produce more roots, greater root density, and extract more water, especially from the lower soil

profile (Morgan and Condon, 1986; Santamaria et al., 1986). As a result, dehydration avoidance is enhanced.

Osmotic adjustment contributes to grain yield in drought stress situations by maintaining or improving harvest index (Ludlow and Muchow, 1990) by one or more of the following effects:

- improved tiller and floret survival and improved seed set (in wheat: Morgan, 1984);
- improved head exertion and reduced spikelet abortion (in sorghum: Santamaria et al., 1986);
- increased assimilate supply during grain filling, by reduced leaf senescence and by maintaining photosynthetic activity of remaining leaves (Santamaria et al., 1986);
- continued root growth and thorough soil moisture extraction (Sharp and Davies, 1979).

Entries with high osmotic adjustment had the following yield advantages over those with low osmotic adjustment:

- in wheat: increases towards 50% as water supply became more limiting (Morgan and Condon, 1986).
- in sorghum: increases of 15–24%, when drought stress occurred during the pre-anthesis or post-anthesis period, respectively (Santamaria et al., 1986).

Osmotic adjustment can therefore contribute to increasing yield stability under water stress conditions. In trials performed under variable moisture regimes in a Mediterranean climate, Blum and Pnuel (1990) found that the variations in yield among cultivars under drought stress were associated mainly with osmotic adjustment as a major physiological attribute. The authors conclude that since, in this particular case, stress occurred during the period of ear growth and development, a greater capacity for osmotic adjustment apparently allowed sustained ear growth under drought stress and the maintenance of relatively larger ears in the higher-yielding varieties.

Genetic variability in osmotic adjustment has been found in wheat, grain sorghum, millet, rice, cotton, and pigeon pea (Ludlow and Muchow, 1990).

Osmotic adjustment also has its limitations (Turner and Jones, 1980): (a) the degree of osmotic adjustment is limited (in sorghum, e.g., it is limited to the range of –5 to –8 bar); and (b) it does not fully maintain physiological and morphological processes.

Ludlow and Muchow (1990) recommend osmotic adjustment “as a highly desirable characteristic for both intermittent and terminal stress environments in modern agriculture”. Blum (1988) points out that osmoregulation is also effective in plant tolerance to salinity and freezing stresses, both of which involve a component of water deficit. Jordan (1983) is less positive in his assessment; he concludes from his review of plant response to water deficits that “little evidence suggests osmoregulation may play a major role in cultivar difference in drought resistance”. However,

studies since 1983 add support to the importance of the role of osmoregulation (Blum, personal communication).

Root-to-shoot ratio (R/S). For short-term water stress situations, a balance between water uptake and loss can be achieved through stomatal closure; basic adjustments must, however, come through adaptation of the ratio between effective root surface and leaf area (Loomis, 1983).

The root–shoot ratio is a very plastic character; plants under conditions of stress tend to increase the ratio (Fitter and Hay, 1987).

A high root-to-top ratio is a very effective means of plant adaptation to water stress (Begg and Turner, 1976): it is easier for the root system of the individual plant to maintain an adequate water supply to a reduced transpiring surface. Brouwer (1963) gave the name ‘functional balance’ to the way in which adjustments in R/S occur. When there is an ample supply of water, assimilates are monopolized for top growth; with increasing moisture stress, shoot growth is the first to be curtailed whilst photosynthesis and root growth continue, and thus the functional balance is maintained.

The functional balance causes a wide variation in R/S; in wheat, e.g., when moisture is not limiting, roots may account for 10% of biomass, whilst under drought conditions they may amount to 30% (Loomis, 1983).

Transpiration efficiency. Transpiration efficiency (TE) is defined as mass or moles of C or CO₂ fixed per unit of water lost from a *leaf*. This contrasts with WUE of a plant or of crops, which is dry matter produced per unit of water lost (Ludlow and Muchow, 1990).

In principle, there should be no cost for higher TE, and it should contribute to yield potential and stability. Ludlow and Muchow (1990) conclude that “this trait has great promise and potential for increasing yield of crops in the semi-arid and arid tropics”.

Dehydration tolerance (low lethal water status)

Ability to withstand desiccation

The degree to which plant parts withstand desiccation is expressed as the relative water content or water potential at which leaves die; these are called critical or lethal values (Ludlow and Muchow 1990). Tolerance of desiccation is essentially a survival trait; the process which reduces the above-ground phytomass in arid habitats has been called ‘survival by death’ by Evenari (1962).

The leaves of some C₄ grasses, with so-called ‘resurrection’ features, that are na-

tive of the arid deserts of Southern Africa, may remain air-dry for several months and recuperate when water again becomes available (Gaff, 1971).

Desert species have a preadapted stem morphology, so that a certain proportion of the shoots and roots can die without endangering other parts, that can still obtain sufficient water to stay alive.

There are also great differences between different plant organs in their ability to withstand desiccation. Seeds that are filled with food reserves but have no vacuoles can survive very long dry periods, often of many years. Buds of higher plants also have no vacuoles, and are very resistant to desiccation. Certain desert plants survive a degree of desiccation that causes the death of their leaves; but the buds on the stems remain alive and resume growth when the drought ends.

In many species of perennial plants, the above-ground parts die off at the onset of the hot, dry season and the underground parts, such as rhizomes, bulbs, corms, and tubers, remain alive but dormant (Vegis, 1963).

Ability to maintain reserves of water in tissues

Certain xerophytes have water reserves in hypertrophic underground organs which are often greatly swollen. In *Pachypodium bispinosum*, a South African plant, the tubers account for 95% of the total weight of the plant, and contain 91% of its water (Walter, 1962).

Succulents are a special group, frequent in the deserts of North and South America and South Africa, rare in the deserts of Asia and the Sahara, and virtually absent from the deserts of Australia. They tend to be preponderant in arid regions which have short rainy seasons annually (Walter, 1962), being able to survive periods of absolute drought during which they are almost completely unaffected by their environment, both aerial and edaphic. This they manage by living very frugally on reserves of water which they accumulate in their storage organs during periods when water is available in the soil. The amount of water conserved, which can be quite considerable, is estimated at 2000 to 3000 litres for a single plant of *Carnegiea gigantea* (Killian and Lemée, 1956).

Cellular level

The factors influencing the dehydration tolerance of plant tissues are mainly at the protoplasmic level. Differences in cellular structure, protoplasmic composition and viscosity, enzyme activity and water retention properties of the cell wall have been suggested as contributing to survival under water stress (Turner and Burch, 1983).

Protoplasmic dehydration

There are great differences between plant species in their ability to endure desicca-

tion, in relation to both the duration and the degree of dehydration. The more water the plant can hold in its tissues under stress conditions, the greater will be the ability of the protoplasm to withstand permanent injury during drought. The 'bound water'* prevents the proteins molecules of active sites from coagulating (Vaadia and Waisel, 1967). As the tissues become desiccated, the protoplasm becomes increasingly dense and its viscosity gradually increases; when dehydration is severe, complete gelation of the protoplasm occurs and finally it may become rigid to the point of brittleness (Levitt, 1972).

Significance of survival for crop plants

Turner and Burch (1983) point out that "survival of severe stress is less important in crop species than in natural communities, because crops that are severely stressed usually yield poorly", a subject that will be addressed in more detail in the following chapter. Seedling survival and survival in the vegetative phase may be important in situations where the probability of rainfall increases with the life of the crop, i.e., prior to flowering or fruiting (Johnson, 1980).

Low lethal water status influences survival, but has no direct effect on yield components. It is suited to intermittent stress environments, because it helps leaves and plants to survive until the next rainfall. There is genetic variability in a number of cultivated plants, but heritability of the trait has not been determined (Ludlow and Muchow, 1990).

Complex drought resistance mechanisms

In the previous sections various mechanisms of adaptation to water deficits have been described individually. This was necessary for the sake of clarity and convenience. Under field conditions, it is rare that plants react to water deficits by relying on a single physiological or morphological trait; usually multiple mechanisms are activated at the same time (Radin, 1983). One example is the photosynthetic pathways that have developed in response to drought.

Photosynthetic pathways and drought resistance

The C₄ and CAM pathways are mechanisms of ecological adaptation; the latter even enables survival under extreme climatic conditions, at least in certain plants.

* Bound water: due to the presence of hydrophilic colloids, a fraction of the water in the tissue is so tightly held, that the energy of the water molecules is apparently reduced to such a low level that other properties are also changed. This fraction is called 'bound water' (Currier, 1967).

The adaptive advantage of the C₄ pathway is especially great under conditions of short and irregular periods of rainfall, frequent diurnal and seasonal water stress, high light intensity, high day temperatures and evaporative demand, i.e., typical hot semi-arid climate conditions. This explains why the major concentration of C₄ plants is in the semi-arid tropics and subtropics, where they have apparently evolved as an adaptation to hot, dry, and possibly saline conditions (Ludlow, 1976).

Where net photosynthesis is not limited by environmental and physiological factors, C₄ grass leaves are not light-saturated at mid-day summer light intensities, whereas leaves of C₃ plants are saturated at one-third to half of these values. This response of C₄ plants is due to a continual decline in stomatal resistance and intracellular resistance with increasing light intensity. The marked difference between leaves of C₄ and C₃ plants is gradually reduced as shading increases. C₄ plants are not able to survive in heavy shade (Ludlow, 1976).

The optimum temperature range for C₄ plants (30–45°C) is considerably higher than that of C₃ plants (10–25°C) (cf. p. 67). Under such conditions, the C₄ plants derive a substantial advantage from their more efficient trapping of CO₂, which occurs during photorespiration (Huber and Sankhla, 1976).

C₄ plants are also highly competitive: under cultural practices that favour C₃ crops, various C₄ weeds grow very well, while permanent pastures of C₄ grasses are almost free of weeds (Black, 1971).

The higher growth rates and water use efficiencies of the C₄ grasses aid survival in semi-arid conditions with low, variable and intermittent rainfall, especially if a minimum amount of C fixation is essential for flowering and seed production in annuals or for the formation of dormant buds and reserve materials in perennials. The tolerance of high temperature without adverse effects promotes early flowering and seed maturity (Ludlow, 1976).

Another advantage under drought conditions is the ability of young leaves of many C₄ plants to withstand leaf water potentials as low as –100 bar and recover without injury after stress is removed (Ludlow, 1976).

From a review of the literature, Huber and Sankhla (1976) conclude that “the C₄ pathway may be looked upon as a complementary mechanism offering selective ecological advantage to the plant”.

Large groups of plants with the CAM photosynthetic pathway have gone to the extreme of keeping their stomata closed almost all day; this adaptation to drought environments is very effective in conserving the water potential of the plants, because relative air humidity is fairly high at night, at the time the stomata are open.

Succulence seems to be a prerequisite for CAM; it provides a high capacity for accumulation of malate in the vacuoles during darkness. This apparently prevents an excess of malate in the cytoplasm, which might otherwise cause a premature feedback inhibition of PEP carboxylase (Ludlow, 1976).

CAM species generally show slow growth rates and low productivity in their natural habitats, i.e., climatic zones where periods of drought alternate regularly with

rainy periods. From this, Kluge (1976) concludes that CAM is not a mechanism for providing high rates of photosynthesis, but rather for maintaining a positive carbon balance during seasons of drought.

Examples are known in which stress caused a shift from C₃ to CAM metabolism (Huber and Sankhla, 1976). This shift is apparently regulated, at least partially, by light, temperature, leaf ontogeny, nutrition, and bioregulants.

Differences between C₄ plants

Crop species with the C₄ pathway may differ, qualitatively and quantitatively, in their drought resistance. Hsiao et al. (1976) have made a detailed comparison of the contrasting behaviour of two major crops, maize and sorghum, under contrasting conditions of adequate water supply and water deficits. The following summary of their findings will serve as an example of how different crops, both with C₄ pathway, differ in their drought resistance.

Crop yields, under irrigation and on stored soil moisture, respectively, give an indication of the overall response of these two crops to soil moisture regimes.

Sorghum clearly has a lower yield potential than maize when soil moisture conditions are favourable; under conditions of a more limited water supply, maize yield is considerably reduced and lower than that of sorghum, which is hardly affected. The relative yield reductions due to the less favourable moisture regimes were 54% for maize, and only 9% for sorghum. It should be stressed that the crops grown without irrigation were submitted to extreme drought conditions. The soil, a deep Yolo clay loam, had been fully wetted to a depth of 3 m before sowing, providing a relatively favourable moisture supply which was progressively reduced during the growing period, but was still sufficient for normal grain formation, as evidenced by the relatively high yields produced by the two crops. There is little doubt that under more extreme conditions the differences between the two crops would have been still more striking.

This experimental evidence is confirmed by practical experience in Israel. Sorghum, grown on stored moisture only, produces high yields (up to 4 ton/ha); under the same conditions, maize usually fails to produce an economic crop.

The first advantage of the sorghum is clearly evidenced in Table 6.1, namely, its ability to increase its harvest index under conditions of limited moisture supply, i.e., to increase the proportion of assimilates diverted to grain formation, a trait visibly lacking in maize.

In addition to the more favourable partitioning of assimilates among competing sinks, sorghum has a greater ability than maize to adjust or maintain grain number in water-limiting conditions.

Sorghum is the more 'plastic' of the two crops in reproductive development: should the number of seeds be reduced by drought, this can be, at least partly, compensated for by its ability to form tillers and branch heads freely. Maize, being determinate in

TABLE 6.1

Grain, yields of maize and sorghum at Davis, CA

| | Irrigated | | Unirrigated | |
|-----------------------|---------------|------|---------------|------|
| | yield (kg/ha) | H.I. | yield (kg/ha) | H.I. |
| Maize (DeKalb XL 22) | 11 300 | 0.47 | 5200 | 0.43 |
| Sorghum (Pioneer 846) | 8780 | 0.48 | 8000 | 0.55 |

After Acevado et al. (1979).

its reproductive growth after the ear has reached a certain size, cannot compensate for stress effects on the number of grains by forming new heads.

Panicle formation on sorghum tillers mature later than those of the main shoot, thereby ensuring that all the panicles are not at the same stage of development if and when water stress occurs; maize does not tiller, and therefore does not have this escape mechanism.

When sorghum is planted at a given population density, it can reduce the number of heads per unit area if soil moisture becomes limiting during the early vegetative stage. Maize is obliged to invest all resources in the number of ears dictated by the planting density, and may therefore fail to fill the young grain in case of terminal drought.

In both crops, most of the dry matter for the grain comes from photosynthates produced after flowering. In sorghum, these are mainly supplied by the panicle and the upper leaves. In maize, the main source of assimilates is the five to six leaves at and above the ear node; an additional quantity may be translocated from lower leaves. The canopy structure of maize allows more light penetration to the lower leaves than with sorghum at the same leaf area index. Water stress hastens the senescence of leaves, which progresses from the base of the stem upward, and will therefore have a more adverse effect on maize than on sorghum.

Photosynthesis is more adversely affected by water deficits in maize than in sorghum: stomata of maize begin to close earlier than in sorghum when water is limiting; therefore sorghum should be able to maintain a normal photosynthetic rate for a longer time than maize when water deficits develop.

There is also a difference in the ability for osmotic adjustment in favour of sorghum, which shows full osmotic adjustment under mild but prolonged stress. Osmotic adjustment of maize under the same conditions is apparently not as complete.

Many authors have assumed that a major advantage of sorghum over maize under drought conditions is due to the characteristics of the root systems of the two crops. Though both root systems are about equal in extent, the ratio of secondary to primary roots is twice as great for sorghum as for maize at various stages of development.

From a review of a number of studies, Hsiao et al. (1976) conclude that the evidence indicates that the differences in the root systems of the two crops are of minor

importance in explaining the differences in behaviour under conditions of water deficit.

In conclusion, it can be stated that the advantage of sorghum over maize under drought stress, with minimal adverse effects, is not due to a single overriding character, but to a fortunate combination of many avoidance and tolerance mechanisms which “allow the plant to avoid excessive tissue water deficits and continue growth and development under mild stress conditions and to tolerate desiccation when the stress becomes severe” (Krieg, 1983).

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