

A CRITICAL EVALUATION OF TRAITS FOR IMPROVING CROP YIELDS IN WATER-LIMITED ENVIRONMENTS¹

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I. INTRODUCTION

Breeding improved genotypes for the arid and semiarid tropics by selecting solely for grain yield is difficult, because of the variability in amount and temporal distribution of available moisture from year to year. The genotypic variance in yield is low under these conditions; plant characters that influence performance have differing opportunities for expression in different years. Plant breeders (Blum, 1983; Rosenow *et al.*, 1983) and crop and plant physiologists (Bidinger *et al.*, 1982; Garrity *et al.*, 1982) believe better adapted and higher yielding genotypes could be bred more

¹This paper is based substantially on one first published by ICRISAT: Ludlow, M. M., and Muchow, R. C. (1988). Critical evaluation of the possibilities for modifying crops for higher production per unit of precipitation. ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). In: Research on Drought Problems in the Arid and Semi-Arid Tropics. Proceedings of the International Consultants Meeting, 17–20 November 1986, pp. 179–211. ICRISAT Center, India. Patancheru, A.P. 502 324, India: ICRISAT.

efficiently and effectively if attributes that confer yield under water-limited conditions could be identified and used as selection criteria. However, there are few examples where this approach has been used, and even fewer where it was successful (Passioura, 1981; Richards, 1982). This is partly due to the difficulty of understanding what causes low grain yields and how putative traits enhance drought resistance and contribute to grain yield in water-limited environments. For example, because final yield is an integral of the growth over the whole season, a trait that influences the ability of the plant to grow during or to survive a period of moisture stress may be relatively unimportant in the context of the total life of the crop.

Too often, traits are advocated based on theory, laboratory experimentation, or correlations (probably more casual than causal) between the presence of the trait and yield in drought-prone environments, without sufficient attempt to demonstrate whether and how the particular trait contributes to final yield. Proline accumulation is a good example of such a trait, which has not proved valuable as a selection criterion. High proline accumulation was advocated as a drought-resistance trait in barley because of its correlation with grain yield in water-limited environments (Stewart and Hanson, 1980). However, subsequent research showed that most of the proline was in dead leaves (Hanson *et al.*, 1979) and hence made no contribution to survival, let alone to grain yield. In addition, few attempts have been made to establish if there is genetic variability for particular traits among genotypes of the crop, and even fewer to study their inheritance. All these steps are necessary to ensure that an increase in yield will occur in the target environment when a trait is introduced into otherwise well-adapted genotypes with good yield potential. However, with few exceptions this rarely has been done. Consequently, it is not surprising that the success rate has been low.

Many traits have been proposed for improving the performance of drought-affected crops (see Seetharama *et al.*, 1983, for references prior to 1983; Clarke and Townley-Smith, 1984; Turner, 1986a,b). We will restrict our coverage of these traits to assessing critically both their demonstrated contribution to grain yield and the proposed benefits, using a framework proposed by Passioura (1977) for analyzing the yield of crops in water-limited environments. In Passioura's terms, grain yield is a function of *water transpired*, *water-use efficiency*, and *harvest index*; these identities are called *components of grain yield* in this paper. In addition, because survival of leaves or plants has an important influence on final grain yield in areas with intermittent water stress, the proposed and demonstrated benefits of traits conferring survival will be assessed using a framework similar to the one proposed by Levitt (1980): *drought escape* and *drought resistance* (*dehydration avoidance* and *dehydration tolerance*). There seems

little point in pursuing a trait unless it can be shown that it either benefits one of the components of grain yield (Passioura, 1986) or contributes to one of the determinants of survival.

With the exception of osmotic adjustment—a trait with many ramifications for both yield and survival—only the direct effects of particular traits are discussed. We have not attempted to assess the antagonistic or synergistic effects arising from the simultaneous presence of two or more traits. A discussion about the need to consider groupings of traits—called *strategies*—is given by Ludlow (1988).

In this review, we describe the components of yield and the determinants of survival against which the proposed and demonstrated contributions by traits are critically assessed. The cost of the traits is also discussed, as well as the impact upon both *potential* (i.e., yield in the absence of water deficits) and *stability* of yield. Then we consider if there is genetic variability for the trait and whether the inheritance has been determined. Finally, we make a judgment about whether a trait is desirable for crops growing in two different moisture environments (*intermittent* and *terminal*), typical of the semiarid tropics in both modern (opportunistic) and subsistence (conservative) agriculture.

We have differentiated between modern and subsistence agriculture mainly by the degree of risk that can be tolerated. Although there are economic imperatives for farmers in modern agriculture to ensure some yield, there is a far greater imperative for the subsistence farmer in developing countries, who has to ensure some yield to prevent starvation. Thus the farmer in the developed country can afford to be a greater risk taker.

The potential value of a trait depends upon the crop and the moisture environment in which it is grown. Clearly we cannot cover all crops and all water-limited environments in this review. Consequently, because of our experience and because of the urgent need to increase food production by breeding superior varieties of crops, particular emphasis has been given to the semiarid tropics. Two contrasting moisture environments are considered. *Intermittent stress* is typical of the wet season in the monsoonal semiarid tropics, when stress can occur at any time and with varying intensities between emergence and maturity, especially on lighter soils. *Terminal stress* is typical of the dry season of the semiarid tropics, where crops are usually grown on heavy soils solely on stored moisture, and where the crop grows and matures on a progressively depleted soil moisture profile. Although we have used information from all dryland crops to assess the value of particular traits, we have given particular emphasis to grain sorghum (*Sorghum bicolor*) as an example of a tropical cereal and cowpea (*Vigna unguiculata*) as an example of a tropical food legume. Both

these crops are grown in the semiarid tropics. However, the approach and most of the information can be applied to any dryland crop. Obviously specific crops will have particular requirements, which may not be covered in a general review such as this. To summarize, we list in order of priority the traits that we believe will increase crop yield in these four water-limited environments.

II. FRAMEWORKS FOR ASSESSING THE VALUE OF TRAITS

A. COMPONENTS OF GRAIN YIELD

Passioura (1977) proposed that grain yield of crops in water-limited environments could be analyzed in terms of three identities that are largely independent:

$$\text{grain yield} = \text{water transpired} \times \text{water-use efficiency} \times \text{harvest index}$$

1. Amount of Water Transpired

In the absence of weeds, the potential amount of water transpired by a crop is the sum of the precipitation during the growing season and the available water stored in the soil at sowing. Depending on seasonal and soil conditions, amounts can be deducted due to direct evaporation from the soil surface, available soil water left at maturity, deep drainage, and runoff (Fig. 1). Because genetic manipulation cannot influence runoff, it is not considered further here.

After extensive analyses, many workers (see, e.g., de Wit, 1958; Fischer and Turner, 1978; Tanner and Sinclair, 1983) have shown that biomass accumulation is linearly related to cumulative transpiration. In theory, this means that to obtain maximum productivity, soil evaporation should be minimized, and crops should extract as much water as possible. However, there are high risks associated with this strategy in environments of variable water supply because the crop may exhaust the available soil water before maturity. Greater yield stability would be achieved with a more conservative strategy, where water use is less than the expected supply.

Since soil evaporation depends largely on the radiation reaching the soil surface when it is wet, a crop that reaches full ground cover quickly in regions where rain is frequent will reduce soil evaporation and ensure that a high proportion of the soil water is used as transpiration. Where there is

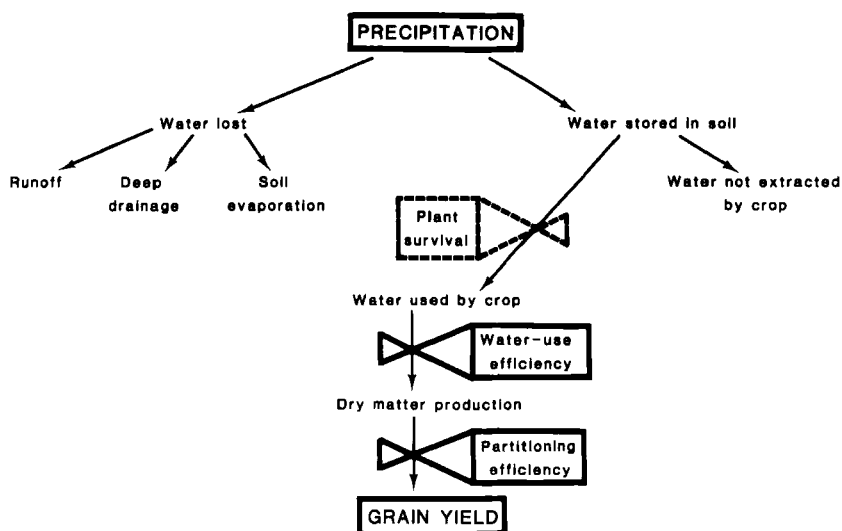


FIG. 1. Schematic relationship between precipitation and grain yield.

little soil evaporation, however—as when growth depends entirely on soil water stored at sowing—or where there is a low expectancy of precipitation during grain growth, rapid early growth could leave insufficient soil water to complete grain filling. In the case of annual row crops, soil evaporation, which depends strongly on precipitation patterns, is highly variable until leaf area index is about 2.5–3. Singh and Russell (1979) estimated that direct evaporation loss from a sorghum crop growing on an alfisol was 21% and 23% of the total seasonal available water during the monsoon season and post-rainy season, respectively. These values compare favorably with the 30–60% estimated loss for mediterranean environments (French and Schultz, 1984; Cooper *et al.*, 1983), but they still represent a considerable loss of potential productivity. It is difficult to assess the scope for further reduction of evaporation losses, because of the high prevailing temperatures and consequent rapid canopy development in the absence of water limitation in the semiarid tropics. There appears more scope to reduce soil evaporation in subtropical and temperate climates where rain falls frequently during the growing season, by selecting for varieties with early vigor.

Although Passioura's approach requires measurement of water transpired, most data simply combine transpiration and soil evaporation. There is an urgent need to estimate soil evaporation so that the potential benefits from manipulating this component might be assessed.

2. Water-Use Efficiency

Water-use efficiency is defined here as the ratio of shoot biomass production (root biomass is rarely measured) to the total amount of water transpired. This has been termed the *T-efficiency* (in contrast to the *ET-efficiency*, which includes soil evaporation) by Tanner and Sinclair (1983), who have thoroughly discussed it from leaf to whole-crop level. They concluded that water-use efficiency was inversely related to the saturation deficit of the air. Differences among crop species are related to carboxylation pathway (being twice as high for C₄ as C₃ species) and the energy required to produce biomass containing different proportions of protein, lipid, and carbohydrate.

Similarly, the apparent difference in water-use efficiency (ET-efficiency) between cultivars of the same species and among several food legumes reported by Muchow (1985) can be related to differences in soil evaporation and in the chemical composition of the dry matter. In addition, Wilson and Jamieson (1985) found that 11 wheat crops had the same water-use efficiency, once allowance was made for saturation deficit of the air. The claim by Maruyama *et al.* (1985) that indica rice showed higher water-use efficiency than japonicas, in pots in the field, is flawed by the absence of any measure of evaporation from the free water surface in each treatment. We are, therefore, not aware of any proven differences in water-use efficiency within a species or within groups of C₃ or C₄ plants in the field (Angus *et al.*, 1983; Tanner and Sinclair, 1983). (See Section III,b,15.)

At the whole-crop level, water-use efficiency appears insensitive to drought, salinity, and soil fertility (de Wit, 1958; Fischer and Turner, 1978; Hanks, 1983; Walker, 1986). This may seem surprising since, in theory, mechanisms at the leaf level—such as leaf movement, increased leaf reflectance, and temporary stomatal closure during periods of peak evaporative demand—should improve water-use efficiency. However, a rise in leaf temperature caused by stomatal closure may increase the difference in water vapor pressure between the crop and the air, which reduces transpiration efficiency. It may also increase maintenance respiration. Both these responses may negate improvement of water-use efficiency associated with stomatal closure. Perhaps more important, the amounts of C fixed and water lost during periods of water stress are probably so small compared with seasonal totals of biomass and transpiration that the effect of a higher water-use efficiency during the stress on seasonal water-use efficiency is negligible. Water-use efficiency could be raised if respiration rate was decreased, if mesophyll conductance was reduced with no change in sto-

matal conductance, and if more dry matter was partitioned to the shoots at the expense of roots (Passioura, 1983, 1986).

3. *Harvest Index*

Harvest index is defined here as the ratio of economic (grain) yield to shoot biomass at maturity. Over the past century, raising the harvest index has improved the genetic yield potential of the major field crops (Gifford *et al.*, 1984). Harvest index depends, among other factors, on the relative proportion of pre- and postanthesis biomass and on the mobilization of preanthesis assimilate to the grain. A severe water deficit at a critical growth stage, such as flowering, greatly decreases seed numbers and harvest index (Inuyama *et al.*, 1976). The pattern of water supply also has a large effect on harvest index. For example, Bond *et al.* (1964) observed in sorghum that with adequate water supply until heading, followed by drought, a large biomass and small harvest index were obtained, while the reverse sequence of water supply resulted in nearly as much grain from much less biomass. Similarly, in crops that rely predominantly on stored water, the harvest index is related to the amount of water available after anthesis (Passioura, 1977).

In summary, relatively few principles underlie crop modifications that provide for more efficient use of precipitation in crop production. Crop breeding should aim to maximize transpiration at the expense of soil evaporation and drainage. Basically this involves extending canopy cover as long as practical to minimize evaporation, matching the crop life cycle to the seasonal water availability, and modifying rooting behavior to increase soil water supply or change the timing of withdrawal. Breeding can influence the partitioning of dry matter to economic yield and the timing of flowering so as to maximize harvest index. Since breeding has failed to increase the maximum photosynthetic capacity of crops (Gifford *et al.*, 1984), the prospect for improved efficiency of water use would seem to be low. However, if transpiration efficiency could be improved and if this were translated to improvements at the crop level, there would be direct benefits for grain yield. The best prospects at the moment for improving grain yield of crops appear to be by increasing the amount of water transpired and maintaining harvest index.

B. DETERMINANTS OF PLANT SURVIVAL

Plants must survive intermittent short-term water deficits if they are to contribute to economic yield. Moreover, in a terminal stress, the longer

- ◆ Drought Escape
- ◆ Drought Resistance
 - Dehydration Avoidance
(Maintenance of Turgor and Volume)
 - maintenance of water uptake
 - reduction of water loss
 - changes in tissue characteristics
 - Dehydration Tolerance
 - protoplasmic tolerance

FIG. 2. Ways plants survive drought. (Adapted from Levitt, 1980.)

leaves and other plant parts can survive during grain filling, the more likely they are to contribute to yield either directly, by supplying carbon to the developing grains, or indirectly, by preventing lodging in sorghum. Consequently, we are interested in how plants survive drought and how traits influence yield by enhancing the determinants of survival (Fig. 2).

To survive periods of water deficits, higher plants may use one of two main strategies (Begg and Turner, 1976; Turner, 1979, 1982, 1986a,b). Desert ephemerals and short season annuals have such a short life cycle that they germinate after rain, grow rapidly, flower, and set seed before the soil water is exhausted in arid environments with low and variable rainfall. These plants are said to *escape* drought or water deficits in their tissues (Fig. 2). The cost of such a strategy however, is lost opportunity and low yield in better than average seasons.

Longer season annuals and perennials survive water stress by one of two *drought resistance* strategies (Fig. 2). The first group *avoids* water deficits in tissues—despite the absence of rainfall and the presence of hot, dry atmospheres—by maintaining cell turgor and cell volume. This can be done by maintaining water uptake, reducing water loss, and changing tissue characteristics, such as osmotic adjustment or an increase in tissue elasticity. The second group resists drought because its tissues are able to *tolerate* dehydration, usually because of superior protoplasmic tolerance of desiccation.

Putative traits that improve yield per unit of precipitation by enhancing plant survival must act through one or more of the determinants given in Fig. 2.

III. CRITICAL ASSESSMENT OF THE CONTRIBUTION TO YIELD OF PUTATIVE TRAITS

A. APPROACHES TO DETERMINE THE CONTRIBUTION OF PUTATIVE TRAITS

It is difficult to obtain unequivocal proof of the value of a trait, so that perceptions are often based on opinion rather than fact. Blum (1983) argues that it is not worth attempting to prove the value of a trait because of the difficulties involved, and that if a trait appears desirable even on theoretical grounds alone, it should be introduced into a breeding program with simultaneous selection for both the trait and high yield under non-stressed conditions. Genotypes are tested in water-limited environments only after the trait and yield potential have been combined. Clearly, there are risks and possible inefficiencies associated with his approach, especially if the trait proves ineffective. Only time will tell whether Blum's more pragmatic approach is effective, and the degree to which the value of traits needs to be assessed before they can be advocated as selection criteria to improve production per unit of precipitation.

A common approach for assessing the value of traits is the comparison of grain yields of *isogenic* or *near-isogenic* lines or populations—genotypes that have a similar genetic background but contrast in the expression of the trait (Richards, 1988). This approach is restricted to traits that are controlled by one or only a few genes, because isogenic lines cannot be developed for quantitatively inherited characters. It is also possible that traits may be expressed differently in different genetic backgrounds. If this is so, the information from isogenic lines may be of limited value. Another approach is to use simulation modeling (Jordan *et al.*, 1983a; Jones and Zur, 1984; Loomis, 1985; Muchow and Sinclair, 1986; Sinclair *et al.*, 1987; O'Toole and Bland, 1988), in which simulations are performed with all other factors being held constant, while the trait is absent or present to varying degrees. The value of maturity, osmotic adjustment, and deep-rootedness in wheat, sorghum, and crops in general have been assessed in this way (Jordan *et al.*, 1983a; Jones and Zur, 1984). Although this approach is rigorous, unequivocal, and intellectually appealing, its application depends upon having an adequate simulation model for the particular crop and sufficient understanding of the trait and its mode of operation. Good simulation models are now becoming available (see, e.g., Sinclair, 1986), but we lack sufficient understanding of many of the putative traits. More research is needed to understand the mode of action of traits and to apply simulation models for assessing their value.

Another, but less satisfactory, approach is to compare lines that differ in a trait while having as similar a genetic background as possible (especially phenology), but which are not necessarily isogenic or near-isogenic. This approach depends upon understanding the steps or processes between the presence or the degree of the trait and grain yield, and establishing the *internal consistency* in correlations for each of the intervening steps. Not only must the presence or strength of the trait be correlated with grain yield, but also there needs to be a continuous and consistent series of correlated steps between grain yield and the degree of expression of the trait. Santamaria *et al.* (1990) and Ludlow *et al.* (1990) have used this approach to assess the contribution of osmotic adjustment to grain yield of sorghum from three maturity groups. For example, there was internal consistency in the following sequence when Texas 671 and E57 were subjected to a preanthesis stress: high osmotic adjustment (E57), better turgor maintenance, more root growth and soil water extraction at depth, higher dry matter production, higher grain number, and higher grain yield (see also Wright *et al.*, 1983b; Morgan and Condon, 1986).

Further discussion on determining the value of traits can be found in Stewart and Hanson (1980), Hanson and Hitz (1982), Richards (1982, 1988), and Passioura (1986).

Here we use evidence from all these approaches where possible to assess critically the contribution of putative traits to grain yield by way of the components of yield or the determinants of survival.

B. PUTATIVE TRAITS

The demonstrated and proposed benefits of each trait for grain yield are assessed in terms of contribution through the components of production (Fig. 1) and the determinants of survival (Fig. 2), yield potential, and stability of yield, together with the cost of production (Table I).

1. Matching Phenology to the Water Supply

Genotypic variation in growth duration is one of the most obvious means of matching seasonal transpiration with the water supply and thus maximizing water transpired. Early flowering tends to give higher yield and greater yield stability than later flowering, if rain does not occur during the latter half of the growing season. Moreover, if it enables a cultivar to escape drought during the critical reproductive stages, harvest index is improved. Development of short season varieties provides benefits where

Table I

Critical Assessment of Putative Traits by Contribution to Components of Yield and Determinants of Survival, including Cost to Production, Contribution to Yield Potential and Stability, and Possibility for Genetic Manipulation, as well as Recommendations for Intermittent and Terminal Stress Environments in Both Modern and Subsistence Agriculture^a

	Matching phenology to water supply	Photo-period sensitivity	Developmental plasticity	Mobilization of preanthesis dry matter	Rooting depth & density	Low root hydraulic conductance	Early vigor	Leaf area maintenance	Osmotic adjustment	Low lethal water status	Reduced stomatal conductance	Leaf movements	Leaf reflectance	Heat tolerance of seedlings	Low epidermal conductance	Transpiration efficiency
<i>Yield components</i>																
Water transpired	+ ^b	+ ^b	+	(0)	+ ^c	-,0	+	(0,+)	+	(0)	-	(0) ^o	0 ^o	(+)	(0) ^o	(0) ^q
Water-use efficiency	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	0	(0)	(0)	(0) ^p	+	(0)	(0)	?
Harvest index	+ ^b	+ ^b	+ ^c	+	+,-	+	0,- ^k	(+,-) ^l	+ ^g	(0)	(0)	(0)	0	(0)	(0)	?
<i>Survival determinants</i>																
Drought escape	+	+	+	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
Dehydration avoidance	(0)	(0)	(0)	(0)	+	+ ⁱ	(-)	-	+,- ^l	(0)	+	+	+	(0)	+	(0) ^r
Dehydration tolerance	(0),	(0)	(0),	(0)	(0)	(0)	(0)	(0)	+	+	(0)	(0)	(0)	?	(0)	0
Cost of trait	(no)	(no)	(no)	(no)	no ^f	no	(no)	no	no	(no)	yes	(no)	(no) ^o	(no)	(no)	(no) ^r

(continued)

Table I (continued)

	Matching phenology to water supply	Photo- period sensitivity	Develop- mental plasticity	Mobiliza- tion of preanthe- sis dry matter	Rooting depth & density	Low root hydraulic conduc- tance	Early vigor	Leaf area mainte- nance	Osmotic ad- justment	Low lethal water status	Reduced stomatal conduc- tance	Leaf move- ments	Leaf reflectance	Heat tolerance of seedlings	Low epidermal conduc- tance	Transpi- ration efficiency
<i>Contribution to yield</i>																
Yield potential	(0)	(0)	(0)	(0)	0, - ^f	0 ^j	(+)	0, -	(0)	(0)	-	(0) ^o	(0)	(0)	(0)	(+) ^q
Yield stability	+	+	+	+ ^d	+ ₀	+	(+, -) ^l	+, - ^l	+ ^g	(+)	(+)	(+)	+	(+)	(+)	(0)
<i>Genetic variability</i>	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
<i>Heritability known?</i>	yes	yes	yes	?	yes	yes	?	yes	yes ^m	?	yes	?	yes	?	?	yes
<i>Recommended for: Modern agriculture</i>																
Intermittent stress	yes	no	yes	yes	yes	no	yes	yes	yes ^g	yes	no	yes	yes ^l	yes ^q	yes	yes
Terminal stress	yes	no	no	yes ^d	yes ^g	yes	yes	yes ^g	yes ^g	no ⁿ	no	no	yes ^l	yes ^q	no	yes
<i>Subsistence agriculture</i>																
Intermittent stress	yes	yes	yes	yes	yes	yes	yes	yes	yes ^g	yes	yes	yes	yes ^l	yes ^q	yes	yes
Terminal stress	yes	yes	no	yes ^d	no ^h	yes	no ^h	no	no ^h	no ⁿ	no	no	yes ^l	yes ^q	no	yes

^aContributions are assessed as positive (+), negative (–), or none (0). Parentheses are used when the contributions are expected from theory or first principles, but where they have not been shown. A question mark is used when information is unavailable or unknown. Cost is defined in terms of carbon or energy.

^bCould be negative in other than average seasons.

^cOnly if hand-harvested in developing countries.

^dAs long as crop does not lodge.

^eOnly if existing root length density or root depth is insufficient to extract all available soil water, and if deep water is recharged each year.

^fIf a unit of C invested in roots results in more water uptake than the reverse of water-use efficiency, the investment will not have a net cost compared with investing that unit of C in the shoot.

^gAs long as available soil water is not exhausted before maturity.

^hRisk of exhausting soil water before maturity is too high.

ⁱUnless low conductance causes relative water content to fall to lethal levels under hot, dry conditions.

^jOnly if seminal roots have low conductance.

^kIf early vigor causes exhaustion of soil water before maturity.

^lPositive if soil water is not exhausted, negative if it is.

^mMorgan *et al* (1986) have suggested that osmotic adjustment is simply inherited.

ⁿUnless the relative water contents at which leaf expansion and photosynthesis cease also decrease, this trait only prolongs time until lethal values are reached, and consequently it makes no contribution to production in a terminal stress situation.

^oGenerally negative, but probably insignificant for crop water use or performance.

^pGenerally positive, but probably insignificant for crop water use efficiency.

^qCould be negative if higher transpiration efficiency is due to transpiration being reduced more than photosynthesis, but production would suffer, and vice versa.

^rCould be positive and “yes” if higher transpiration efficiency is due to transpiration being reduced more than photosynthesis, but production would suffer, and vice versa.

^sIn environments where soil surface temperature cause seedling mortality.

^tThe scope for improvement may be small if current varieties are glaucous or bloomed.

rainfall is reasonably predictable, but in unpredictable environments, potentially transpirable water may be left in the soil at maturity in better years, and yield is sacrificed. This is shown in the study by Jordan *et al.* (1983a) on sorghum and by that of Muchow and Sinclair (1986) on soybeans, where simulated yields for an early maturing genotype were higher only when yields were reduced by at least 40% by low water supply. In contrast, later flowering may be beneficial where drought occurs early in the growing season or where grain maturation is delayed until after the humid season has ended, lowering the incidence of grain molds (Curtis, 1968).

Water balance models can be used to predict the average length of the growing season; for example, Cocheme and Franquin (1967) used rainfall and potential evapotranspiration data to estimate the duration of the growing season for adapted crops in the Sahelian and Sudanian zones of West Africa. They estimated that in the northerly zones, cultivars were needed that could mature in only 70 days, whereas growing seasons exceeding 200 days were available in the subhumid zone to the south. While phenology appropriate for the expected water supply is a valuable trait, particularly in terminal stress situations, it is a conservative trait and may contribute to lower yields in unpredictable intermittent stress situations, though yield stability would be improved. There is genetic variability for phenology, and the inheritance is known in some cases (Fery, 1980).

2. Photoperiod Sensitivity

Photoperiod control provides a mechanism whereby the time of flowering coincides with the average date of the end of the rainy season. This has been shown for sorghum (Bunting and Curtis, 1970), bulrush millet (Cocheme and Franquin, 1967), and cowpea (Summerfield *et al.*, 1974) in the Sudanian and Sahelian zones of Africa. Photoperiod control provides similar benefits to matching phenology to the soil water supply, as discussed earlier. However, a major problem with photoperiod-sensitive cultivars is that they are narrowly adapted. Consequently, many cultivars must be available for different latitudes and rainfall regimes or for planting during different seasons. Moreover yields are sometimes conservatively low.

We believe, therefore, that it is an appropriate trait for both intermittent and terminal stress environments in subsistence agriculture, but of less importance in modern agriculture. There is genetic variability for this trait (Curtis, 1968), and its inheritance is known in some cases (Fery, 1980).

3. *Developmental Plasticity*

Developmental plasticity is the mechanism whereby the duration of the growth period varies depending on the extent of water deficit. Drought-induced early maturity may be advantageous in dry years. However, because it is a facultative response the plant is still able to respond to longer seasons and produce larger yield during wetter years. Turk and Hall (1980) observed differences between harvest dates as large as 21 days for cowpea that were sown at the same time but were grown under limited or abundant water supply. In addition, Lawn (1982a) and Sinclair *et al.* (1987) found that the developmental plasticity of cowpea and mung bean contributed to their superior performance over soybean in water-limited environments. Developmental plasticity ensures that all the available water is transpired.

Indeterminateness in flowering could also be worthwhile where water supply during flowering is uncertain or total seasonal supply is highly variable, because this permits fruiting to occur in flushes during favorable periods. Determinate crops have only a single chance for successful reproduction, unless lateral flower heads and panicles on tillers are produced. Most of the sorghums grown in the semiarid tropics do not produce tillers (Seetharama *et al.*, 1982), whereas tiller number in millet adjusts to the water supply (Mahalakshmi and Bidinger, 1986).

Plasticity in the length of the growing season, indeterminacy, and tillering and branching all have the disadvantage of uneven maturation, and harvest index tends to be low with mechanized harvesting. However, delayed reproduction until water deficits are relieved combined with hand harvesting during the growing season in subsistence agriculture could increase the harvest index. Developmental plasticity would seem advantageous for genotypes in both modern and subsistence agriculture where unpredictable intermittent water deficits occur, but it would be of little advantage in terminal stress situations where late rains are unlikely to occur.

4. *Mobilization of Preanthesis Assimilate to Grain*

The relationship between C accumulation and the amount of water transpired (Tanner and Sinclair, 1983), and the correlation between harvest index and postanthesis water use (Passioura, 1977) suggest that grain yield is strongly dependent on biomass accumulation after anthesis in water-limited environments. However, some workers (Blum *et al.*, 1983b;

Turner and Nicholas, 1988) have shown that the contribution to yield of preanthesis assimilate can be significant under drought. It is difficult to assess accurately from biomass data the absolute contribution to grain yield of dry matter losses in other plant parts, particularly from leaf, and from root, which are seldom measured. Bidinger *et al.* (1977) observed that up to 20% of preanthesis assimilate can be transferred to the grain in water-stressed wheat. In contrast, values up to 80% have been recorded in grain sorghum subjected to water stress during grain filling (Santamaria, 1987). Significant retranslocation of preanthesis assimilate has been shown by Muchow (1989) in sorghum and pearl millet, but not in maize. A high transfer of assimilates to the grain would maximize the harvest index and reduce the proportion of dry matter produced early in growth that is left as stover. This trait would have no effect either on the amount of water transpired and water-use efficiency, or on any survival trait.

Mobilization of assimilate in response to water deficits per se should not affect yield potential. However, under well-watered conditions, Daniels *et al.* (1982) observed that high grain yield in spring barley was associated with large positive increases in stem dry weight after anthesis, indicating that there was more assimilate available than that required to fill the grains. Thus cultivars with a high capacity for storing assimilate in the stem may have a low yield potential because of a lower sink strength. The importance of this finding for water-limited environments depends upon whether cultivar differences in assimilate partitioning are similar under well-watered and water-limited conditions. Assimilate mobilization would tend to improve yield stability by acting as a buffer against the effects of water deficits on current assimilation. The exception to this would be where mobilization results in increased susceptibility to lodging (e.g., in sorghum, Rosenow *et al.*, 1983).

Blum *et al.* (1983b) have suggested that there may be useful genetic variation in mobilization that offers scope for improvement in wheat. Constable and Hearn (1978) found large differences between two soybean cultivars in the effect of water deficits on the contribution of stem storage to yield. Wright *et al.* (1983a) found no difference between two sorghum cultivars in mobilization, but Santamaria (1987) found considerable mobilization of preanthesis dry matter when accessions of grain sorghum were subjected to water stress during grain filling. Accessions with high osmotic adjustment retranslocated more preanthesis assimilate to grain than those with low osmotic adjustment. Although the evidence is inconclusive, we cautiously recommend this trait in the four stress situations. However, further work is required to assess the consequences of this trait on yield potential and lodging (in some crops) and upon root growth and nitrogen fixation in food legumes, particularly in intermittent stress situations.

5. Rooting Depth and Density

Differences in rooting patterns change the amount and timing of water availability to the crop. Greater depth and extent of soil water extraction could increase the amount of water transpired; if this results in the avoidance of water deficits at critical growth stages, it could increase harvest index. Deeper roots could also reduce some of the water lost by deep drainage. The traditional view is that a large vigorous root system, through avoidance of plant water deficits, is a major feature of high yield in water-limited environments. The implicit assumptions here are that water is available deep in the soil profile and is replenished each year, and that the existing root length density is insufficient to extract all the water (Clarke and Townley-Smith, 1984). If these conditions do not apply, then greater rooting depth and density will have no effect on the amount of water transpired and may reduce shoot dry weight or harvest index, because biomass is partitioned to roots at the expense of shoots.

Some evidence suggests deep roots may have additional benefits for water extraction and root function because water uptake continues at night, resulting in an increase in the soil water content of upper soil layers and presumably of roots in these layers (Richards and Caldwell, 1987). The water in these upper layers is extracted the following day. As well as aiding water extraction, this "hydraulic lift" would keep roots alive in the upper layers where most of the nutrients occur and hence would promote nutrient uptake. It may also reduce the production of hormone signals from the roots, which reduce leaf growth and stomatal conductance (Turner, 1986a).

Where water remains in the soil at maturity, usually below the root zone—as in some parts of the semiarid tropics when crops are grown on stored water following the monsoon season—greater rooting depth should lead to improved stability in grain yield. However, where the soil is not replenished at depth between crops, greater rooting depth would be of little advantage, and could even be disadvantageous in limiting the frequency with which the crop may be grown (Bremner *et al.*, 1986). To take account of yearly variation in weather, Jordan *et al.* (1983a) used the crop simulation model SORGF to assess the consequences of deep rooting in sorghum. The simulations showed that deeper roots increased yield by 20% in about one third of the 30 years considered, because in wet years soil water was not limiting and in the very dry years there was little available water at depth. Similarly, an increase in the simulated root zone depth has been shown to increase leaf area, growth, photosynthesis and transpiration (Jones and Zur, 1984), and yield (Muchow and Sinclair, 1986) of crops under drought. The assimilate cost of deeper rooting was not incorporated

into these models, so that the yield advantage may be overestimated.

Passioura (1982, 1983) has questioned the value of deep roots, because the water transpired to produce C for the extra root growth may offset the extra water gained by deep roots. Furthermore, the costs of root growth and maintenance represent clear diversions of assimilate, which might have been used for shoot growth, and thus may decrease yield potential. Passioura (1983) concluded that selection for a smaller root system—particularly in the topsoil, where rooting densities appear much larger than what is needed to extract all the water at a reasonable rate—might actually increase the above-ground yield. Such a proposal has merit in soils where crops extract all the available water from the soil each year. Moreover, it is supported by the observation of Blum *et al.* (1983a) that the only wheat variety in their study that did not show promoted root growth under mild stress using polyethylene glycol (PEG) solutions had the largest top growth. It is difficult to resolve the questions of the C cost of a deeper root system and the consequences on yield potential. Sorghum roots weigh about $50 \mu\text{g cm}^{-1}$ (Merrill and Rawlins, 1979), so an additional 50 cm of roots at a density of 0.5 cm cm^{-3} would require only 125 kg ha^{-1} more dry matter plus some additional respiration cost. This cost seems small when above-ground biomass at maturity can exceed $10,000 \text{ kg ha}^{-1}$ (Wright *et al.*, 1983a; Muchow, 1988, 1989). Alternatively, a deeper root system could have little additional assimilate cost if the root length density was distributed more uniformly down the soil profile (i.e., fewer surface roots and more at depth). Furthermore, several workers have shown that a greater rooting depth is associated with improved performance under water-limited field conditions (e.g., sorghum, Wright and Smith, 1983; wheat, Hurd, 1974; corn, Lorens *et al.*, 1987).

Genotypic variation in root characteristics of crop plants has been reviewed extensively by O'Toole and Bland (1988); variation occurs in both monocotyledons and dicotyledons. Many root characteristics have been shown to be under genetic control and quantitatively inherited.

Measurements of rooting depth and root length density to not necessarily given an estimate of the ability of a genotype to extract soil water. A root length density greater than $0.5 \text{ cm root cm}^{-3}$ soil can be adequate for complete extraction of available water, though many crops have rooting densities to much greater values of two to three, particularly in the surface layers (Passioura, 1982). The fact that root length densities can vary from 0.3 to $6 \text{ cm root cm}^{-3}$ soil in a range of temperate cereals and legumes, with no effect on soil water extraction (R. A. Richards, personal communication), suggests that root length densities may be in excess of requirements in some crops and that little will be gained by increasing root length density. However, water is frequently left behind in the subsoil by a

water-limited crop despite the fact that roots can be present at depth (e.g., sorghum, Jordan and Miller, 1980). Root length density at depth may be insufficient to extract all the water, though calculations by Passioura (1983) suggest that the frequencies of sorghum roots in the deeper profile should be sufficient to extract all the water available—unless only a portion of the roots is extracting the water, or the roots are constrained to certain limited regions of the soil, such as fracture planes and the channels of former roots or earthworms. Alternatively, the hydraulic resistance to water flow in the plant may limit water uptake by the crop, and this could affect the amount extracted. Indirect measurements of root activity, such as measurements of water extraction by water depletion methods (e.g., neutron moderation) are very prone to errors associated with the separation of extraction and drainage (Stone *et al.*, 1973), unless deep soils that have a lower layer with low hydraulic conductivity are used. Also the growth of roots into deep soil layers is clearly a function of both genotype and environment; the interaction between the two often makes it difficult to distinguish genotypic differences in root growth (Gulmon and Turner, 1978).

Given the potential for increasing the amount of water transpired, greater rooting depth and density are recommended in opportunistic situations, despite the possible risk of running out of water and the possible C cost on above-ground growth. In conservative situations of intermittent stress, greater root activity should enhance stability by reducing the incidence, and slowing the development, of water deficits. However, the risks of depleting water before maturity would make greater rooting depth and density undesirable in a terminal stress situation in subsistence agriculture.

6. Root Hydraulic Conductance

Decreased root hydraulic conductance has been proposed as a valuable trait by Passioura (1972, 1977) for crops growing predominantly on stored soil water. By restricting early water use, more water is available for grain filling, thus minimizing the decrease in harvest index. This trait should not affect the amount of water transpired in terminal stress situations, where the soil water store is exhausted at maturity, but in intermittent stress situations it may result in reduced uptake and less water transpired. In terms of survival determinants, low root hydraulic conductance should enhance dehydration avoidance, providing the lower conductance does not result in the relative water content reaching the critical value at which leaf death occurs.

In wheat, decreased root hydraulic conductance can be achieved by decreasing the diameter of the main xylem vessel in the seminal roots (Richards and Passioura, 1981a,b). Subsequent work has shown that in dry environments, wheat lines with small xylem vessels yielded more than lines with larger vessels (Richards, 1988). In good seasons, there was no yield penalty in having small xylem vessels, as the nodal root system overrides the effect of small xylem vessels in the seminal roots when the topsoil is wet. Thus in wheat this trait would increase yield stability but have no effect on yield potential in terminal stress situations. In sorghum roots, hydraulic conductance is likely to depend on the number of fully functional nodal roots, as the seminal root system ceases axial growth about two weeks after emergence (Blum *et al.*, 1977; Bremner *et al.*, 1986). The number of nodal roots penetrating deep into the profile depends on the surface soil water content during the early stages of nodal root growth (Blum and Ritchie, 1984). This environmental effect, combined with the relatively large size of these xylem vessels (R. A. Richards, personal communication), suggests that there may be little avenue for manipulating root hydraulic conductance in sorghum. Similarly, in dicotyledons root hydraulic conductance tends to be high since the capacity for secondary thickening may lead to large xylem cross sections (see, e.g., Meyer and Ritchie, 1980).

There is genetic variation for this trait in wheat, and it is heritable (Richards, 1988).

This trait is recommended in some cereals for both opportunistic and conservative terminal stress situations so that sufficient water remains for grain filling, leading to enhanced grain yields. In intermittent stress situations, reduced water uptake via lower conductance would seem disadvantageous, though in conservative situations this trait would slow the development of water deficits and enhance yield stability.

7. *Early Vigor*

Genotypes with early vigor and good seeding establishment tend to enhance transpiration at the expense of direct soil evaporation, particularly where the surface soil is wet by frequent rains. For 22 wheat lines growing on light-textured soils in a mediterranean-type environment, Turner and Nicholas (1988) found that vigorous early growth resulted in high dry matter yields by anthesis and improved grain yields with no decrease in harvest index. They suggested that on the deep sandy soils, vigorous early growth enabled greater root development, so that yields were not restricted by water limitations at the end of the season. If this

water use occurred in the early part of the growing season, which is cool, then early vigor may increase water-use efficiency. However, in some situations, early vigor may result in rapid early water use, followed by severe water deficits at critical growth stages and consequent reductions in harvest index. This would be the situation for crops growing on a limited store of soil water, using the arguments of Passioura (1977). In terms of survival determinants, this trait would have a negative influence on dehydration avoidance due to increased water use, commensurate with greater leaf area.

Early vigor would be expected to have a positive influence on yield potential due to increased radiation interception. This trait is particularly relevant for cereals in the tropics, where high temperature is associated with rapid development and the yield potential of the crop is largely set in the first two to three weeks after sowing (Rawson, 1986). Early vigor may have a positive or negative effect on yield stability depending on the pattern of water availability, as discussed earlier. No cost to production would be associated with this trait per se. Early vigor is recommended for an ideotype in all situations except for conservative terminal stress environments in subsistence agriculture, where conservation of early water use would enhance yield stability.

8. *Leaf Area Maintenance*

Reduced leaf growth and accelerated leaf senescence are common responses to water deficits, and they both reduce leaf area. Although these responses tend to enhance survival by conserving water, they can be detrimental to productivity upon the relief of water deficits if leaf area index falls below three, because radiation interception and transpiration as a proportion of evapotranspiration increase up to this value. Consequently, maintaining leaf area is seen as a trait contributing to yield, but at the same time as a potential threat to survival. Maintenance of leaf area is determined by lethal leaf water status (discussed later), the N economy of the plant, and sink demand by the developing grains.

Where water deficits are unrelieved, as in terminal stress situations, leaf area maintenance has no effect on the amount of water transpired; a larger leaf area only exhausts soil water more rapidly. However, it may *decrease* harvest index if the soil water supply is exhausted before maturity. On the other hand, if it allows more time to retranslocate preanthesis dry matter, leaf area maintenance could *increase* harvest index. Where water deficits are relieved, as in intermittent stress situations, leaf area maintenance would increase the amount of water transpired at leaf area index less than

three, and would increase the harvest index if this results in greater radiation interception during grain filling. In terms of survival determinants, leaf area maintenance would lower dehydration avoidance by maintaining water loss.

Leaf area maintenance under water deficits per se should have no effect on yield potential. However, expression of this trait in terminal stress situations may be associated with low yield potential, because low yielding sorghum genotypes, with a small grain sink size relative to vegetative growth, remained green ("stay-green" or "non-senescing") during postflowering drought compared with high grain-yielding genotypes (Rosenow *et al.*, 1983). The nonsenescing cultivars also tend to be resistant to charcoal rot and stalk lodging. Leaf area maintenance would improve yield stability in intermittent stress situations due to better radiation interception when water is available, whereas the opposite would be the case in terminal stress situations, because leaf area maintenance would increase the rate of water use and increase the probability of the crop running out of water before maturity. Consequently, leaf area maintenance is recommended for an ideotype in intermittent stress situations but not in terminal stress situations, where soil water may be exhausted before maturity.

There is genetic variation for leaf area maintenance, and it is under genetic control in grain sorghum (Duncan *et al.*, 1981; Rosenow *et al.*, 1983).

9. Osmotic Adjustment

Osmotic adjustment results from the accumulation of solutes within cells, which lowers the osmotic potential and helps maintain turgor of both shoots and roots as plants experience water stress. This allows turgor-driven processes, such as stomatal opening and expansion growth, to continue, though at reduced rates, to progressively lower water potentials (Hellebust, 1976; Turner and Begg, 1978; Zimmerman, 1978; Turner, 1979, 1982, 1986a,b; Turner and Jones, 1980; Ludlow, 1980a, 1987; Blum *et al.*, 1983a; Wyn Jones and Gorham, 1983; Morgan, 1984). Osmotic adjustment is not an inherited trait, but the capacity to adjust when the plant experiences water stress is inherited. Thus it is an inducible or facultative rather than a constitutive trait. The ways in which osmotic adjustment in roots, shoots, and panicles influences plant processes and grain yield in sorghum are summarized in Fig. 3.

Osmotic adjustment has no effect on water-use efficiency (Morgan and Condon, 1986; McCree and Richardson, 1987; D. J. Flower, personal

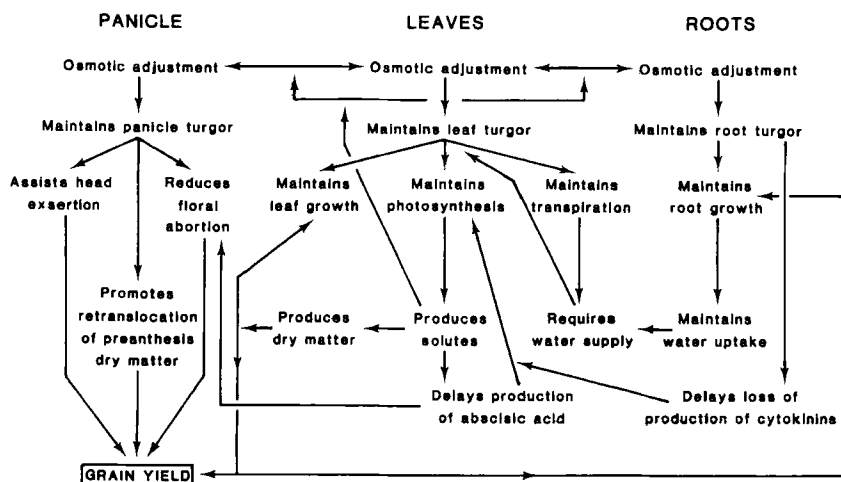


FIG. 3. Schematic diagram of the possible consequences of osmotic adjustment of panicles, leaves, and roots in grain sorghum. (Adapted from Turner, 1986a.)

communication; Ludlow *et al.*, 1990; Santamaria *et al.*, 1990), but it contributes to grain yield in water-limited conditions by increasing the amount of water transpired and by minimizing the reduction in harvest index. Increases in water transpired result from stomatal adjustment, maintenance of leaf area, and increased soil water uptake. Osmotic adjustment reduces the rate of leaf senescence (sometimes called stay-green character in grain sorghum) (Wright and Smith, 1983; Morgan, 1984; Hsiao *et al.*, 1984; Blum and Sullivan, 1986), because it increases both avoidance and tolerance of dehydration (discussed later). Furthermore, osmotic adjustment appears to be the main mechanism of stomatal adjustment, a process that allows stomata to remain partially open at progressively lower leaf water potentials as water stress increases (Ludlow, 1980a, 1987; Ludlow *et al.*, 1985). This does not, however, result in more C fixed if accompanied by a rapid decline in leaf water status (McCree and Richardson, 1987).

Genotypes of wheat and sorghum with high osmotic adjustment produce more root biomass and greater root length density and extract more soil water (particularly from lower parts of the soil profile), than do genotypes with low osmotic adjustment (Wright *et al.*, 1983a; Morgan and Condon, 1986; Santamaria, 1987). For example, Morgan (1984) reported increases in transpiration of 26 mm for wheat growing on a clay-loam soil, and 24 mm and 64 mm for two sorghum crops growing on a heavy clay soil, associated

with the higher osmotic adjustment. The enhanced root growth results from maintenance of turgor by osmotic adjustment in the *root* (Turner, 1986a), and from additional C fixed associated with osmotic adjustment in the *shoots*, which allows photosynthesis to continue, though at a reduced rate, as leaf water potential falls (Ludlow, 1987).

Osmotic adjustment has been shown to maintain harvest index in wheat (McGowan *et al.*, 1984; Morgan and Condon, 1986) and sorghum (Ludlow *et al.*, 1990; Santamaria *et al.*, 1990), and probably also in barley (Legg *et al.*, 1979), subjected to mild water deficits, and to increase it in wheat subjected to high water deficits (Morgan and Condon, 1986), compared with unstressed plants. Maintenance of harvest index by high compared with low osmotic adjustment involves several specific effects (Fig. 3):

1. Improved tiller and floret survival, and better seed set in wheat (Morgan, 1984).
2. Improved head exertion and reduced spikelet abortion in sorghum (Wright and Smith, 1983; Santamaria *et al.*, 1990).
3. Increased assimilate supply during grain filling by reducing leaf senescence (Wright and Smith, 1983; Morgan, 1984; Santamaria *et al.*, 1986) and by maintaining photosynthetic activity of remaining leaves (Hsiao *et al.*, 1984).
4. Increased use of preanthesis assimilates in grain filling (Wright *et al.*, 1983a; Ludlow *et al.*, 1990).

McCree and Richardson (1987) found that cowpea (low osmotic adjustment) fixed as much C as sugar beet (high osmotic adjustment) when grown in pots and deprived of water. Such a result is not unexpected, because they used the same amount of water, but sugar beet used it faster. Unless there were differences in water-use efficiency, the C gain would be similar. Furthermore, enhanced root growth, better soil water extraction, and greater water use of sugar beet could not have been expressed in pots.

Some of the consequences of osmotic adjustment promote dehydration avoidance, and some reduce it (Fig. 3). The continued water loss caused by maintenance of green leaf, delay of leaf rolling (Hsiao *et al.*, 1984), and stomatal adjustment reduces dehydration avoidance. An inevitable consequence is that leaf water potential falls progressively (Morgan, 1984), and this can cause leaf and plant death if critical leaf water potentials or relative water contents are reached or if the soil water is exhausted, irrespective of the dehydration tolerance of the species (Ludlow *et al.*, 1983; M. M. Ludlow, unpublished data). Thus species like soybean and some forage legumes, which have high osmotic adjustment and high dehydration tolerance, die before other species, such as cowpea and siratro, that lack these attributes (Ludlow *et al.*, 1983; Sinclair and Ludlow, 1986). However,

when osmotic adjustment promotes root growth and exploration, and consequently soil water extraction, dehydration avoidance is enhanced. The balance between these two opposing effects will determine whether osmotic adjustment improves or reduces dehydration avoidance. This will vary with species, soil type, environment, and timing of water stress during the development of the crop.

Richardson and McCree (1985) and McCree (1986) have shown that the metabolic cost of storing photosynthate and using it for osmotic adjustment in grain sorghum was *less* than the cost of converting it to new biomass. This suggests that there is no particular cost of osmotic adjustment above that of normal growth. For this reason, and because osmotic adjustment is an inducible trait that occurs only when stress develops, there should be no loss of yield potential. However, the greatest contribution of osmotic adjustment is to the stability of yield under water-limited conditions. Averaged over three maturity groups, entries of grain sorghum with high osmotic adjustment had up to 34% and 24% higher yield when water stress occurred during the preanthesis and postanthesis periods, respectively, than entries with low osmotic adjustment (Ludlow *et al.*, 1990; Santamaria *et al.*, 1990). Similarly, in wheat the advantage of high compared with low osmotic adjustment increased by up to 50% as water supply became more limited in dryland crops (Morgan, 1983; Morgan *et al.*, 1986).

Genetic variability in osmotic adjustment has been found in wheat (Morgan, 1977, 1983, 1984; Blum *et al.*, 1983a; Morgan and Condon, 1986; Morgan *et al.*, 1986), grain sorghum (Ackerson *et al.*, 1980; Wright and Smith, 1983; Santamaria *et al.*, 1986; Blum and Sullivan, 1986), millet (Henson, 1982), cotton (Karami *et al.*, 1980), rice (Turner *et al.*, 1986b), soybean (M. M. Ludlow, unpublished data), and pigeonpea (Flower and Ludlow, 1987). Although there is at present insufficient data to enable conclusions about the heritability of osmotic adjustment, data for wheat are consistent with the proposition that only one or a few genes are involved, and that the trait is simply inherited (Morgan, 1983; Morgan *et al.*, 1986).

Grumet *et al.* (1987) reported that lines of barley selected for high osmotic adjustment to salinity stress had slower growth and lower total dry matter production and grain yield than did lines with low osmotic adjustment. However, expression of the 0.1 MPa difference in osmotic adjustment between the two groups was not measured in any experiment. Furthermore, if that difference occurred because it is a constitutive character, as the authors propose, it is different from the facultative osmotic adjustment discussed in this section.

Provided that the aspects of osmotic adjustment that reduce dehydration avoidance and promote transpiration do not exhaust the soil water before

maturity, we see osmotic adjustment as a highly desirable characteristic for both moisture environments in modern agriculture and intermittent stress environments in subsistence agriculture, where a greater risk of low yield can be tolerated. However, it is questionable whether it is a desirable trait for terminal stresses in subsistence agriculture, if it is associated with an increased risk of exhausting soil water. When the probability of exhausting the soil water supply is low, then the trait is desirable in this environment as well. We are more confident of recommending this trait because, unlike most other traits, the association with components of yield, determinants of survival, and yield have been *demonstrated* rather than merely postulated. Apart from the risk of exhausting the soil water supply and the need to develop rapid screening procedures, we see few problems in such a trait being used in dryland crop breeding programs with good prospects of increasing potential yield and stabilizing yields during drought.

10. Low Lethal Water Status

The degree to which plant parts withstand desiccation is expressed as the relative water content or water potential at which leaves die; these have been called *lethal values*. Low lethal water status refers to more negative leaf water potentials and low relative water content. The criterion for deciding when to measure critical values varies: when 50% of leaves of the plant are dead, when 50% of the surface area of a leaf is dead, or when there is only one leaf remaining on a plant subjected to a slow soil-drying cycle (Ludlow *et al.*, 1983; Flower and Ludlow, 1986). Some work has shown that leaves die when they reach a critical relative water content rather than when they reach a critical leaf water potential (Flower and Ludlow, 1986; Ludlow, 1988). Similarly, while the leaf water potential at which leaves of 33 C₄ forage grasses died varied between -9 and less than -13 MPa, the relative water content was 25 ± 1 (SE)% (Z. Baruch, M. M. Ludlow, and J. R. Wilson, unpublished data). It is interesting to note that both cowpea and sorghum are very sensitive to dehydration. Consequently, their ability to survive periods of water deficits in the semiarid tropics must be due to avoidance rather than tolerance of water deficits (Santamaria *et al.*, 1986; M. M. Ludlow, R. G. Kerslake, and D. J. Flower, unpublished data).

Because low lethal water status influences survival, it has no *direct* effect on yield components. However, it contributes to dehydration tolerance and to leaf survival of intermittent water stress (Flower and Ludlow, 1986; Sinclair and Ludlow, 1986), and hence to yield stability. Turner

(1979) questioned whether considerable research effort to increase tolerance was warranted, arguing that dehydration tolerance and yield potential were "mutually exclusive." He based this conclusion on the fact that xerophytic plants, which are reputed to have high dehydration tolerance, grow slowly and have low yields (Begg and Turner, 1976; Fischer and Turner, 1978). Although such a relationship may exist, there is no *a priori* reason why it should be causal. In fact, within agricultural plants—a more relevant comparison than between agricultural plants and desert species—there is no clear relation between dehydration tolerance and yield. The lethal leaf water potential of C_4 grasses varies from -3 MPa in sorghum and millet (Sullivan and Eastin, 1974; Santamaria *et al.*, 1986) to -13 MPa in a range of forage grasses (Ludlow, 1980b; Wilson *et al.*, 1980; Z. Baruch, M. M. Ludlow, and J. R. Wilson, unpublished data), but these C_4 grasses have a similar yield potential for dry matter production. Similarly, although the lethal leaf water potential of food legumes varies from -1.8 MPa in cowpea (Sinclair and Ludlow, 1986) to -6.3 MPa in pigeonpea (Flower and Ludlow, 1986) and ca. -9 MPa in peanut (M. M. Ludlow and R. G. Kerslake, unpublished data), they do not differ appreciably in yield potential for dry matter production (Lawn, 1982b; Angus *et al.*, 1983; Muchow, 1985).

There is genetic variability in lethal leaf water potential in grain sorghum (Sullivan and Eastin, 1974; Blum, 1979; Sullivan and Ross, 1979; Jordan and Sullivan, 1982; Santamaria *et al.*, 1986), wheat (Blum and Ebercon, 1981), pigeonpea (Flower and Ludlow, 1987), and cotton (Quisenberry *et al.*, 1981). Although heritability of this trait has not been determined, the "relatively consistent performance of some parents [that differed in lethal leaf water potential] in hybrid combination suggests that selection for high or low desiccation tolerance is an attainable goal in a breeding program" (Jordan and Sullivan, 1982). However, we are not aware of any program where low lethal water status is used as a selection trait, despite the facts that both cowpea and grain sorghum have poor desiccation tolerance and there is no proven cost of this trait for potential yield.

High desiccation tolerance is suited to both intermittent stress environments, where it assists survival of leaves and plants until the next rain. However, we do not believe it would contribute substantially in terminal stress environments, because it only lengthens the time between when growth and photosynthesis cease and when leaves die, and this makes no contribution to dry matter production. For example, leaf turgor is lost at -2.5 MPa in pigeonpea, and both leaf expansion and net photosynthesis cease at -2 and -3.5 MPa, respectively, whereas leaves do not die until -6.3 MPa (Flower and Ludlow, 1986; Flower, 1986). If, however, it allows time for preanthesis dry matter to be retranslocated, it would contribute to harvest index and hence grain yield in a terminal stress environment.

11. *Reduced Stomatal Conductance*

Various stomatal characteristics, such as low conductance, high sensitivity to leaf water status and saturation deficit, and abscisic acid (ABA) accumulation, have been suggested as desirable traits to improve the yield of crops in water-limited environments (Jones, 1979, 1980, 1987; Turner, 1979, 1982, 1986a,b; Clarke and Townley-Smith, 1984). All these characteristics reduce water loss and lower the probability of desiccation. Moreover, they have the attractive feature that they are reversible when the stress has abated. However, because stomata influence the influx of CO₂ into leaves as well as the loss of water vapor, reductions in stomatal conductance to conserve water inevitably mean lowered photosynthetic rate. Consequently, the usefulness of reduced stomatal conductance depends upon this trade-off between loss of production and the need to prevent dehydration. Inherently low stomatal conductances and a reduction of stomatal conductance in response to low leaf water potential, high saturation deficit, and high ABA production reduce crop water loss (Jarvis and McNaughton, 1986). For example, the crop water use of cowpea (203 mm) mung bean (247 mm) and soybean (328 mm) crops until 64 days after sowing is consistent with the differential sensitivity of their stomates to water deficits (Lawn, 1982a; R. C. Muchow and M. M. Ludlow, unpublished data). However, the reduction is not as much as might be expected because most short, uniform agricultural crops are not as well coupled with the atmospheric environment as is tall, rough vegetation, and the reduction of water loss in crops is proportionately much less than the reduction of stomatal conductance (Jarvis and McNaughton, 1986).

In leaves with osmotic adjustment, stomata remain partially open to progressively lower water potentials. This stomatal adjustment, therefore, has the opposite effect to the traits just discussed, because it promotes continued water loss and a progressive decline in leaf water potential. Stomatal adjustment also promotes growth of grain sorghum during water stress (Blum and Sullivan, 1986).

While theory predicts an increase in transpiration efficiency as stomata close, this rarely occurs under field conditions because the resulting rise in leaf temperature increases the leaf-air vapor pressure difference, which lowers transpiration efficiency (see Section III,B,15). Also the poor coupling between agricultural crops and the atmosphere will militate against improvements in water-use efficiency by stomatal closure. Therefore, it seems unlikely that stomatal closure will increase water-use efficiency.

The main response to reduced stomatal conductance, by whatever means, is avoidance of desiccation (Blum *et al.*, 1981; Ludlow *et al.*, 1983).

For example, cowpea, which has stomates more sensitive to water deficits, avoids desiccation better than mung bean, which in turn avoids better than soybean and pigeonpea (Lawn, 1982a; M. M. Ludlow, R. G. Kerslake, and D. J. Flower, unpublished data). Lowered conductance should improve the stability of yield, because it reduces water loss and lowers the probability of exhausting the soil water before maturity. However, it will reduce yield potential—the reduction being worse in plants with inherently low conductance than in ones where stomates close in response to lowered leaf water potential, high saturation deficit, or ABA accumulation, which are reversible. Consequently, because of the trade-off between CO_2 and H_2O exchange, a reduced stomatal conductance will have a production cost. This trade-off could be acceptable for subsistence agriculture in intermittent stress environments if it prevents crops from dying before the next rainfall, and in terminal stress environments if it prevents exhaustion of soil water before maturity. We believe, however, that the cost of these stomatal traits is high for comparable environments in modern agriculture.

Genetic variability has been demonstrated in various stomatal characteristics (Jones, 1980, 1987; Clarke and Townley-Smith, 1984), and though there are no definitive studies, it appears that they are highly heritable (Roark and Quisenberry, 1977; Jones, 1987). However, obtaining consistent measurements of stomatal characteristics in the field is very difficult (Bennett *et al.*, 1987). Jones (1979, 1987) has discussed the attendant problems and limitations of attempting to select for stomatal traits. One such problem is the lack of stomatal response to water deficit after flowering in grain sorghum (Garrity *et al.*, 1984). Jones concludes that it would be better to select for characteristics closer to yield or survival than to select for stomatal traits. Some evidence (Turner, 1986a; Bennett *et al.*, 1987), which suggests signals from roots in response to soil dehydration can override the control of stomatal conductance by leaf water status, is an added complication. Despite the potential benefits of stomatal traits and the existence of genetic variability, it is premature to consider them as selection criteria.

12. Leaf Movements

Leaf movements include rolling, folding, and wilting (floppiness), as well as diaheliotropic and paraheliotropic movements in response to water deficits (Rawson, 1979; Begg, 1980; Wilson *et al.*, 1980; Ludlow and Bjorkman, 1985). Like glaucousness and hairiness, leaf movements help shed radiation incident on leaves and reduce leaf temperatures and water

loss (O'Toole *et al.*, 1979). Consequently, they increase avoidance of dehydration (Begg, 1980; Fisher and Ludlow, 1983; Ehleringer and Forseth, 1980; Forseth and Ehleringer, 1980) and should contribute to stability of yield in environments with intermittent water stress, by enhancing the survival of plants until the next rain falls. However, because these leaf movements do not occur in the absence of water stress, and because they are reversible and light interception returns to normal after the stress is relieved (Turner *et al.*, 1986a), there would be no yield penalty. Because leaf movements are essentially survival traits, they have little direct influence on the yield components. In rice, cultivars with more leaf rolling maintained higher leaf water potentials (increased avoidance of dehydration), but this had no detectable effect on water transpired or dry matter produced during a 10-day stress (Turner *et al.*, 1986b).

Leaf movement would seem to be a desirable trait in intermittent stress environments, because it enhances survival until the next rainfall. However, we see no benefit from it in terminal stress environments where it will only reduce the rate of water loss and delay the time until the water runs out—unless it allows more time to retranslocate preanthesis dry matter. Moreover, if leaf movements occur only after stomates are closed they will not enhance production. If, however, leaf movements prevent leaf death by high temperatures or if they allow the crop to survive into the cooler part of the season when water-use efficiency is enhanced, the trait would also be valuable in terminal stress environments.

There is genetic variability in the capacity for leaf rolling in grain sorghum (Begg, 1980; Santamaria *et al.*, 1986) and rice (Change *et al.*, 1974; Turner *et al.*, 1986a). Although there are obvious differences among tropical food legumes in their ability for paraheliotropic leaf movements (Lawn, 1982a; M. M. Ludlow and R. C. Muchow, unpublished data), we are not aware of any studies to characterize differences among genotypes of the same species.

We have observed that appreciable paraheliotropic leaf movements do not occur in the tropical forage legume siratro (*Macroptilium atropurpureum*) until stomates are almost closed (M. M. Ludlow, unpublished data). Blum and Sullivan (1986) also found that leaf rolling did not occur until after stomatal closure in sorghum and millet. The linkage between these two responses could be through leaf turgor. Consequently, it may not be possible to breed or select for either separately. However, because these traits may have co-evolved to reduce leaf temperature after stomates have closed, it may be undesirable to do so in any case.

Blum and Sullivan (1986) advocated that before heading in grain sorghum (leaf rolling does not occur after heading), leaf rolling could be used as a selection criterion for osmotic adjustment, because high osmotic

adjustment was negatively correlated with the relative water content when leaves rolled—the lower the relative water content at which rolling occurs, the higher the osmotic adjustment.

13. Leaf Reflectance

Leaves of different species, and ad- and abaxial leaf surfaces, vary considerably in the extent to which they reflect visible light. Increased leaf reflectance reduces leaf temperature, the leaf–air vapor pressure difference, and hence water loss (Johnson *et al.*, 1983). In wheat, for example, glaucous leaves were 0.7°C cooler than nonglaucous leaves, and the rate of leaf senescence was lower in the former (Richards *et al.*, 1986). The reflectance is caused by the presence of epicuticular wax; the trait is called *glaucous* (cf. *nonglaucous*) in wheat and *bloomed* (cf. *nonbloomed* or *bloomless*) in grain sorghum. As well as increasing reflectance, the epicuticular wax is thought to lower epidermal conductance (Blum, 1975; Jordan *et al.*, 1984). Bloomed grain sorghum leaves have lower rates of photosynthesis and transpiration than nonbloomed leaves, but because transpiration is reduced more than photosynthesis, transpiration efficiency increases in leaves of grain sorghum (Chatterton *et al.*, 1975) and in ears of wheat (Richards *et al.*, 1986). Nighttime transpiration is reduced as well (Blum, 1975; Richards *et al.*, 1986), presumably because of lower epidermal conductance. The net result of these responses is an increased water-use efficiency, but no effect on water transpired or harvest index (Richards, 1983, 1988; Richards *et al.*, 1986).

The glaucous or bloom character increases the stability of yield in water-limited environments (Jordan and Sullivan, 1982; Johnson *et al.*, 1983; Richards, 1983), and even though it has not been shown conclusively, Richards *et al.* (1986) argue that it probably will not reduce potential yield. Theoretically, glaucousness should have a cost to production because of the reduced photosynthesis associated with the increased reflectance. However, a number of factors could compensate for this potential loss. First, if the reflected light is absorbed by lower leaves in the canopy, the light may not be lost, and the efficiency of light use could be increased. Second, the accompanying lower transpiration rate both in the light and the dark may mean that leaves can photosynthesize longer into the stress. For example, Richards *et al.* (1986) have calculated that a reduction of 0.5°C for six hours per day could extend the duration of grain filling by more than three days. Third, the accompanying benefits, such as lower epidermal conductance and lower leaf senescence, may also contribute to longer duration of photosynthesis. Increased reflectance usually

results from the onset of water stress and is therefore an inducible trait. Although the waxiness does not disappear when stress is relieved, the most reflective surfaces, which are exposed during the stress, are usually abaxial, and they are less exposed after stress is relieved.

There is genetic variation in the bloomed trait in grain sorghum (Ebercon *et al.*, 1977; Jordan *et al.*, 1983b) and in glaucousness in wheat (Richards 1983), and the inheritance of this trait is understood for these two cereals. However, the heritability of bloom in sorghum is quite low (Jordan *et al.*, 1983b). Moreover, the amount of epidermal wax is strongly influenced by the environment (Jordan and Sullivan, 1982; Jordan *et al.*, 1983b), increasing with the degree of water stress.

The contribution of epidermal wax to dehydration avoidance is an advantage in environments with intermittent water stress. Moreover, its contribution to improved water-use efficiency is an advantage in all four situations. Many of the current cultivars of wheat (Richards, 1983) and grain sorghum (Jordan *et al.*, 1983b) have some degree of epidermal wax, and the yield advantage of bloomed or glaucous over nonbloomed or nonglaucous is a maximum of 15% in grain sorghum (Jordan *et al.*, 1983), 16% in barley (Baenziger *et al.*, 1983), and 7% in wheat (Johnson *et al.*, 1983). Therefore, the yield gain by increasing the epidermal wax content of an already bloomed or glaucous cultivar may be small.

We are not aware of any studies on the epidermal wax content of tropical food legumes, though visually there are differences in leaf reflectance among food legumes, among genotypes of the same legume, and between the ad- and abaxial leaf surfaces.

14. Epidermal Conductance

Water vapor is lost from leaves through parallel pathways via stomata and the leaf cuticle. When stomata are open, most of the water is lost through that pathway. When stomates are closed, the main pathway of water loss is by way of the cuticle. However, there may still be some loss through incompletely closed stomates either over the whole leaf surface or in patches. For this reason, we use the term *epidermal* rather than *cuticular conductance*. When stomates are closed, water loss from the leaf is determined by the epidermal conductance and the saturation deficit of the air. In these circumstances, leaf survival depends upon the rate of water loss, and the difference in relative water content at which stomates close and at which leaves die. Therefore, epidermal conductance is one of three plant parameters that govern the survival of leaves.

Low epidermal conductance enhances avoidance of dehydration of

leaves and, therefore, will promote leaf survival (Sinclair and Ludlow, 1986). This should assist stability of grain yield. Moreover, because low epidermal conductance will not influence water loss when stomates are open, this trait should not entail a cost. Consequently, it should not reduce yield potential. The main advantage of low epidermal conductance would be to enhance survival in intermittent stress environments in both modern and subsistence agriculture.

Variation in epidermal conductance has been found in rice (Yoshida, 1975; Yoshida and De Los Reyes, 1976; O'Toole *et al.*, 1979), grain sorghum (Blum, 1979; Jordan *et al.*, 1984), and soybean (Paje *et al.*, 1988). However, we are not aware of any studies on its inheritance. As with bloom on leaves, the environment has a very strong influence on epidermal conductance (Paje *et al.*, 1988)—especially temperature, relative humidity, and water stress. Part of the variation could be associated with different amounts of epicuticular wax (Blum, 1975). However, there is not always a good correlation between the two (Jordan *et al.*, 1984). In sorghum, epidermal conductance increases with stomatal density (Muchow and Sinclair, 1989), and these workers hypothesized that once stomata reached minimum aperture, water loss from the cuticle above guard cell teichodes becomes a significant source of leaf water loss.

15. Transpiration Efficiency

Transpiration efficiency is defined as mass or moles of C or CO₂ fixed per unit of water lost from a *leaf*. This contrasts with water-use efficiency of plants or crops, which is defined as dry matter produced per unit of water lost. Consequently, transpiration efficiency depends upon the balance between photosynthesis and transpiration, which in turn determines the partial pressure of CO₂ (p_i) in the intercellular spaces of leaves (Farquhar *et al.*, 1988). More precisely, p_i is determined by the relationship between the stomatal conductance (g) and the assimilation rate (A) of the leaf. Increases in A relative to g cause p_i to fall and transpiration efficiency to increase. For example, values of p_i are lower in C₄ than in C₃ plants, and hence transpiration efficiency is higher in C₄ plants (Ludlow and Wilson, 1972; Tanner and Sinclair, 1983).

Farquhar *et al.* (1982) have shown that p_i is related to the extent to which ¹³C, the naturally occurring stable isotope of carbon, is discriminated against in comparison to ¹²C during photosynthesis in C₃ plants. This discrimination (Δ) should theoretically be inversely proportional to the transpiration efficiency of leaves (Farquhar and Richards, 1984). Thus, the

less the discrimination against ^{13}C , the lower the p_i and the higher the transpiration efficiency. They subsequently confirmed that Δ was inversely proportional to water-use efficiency in wheat, barley, cotton, sunflower, and peanuts in pot experiments (Richards, 1988; Farquhar *et al.*, 1988; J. Virgona and G. D. Farquhar, personal communication).

Early field attempts with wheat, however, could not confirm these results, though soil water was not measured. In fact, the opposite results were inferred (Condon *et al.*, 1987). This arose because lines with low Δ (and hence potentially high transpiration efficiency and water-use efficiency) had slow early growth, which increased water loss by soil evaporation, compared with lines with high Δ . The slow growth also meant that lines with low Δ used relatively more of their water during the hotter, drier part of the growing season, which also reduces transpiration efficiency (Condon *et al.*, 1987). Both these associated characteristics presumably negated the potential benefits associated with low Δ . In addition, no association was found between Δ and water-use efficiency among genotypes of peanuts subjected to water stress in the field (S. C. Chapman, K. S. Fischer, and M. M. Ludlow, unpublished data). More recently, however, in situations where soil evaporation was minimal, Δ was found to be negatively correlated with dry matter production in wheat (R. A. Richards, personal communication) and with dry matter production and water-use efficiency in well-watered peanuts grown in mini-lysimeters within a field canopy (Wright *et al.*, 1989). Both these observations suggest that Δ may be correlated with water-use efficiency in the field. However, the amount of water used was not measured in the wheat study, and the peanuts were not subjected to water stress. Work is continuing in order to establish an unequivocal link between Δ and water-use efficiency of water-stressed crops in the field.

This work of Farquhar and Richards (1984) is in apparent conflict with the conclusion of Tanner and Sinclair (1983) that there was little scope to improve the water-use efficiency of crops by selecting for a higher transpiration efficiency of leaves. Tanner and Sinclair's analysis was based on the assumption from the earlier work of Wong *et al.* (1979) that p_i did not vary among C_3 or C_4 plants. Since Tanner and Sinclair's analysis was published, variation in p_i has been found among genotypes of the same species. (See references in Condon *et al.*, 1987.)

In theory, transpiration efficiency should not influence water transpired, except if high transpiration efficiency is achieved by high g relative to A , when water use would be reduced and dehydration avoidance enhanced. As already discussed, higher transpiration efficiency is associated with higher water-use efficiency of several crop species when grown in pots, of wheat in the field when soil evaporation was low, and of well-watered

peanuts in the field. However, more work is required to establish an unequivocal relationship for water-stressed crops in the field. While negative correlations between Δ and water-use efficiency of potted plants in both the glasshouse and the field have been found among peanut genotypes, low Δ (high transpiration efficiency) was associated with low harvest index and low economic yield (R. Shorter, personal communication; G. C. Wright, personal communication). In addition, there are indications of a similar relationship with harvest index for a limited number of wheat genotypes (R. A. Richards, personal communication). However, one peanut genotype (Q18801) has both high transpiration efficiency and high harvest index (G. D. Farquhar, personal communication). Obviously, there is a need to establish whether this potentially deleterious association between transpiration efficiency and harvest index is causal or casual. Theoretically, there should be no cost of higher transpiration efficiency, and it should contribute both to yield potential and stability of yield.

There is genetic variability in transpiration efficiency in wheat, barley, cotton, peanuts, and sunflower (Richards, 1988; Farquhar *et al.*, 1988; J. Virgona and G. D. Farquhar, personal communication). Corresponding variation in water-use efficiencies of potted plants were 2–3.7 mmol C mol H_2O^{-1} and 0.8–1.7 mmol C mol H_2O^{-1} for wheat and peanut, respectively. The nature of inheritance of transpiration efficiency is largely unknown at present, except that it is not under simple genetic control. Nevertheless it is under strong genetic control, with broad sense heritabilities between 60% and 90% (Farquhar *et al.*, 1988; Martin and Thorstenson, 1988).

If improved transpiration efficiency increases water-use efficiency of crops in the field, this would be a very desirable trait in both stress environments in both modern and subsistence agriculture. Moreover, the fact that Δ can be determined from a single plant part ensures that large breeding programs could select for this trait (Richards, 1988). While the trait has great promise and potential for increasing yield of crops in the semiarid and arid tropics, there is a need for further work to demonstrate unequivocally that selecting for a low Δ (high transpiration efficiency) will result in higher water-use efficiency, dry matter yield, and economic yield under water-limited conditions. Moreover, the inverse relationship between Δ and harvest index needs to be investigated. Otherwise selecting for Δ will result in lower, not higher, economic yields.

16. High Temperature Tolerance

High temperature tolerance has often been advocated as a highly desirable trait for tropical cereals, such as maize, sorghum, and millet (Sullivan,

1972; Sullivan and Ross, 1979; Jordan and Sullivan, 1982). We make a distinction between high temperature tolerance of leaves and of germinating seedlings. In addition, we are concerned with temperature that threaten survival rather than those that influence growth and development.

In many areas of the semiarid tropics, soil surface temperature may exceed 60°C (Peacock, 1982). Such temperature can cause considerable seedling mortality—more in maize than in grain sorghum—which ultimately limits yield because of poor stand density (Peacock, 1982; McCown *et al.*, 1980, 1982). In addition, the growth of surviving seedlings is sometimes impaired for the life of the crop. Similarly, germination and seedling emergence of cowpea (Onwueme and Adegoroye, 1975) and soybean (Emerson and Minor, 1979) are impaired by high soil temperature.

Improved high temperature tolerance would enhance grain yield by promoting water transpired, because of a better plant population. Moreover, it should contribute to yield stability without penalty for yield potential. Genetic variability has been found in grain sorghum (Wilson *et al.*, 1982). However, the inheritance of this trait is unknown. It seems to us a very desirable trait for crops grown in those areas of the semiarid tropics where excessive soil temperatures can occur.

The case for high temperature tolerance of leaves is more equivocal. Leaf temperature of sorghum often exceeds 40°C in the semiarid tropics, and values as high as 55°C have been recorded (Peacock, 1982). Some results (M. Paje, M. M. Ludlow, J. M. Peacock, and R. G. Henzell, unpublished data) indicate that irreversible high temperature injury does not occur in high temperature-acclimated grain sorghum until the temperature reaches 52–55°C. Consequently, injury from high temperatures will occur only under extreme conditions. We believe leaf firing during drought is mainly due to desiccation, because grain sorghum leaves are relatively sensitive to dehydration compared with other crops (Santamaria *et al.*, 1986).

Sullivan and Ross (1979) reported a good correlation between high temperature tolerance and grain yield under hot, dry conditions in the field. However, this trait does not seem to have been used as a selection criterion in breeding programs. Passioura (1986) argues that such a trait is “contrived,” with no well-articulated connection with grain yield. While theoretically high temperature tolerance of leaves should enhance their survival and contribute to yield by maximizing the amount of water transpired, there have been no studies to demonstrate a causal relationship between high temperature tolerance and grain yield. Until that is done it cannot be considered as a desirable trait.

17. Other Traits

We have omitted several traits from detailed discussion because we do not believe they have been sufficiently well studied to be considered. Cell size and tissue elasticity are two such putative traits. It has been proposed that small cells are more tolerant of dehydration (Iljin, 1957) and that they enhance osmotic adjustment and turgor maintenance (Cutler *et al.*, 1977; Turner and Jones, 1980). Neither the cost nor the value of the trait has been investigated, and no genetic variability has been identified. High tissue elasticity, in theory, assists in volume maintenance by reducing the change in volume per unit of change in turgor. While elasticity varies among species, no genetic variability has been reported within a species (Turner, 1986b).

Another such trait is the maintenance of high leaf water status, as shown by small leaf-air temperature differences measured by infrared thermometry (Blum *et al.*, 1982). The principle of the technique is that when stomates close because of reduced leaf water status, leaf temperature rises above ambient air temperature. However, although Blum *et al.* (1982) found significant relationships between leaf water potential and leaf temperature, they did not always find significant relationships between diffusive resistance and leaf temperature. Therefore, the basis of differences in leaf temperature may not have been due to differences in water status. Furthermore, some evidence (Turner, 1986a) suggests that diffusive resistance can rise in response to soil dehydration, independent of changes in shoot water status. There are also many technical problems associated with infrared thermometry; leaf temperature is influenced by wind speed, cloudiness, saturation deficit of the air, and the degree of canopy cover, as well as leaf water status. Attempts to use infrared thermometry in rice (Turner *et al.*, 1986a) and in wheat (Turner and Nicholas, 1986) have been unsuccessful. While Blum *et al.* (1982) used this approach to find genotypes of wheat with good dehydration avoidance (i.e., cooler leaves) through more effective water uptake, Chaudhuri *et al.* (1986) found that grain yield was greatest in the genotypes of grain sorghum and millet with the *higher* leaf temperature. Obviously more work is needed before maintenance of leaf water status as measured by infrared thermometry can be considered as a desirable trait.

C. COMBINATIONS OF TRAITS

The effects of the simultaneous occurrence of two or more traits have not been considered because they are specific to crop, environment, and

farming system. Although most of the traits that influence production can be considered as separate entities, the same cannot be said for those influencing survival. There is good evidence that traits are linked in *strategies* varying from extreme avoidance (e.g., cowpea) to extreme tolerance (e.g., pigeonpea and peanut). The lethal leaf water status is a key determinant of the strategy; crops with high lethal water status have an extreme avoidance strategy, and those with low status have an extreme tolerance strategy (Ludlow, 1988). Crops with high lethal water status have well-developed traits for enhancing water uptake and reducing water loss. In contrast, those with a low lethal water status have less-developed avoidance traits, and they usually have considerable osmotic adjustment (Ludlow, 1980a,b, 1988; Ludlow *et al.*, 1983).

IV. RECOMMENDATIONS

Table II lists the traits that we believe will increase yield of grain sorghum and cowpea in the four nominated situations. The recommendations are based primarily on the data in Table I, with most emphasis being given to traits that have been shown to contribute to grain yield or one of more of the determinants of survival or production, and to those with a good theoretical basis. Inclusion of traits in the recommended list is a matter of personal preference, but we have attempted to justify our decisions with fact or argument. Obviously readers are free to alter the ranking in accordance with their knowledge or experience.

Grain sorghum and cowpea have several similarities: their leaves are sensitive to dehydration (Sinclair and Ludlow, 1986; Santamaria *et al.*, 1986), and they both exhibit an avoidance strategy to water stress. However, whereas grain sorghum has few tillers in the tropics and is botanically determinant, cowpea is indeterminant. Consequently, sorghum has only limited developmental plasticity compared with cowpea. Traits for these two crops are considered for intermittent and terminal stress environments in both modern and subsistence agriculture.

Survival traits are of limited value in a terminal stress because they only delay the time until the plant dies or matures and may not contribute to yield. Hence we have included them only in the environments with intermittent water stress. In these two cases, they are given higher emphasis for subsistence than for modern agriculture because they are conservative and ensure some yield, even if they have a cost to production. However, within both intermittent stress situations the relative rankings will depend upon the probability of the crop experiencing periods of water deficit sufficient

Table II

Recommended Traits, in Order of Priority, for Both Grain Sorghum and Cowpea Grown in Intermittent and Terminal Stress Environments in Both Modern (Opportunistic) and Subsistence (Conservative) Agriculture; Traits Specifically for Cowpea are Shown in Parentheses

Modern agriculture ^a		Subsistence agriculture ^a	
Intermittent stress	Terminal stress ^b	Intermittent stress	Terminal stress ^b
1. Matching phenology to water supply	1. Matching phenology to water supply	1. Matching phenology to water supply	1. Matching phenology to water supply
2. Osmotic adjustment of shoots and roots	2. Osmotic adjustment of shoots and roots	2. (Developmental plasticity)	2. Mobilization of preanthesis dry matter
3. Rooting depth and density	3. Rooting depth and density	3. Osmotic adjustment of shoots and roots	3. Increased leaf reflectance ^d
4. (Developmental plasticity)	4. Increased leaf reflectance	4. Rooting depth and density	4. Photoperiod sensitivity ^d
5. Early vigor	5. Early vigor	5. Increased leaf reflectance	
6. Leaf area maintenance	6. Mobilization of preanthesis dry matter ^d	6. Low lethal water status	
7. Increased leaf reflectance ^c		7. Leaf movements	
8. Low lethal water status		8. Low epidermal conductance	
		9. Early vigor	
		10. Leaf area maintenance	
		11. Photoperiod sensitivity	

^aSeedling tolerance of high temperature is an important trait in environments where soil surface temperature at emergence exceeds 50°C.

^bWhen lodging of grain sorghum is a problem in a particular environment, any trait that is shown to reduce lodging is desirable. It remains to be shown whether stay-green is such a trait without a yield penalty.

^cThe scope for improvement may be small if current varieties are glaucous or bloomed.

^dCould be disadvantageous for grain sorghum in some environments if it promotes lodging.

to endanger its survival. The probability of such lethal deficits depends upon the frequency and intensity of rainless periods. Moreover, it will be higher on light soils with low water-holding capacity than on heavy soils.

Apart from developmental plasticity—a desirable trait for the indeterminate cowpea—the remaining traits chosen are common to both cowpea and grain sorghum. In contrast to Section III, where the value of each trait was assessed, in this section we attempt to rank in order of priority the traits that we believe are important for each species in each of the four situations.

The most important trait, we believe, is matching the crop phenology to the average water supply of the environment and ensuring that critical developmental stages occur in the periods of higher probability of adequate water supply. This is easier in a terminal stress than in an intermittent stress situation, because the timing of the stress is unpredictable in an intermittent rainfall environment. Consequently, although it is not possible to select for specific phenologies, it is possible to do so in a more general sense, such as ensuring that grain filling occurs after the rains have ceased to reduce the occurrence of head mold in sorghum. By selecting for a phenology to suit the average water supply, yield may be lost in better than average years, and yield may be depressed in low rainfall years. However, selecting for any other phenology is, we believe, fraught with even more danger.

The next most important traits in three of the four situations are osmotic adjustment and rooting characteristics, which maximize water extraction. Neither is recommended for terminal stresses for subsistence agriculture because of the risk of exhausting the soil water, except if available soil water remains at maturity of current varieties. Osmotic adjustment is marginally preferred over inherently deep roots and high root length density for two reasons. First, osmotic adjustment confers other benefits—such as better panicle exertion and continued photosynthesis during stress—has no known costs, is induced only by water stress, and is lost after stress is relieved. Second, a deep and dense root system may be beneficial during periods of stress, but there may be a dry matter cost to the plant, which could reduce yield potential.

Although both these traits associated with the roots will tend to maximize evapotranspiration, early vigor should reduce evaporation and maximize transpiration, especially on lighter soils (Turner and Nicholas, 1988). Mobilization of dry matter (both C and N) accumulated before anthesis is seen to be of value in terminal stresses.

Maintenance of leaf area (stay-green character in sorghum) is a positive trait in intermittent stress environments, because it ensures leaf area for

growth when the stress is relieved. However, it seems of less importance under terminal stress, because it promotes water loss and increases the probability of the crop exhausting the soil water during grain filling. This applies more to subsistence than to modern agriculture. Maintenance of green leaf area is a very important trait in grain sorghum if it prevents lodging, or if it allows more time to mobilize preanthesis dry matter.

Increased leaf reflectance is seen as a desirable trait in all four situations because it has no cost and is likely to produce small but important yield increases. There may, however, be limited scope for improvement because many current cultivars have some degree of waxiness. Its importance is greater in terminal than in intermittent stresses, and in subsistence compared with modern agriculture.

Photoperiod sensitivity is seen to be a useful conservative trait that contributes to yield stability in subsistence agriculture. However, opportunities for higher yields in above-average seasons may be lost in sorghum, but not necessarily in cowpea. The need to have different cultivars for different latitudes also detracts from its value in modern agriculture.

Several of the traits that promote water uptake and water loss—such as osmotic adjustment, deep roots, early vigor, large leaf–air temperature difference, and leaf area maintenance—are seen as desirable, more so in intermittent than in terminal stresses, as long as the water supply is not exhausted. If they endanger survival they could be seen as undesirable. Their relative importance obviously depends upon the probability of rainless periods and the nature of the soil.

In addition to these characteristics for cowpea, we believe developmental plasticity is a very important characteristic for intermittent stress environments, but not for terminal stresses. Furthermore, it is more important in subsistence agriculture, where grain can be hand-harvested, than in modern agriculture where uneven maturity causes problems for machine harvesting.

Other traits are potentially important for each of the four situations but are not listed because there is either insufficient experimental evidence or insufficient theoretical analysis to support them at present. Because of the uncertainties about the association between Δ , water-use efficiency at the crop level, and harvest index, we have not included transpiration efficiency. Clearly, if this association can be proved, transpiration efficiency is recommended for all four situations, because it should enhance yield in any moisture environment. Such a prospect is an exciting possibility for improving crop yields in water-limited environments. Low epidermal conductance and leaf movements are also potentially useful traits in intermittent stress environments of modern agriculture.

V. CONCLUSIONS

Too much has been written about putative traits for drought resistance in crops, and too little analysis of their actual as opposed to their potential value has been done. There is much *information* about various traits, but less *knowledge* and even less *understanding* of their real worth. Only recently have attempts been made to assess their benefit by mathematics, simulation modeling, use of near-isogenic lines, or other techniques discussed here. Before putative traits are proposed for inclusion in breeding programs, their benefit for grain yield should be assessed in terms of the components of yield and the determinants of survival. Unless they make a contribution to one or more components or determinants, there seems little use in breeding for them. Simulation models promise to be a very powerful tool for critically assessing the value of putative traits. However, more work is needed in the development and testing of suitable models, and in their application for this purpose. Use of near-isogenic populations as opposed to isogenic lines also appears to hold great promise.

More agroclimatic work is required to define the various moisture environments, especially in terms of the amount, frequency, and probability of rainfall and of the expected soil moisture regime in average seasons. This is necessary so that the most appropriate phenology can be devised. Better techniques are required to measure soil water extraction and soil evaporation, so that the amount of water transpired by present cultivars can be determined and an estimate made of available soil water at maturity, as a basis for deciding upon traits to increase water transpired or traits to meter crop water use during development. If all available soil water is not used and is recharged each year, increasing water transpired seems the most direct and potentially the most important way of increasing grain yield.

Because of the success by Morgan with osmotic adjustment in wheat and by Passioura and Richards with low hydraulic conductance of the seminal roots of wheat, we are confident that traits can be identified that will lead to higher yields of dryland crops. Although it has been stated many times before, the probability of such success is greatly enhanced by the close cooperation of physiologists, plant breeders, and geneticists.

ACKNOWLEDGMENTS

We would like to thank colleagues who supplied us with preprints of papers in press or with unpublished data. The helpful comments of Jim Morgan, Richard Richards, Mike Foale, and Bob Lawn on the manuscript are gratefully acknowledged. Finally, we wish to thank ICRIAT for permission to revise the manuscript prepared by us for one of its internal reviews so that it could reach a wider audience.

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