

Targeting Sorghum Improvement in Drought-Prone Environments: Approaches and Progress

R.C. Muchow*, M. Cooper, F.R. Bidinger,
G.L. Hammer, A.K. Borrell and S.C. Chapman

Abstract

Grain sorghum is grown in environments of highly variable water supply, both within and between seasons. This variability, coupled with associated genotype-by-environment (GxE) interactions, results in unclear definition of both target environment(s) and traits that may be used as selection criteria, causing slow progress in breeding for drought resistance. This paper reviews new approaches to characterize environments in terms of the incidence of water deficits and to assess the value of traits for improvement of drought resistance. Sorghum simulation models are powerful tools to characterize types of environmental challenges and their frequency of occurrence at different locations. Models also are being used to assess hypotheses about trait action and their value, and to develop optimal combinations of traits for different environmental challenges. Further research involving physiologists, agronomists, and plant breeders using integrated systems analysis will realize the potential of these approaches and improve the efficiency of selection in drought-prone environments.

Rainfed production of grain sorghum is a risky enterprise due to high rainfall variability, both within and between seasons (Muchow et al., 1991; 1994). Plant breeders face considerable challenges in improving sorghum performance in these regions for two reasons: 1) climatic variability and the associated genotype-by-environment (GxE) interactions, which often result in unclear definition of the target environment(s); and 2) lack of definitive knowledge of which plant traits for drought resistance are relevant to particular environments. Consequently, progress in genetic improvement in drought-prone environments has been relatively slow (Cooper and Hammer, 1996). Im-

portant questions are: what new approaches are available to assist the plant breeder in targeting selection for drought-prone environments and what recent advances in physiological knowledge are relevant to this endeavor? Bidinger et al. (1996) set out the physiological basis of GxE interaction in crop adaptation and argue that real opportunities lie both in understanding the environmental control of crop growth and in developing simplified approaches to modeling. These approaches include better analysis of multi-environment trial (MET) data sets, better understanding of resources and challenges in target environments, and better understanding of the adaptive value of plant traits in specific environments.

Muchow et al. (1996a) recently reviewed the considerable advances in our understanding of the physiology of grain

R.C. Muchow and S.C. Chapman, CSIRO St Lucia, QLD, Australia; M. Cooper, Dept Agric, UQ, St Lucia, QLD, Australia; F.R. Bidinger, ICRI-SAT, Patancheru, AP India; G.L. Hammer, QDPI/APSRU Toowoomba QLD Australia; and A.K. Borrell, QDPI Warwick QLD Australia.*Corresponding author.

sorghum. In the past, physiology was viewed largely as a retrospective discipline in explaining plant function. Physiological research now tends to be more focused on providing knowledge about plant and crop processes to underpin sustainable and profitable production and assist in breeding better adapted plants. Quantitative knowledge of the physiology of yield accumulation contributes to the development of crop growth simulation models that can be used to assess improved crop management options, characterize environments, assist multi-environment testing, and evaluate potentially useful traits (Hammer et al., 1996a,b). Enhanced modelling capability and better databases, particularly of historical climatic data, have been central to recent progress in better targeting sorghum improvement in drought-prone environments.

In reviewing approaches and progress, we consider three key questions in this paper:

- 1) How can we best define the target environment(s)?
- 2) How can better characterization of environments improve the efficiency of METs?
- 3) How can we better evaluate which traits for improving drought resistance in grain sorghum are likely to be beneficial in different environments?

Defining the Target Environment(s)

Comstock (1977) discussed the concept of a target population of environments (TPE) for breeding programs. The TPE can be defined as the complete set of

“types” of environments within the geographical area targeted by a breeding program. The types of environmental factors encountered within the TPE play a dominant role in determining crop performance, genetic variation for quantitative traits, and therefore the relative performance of genotypes. An important challenge in plant breeding is to evaluate genotypes across variable environments in a manner that allows assessment of their adaptation within the TPE. This is traditionally done using METs. One factor influencing the efficiency of this approach is GxE interaction (Cooper et al., 1993). When GxE interactions are a large source of variation, the TPE consists of a complex mixture of different types of environments. If some of these environments are repeatable and important in the TPE, then the TPE can be resolved into sub-populations. Breeding for target environments may therefore be considered as breeding for specific adaptation to those types of environments that occur frequently within the TPE. A successful example of this breeding strategy is breeding for resistance to sorghum midge (*Contarinia sorghicola*) for the Australian TPE (Henzell, 1992).

Water availability is a major environmental factor responsible for GxE interactions for yield in grain sorghum. Better characterization of environments in terms of the severity and frequency of occurrence of water deficits offers the potential to improve the efficiency of selection within METs. This may lead to better choice of environments for field trials, thereby increasing gains from selection. Muchow et al. (1996b) and Cooper and Chapman (1996) outline an approach using crop simulation models coupled to

historical climatic data to define the spectrum of environmental challenges in the TPE, and then use pattern analysis to group environments in terms of types and frequency of occurrence of water deficits. This information then can be linked with spatial databases (Chapman and Baretto, 1996) to identify testing locations that either best represent the target environment(s) or present specific challenges to germplasm under test. Case studies of the approach using simulation modelling and pattern analysis to characterize sorghum environments are given below.

Muchow et al. (1996b), using 96-101 years of historical climatic data for two rainfed sorghum-growing sites in Queensland, Australia, concluded that the grouping of environments by a relative transpiration index accounted for a higher proportion of the yield variation among years than did groupings based on indices derived from a simple water balance model or direct climatic variables. Relative transpiration (RT, 0-1.0) is the ratio of actual transpiration to potential transpiration; RT values less than 1.0 indicate that water deficit is restricting crop growth. Muchow et al. (1996b) used the grain sorghum model of Hammer and Muchow (1994) to calculate daily RT using a defined cropping system (i.e., soil type, total available soil water in profile [tsw], initial available soil water [asw], cultivar, density, nutrient supply, and sowing window based on rain occurrence). The weekly RT value was calculated as the mean of the corresponding daily values to determine the weekly patterns of water deficit during the crop cycle for each year at each site. Pattern analysis (DeLacy, 1981) was used to identify the major types of water deficit pattern, and

the frequency with which these types occur was then inferred by the size of the groups (Figure 1).

In the case study at Emerald, five groups of water deficit patterns were identified (Figure 1). Groups 174, 176, and 177 were of similar and higher frequency than groups 170 and 173. Groups 174 and 177 showed terminal water deficit of varying intensity, while water deficit was least in group 176. Four groups were identified at Dalby (Figure 1). Group 190 had the least water deficit but occurred most frequently, whereas groups of varying terminal water deficit occurred 49% of the time. Table 1 shows the group profiles and simulated grain yield at Dalby for the years 1985 to 1989. In field trials conducted at Dalby over the three years 1987 to 1989, the pattern analysis classified these seasons as group 190 (i.e., little water limitation, Figure 1). An important question to the plant breeder is how frequently does this environment occur. Figure 1 shows that it occurs 38% of the time, not 100% of the time, as was the case in these three years (Table 1), suggesting that genotype performance in those years would not necessarily be predictive of long-term genotype performance.

Cooper and Chapman (1996) used a similar approach to examine the patterns of water deficit at seven sites in Queensland over the historical climatic record. Out of the 660 seasons (totaled over the seven locations) that the sorghum crop was simulated, five patterns of water deficit were identified (Figure 2). In the four southern sites (Bongeen, Bowenville, Condamine, and Dalby) 60% to 90% of seasons had little or no stress (Group 507), whereas in central Queensland, less than

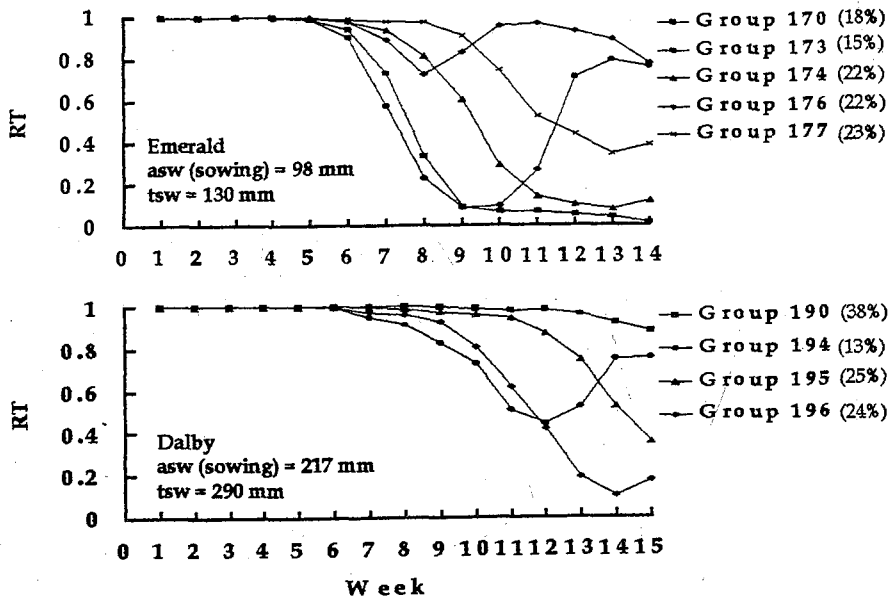


Figure 1. Pattern of water deficit based on relative transpiration (RT) over time for two rainfed sites in Queensland, Australia. Source: Muchow et al. (1996b)

Table 1. Group profiles based on relative transpiration and simulated grain yield from 1985 to 1989 at Dalby, Australia.

Year	1985	1986	1987	1988	1989
Group	196	195	190	190	190
Grain yield (t ha ⁻¹)	1.85	5.56	6.37	6.21	6.23

Source: Muchow et al. (1996b).

30% of seasons were characterized as no stress. Groups showing terminal stress (Groups 509 and 512) occurred to differing degrees at all locations, while mid-season water deficit (Groups 510 and 511) occurred only at the central Queensland sites (Figure 2).

Given this insight, it would seem difficult to design a MET to account for the different mixture of season types in each region. Trials in southern Queensland would tend to indicate a high frequency of

low stress sites, so the results from these would probably not be relevant in central Queensland, and vice versa. Sampling would be even more difficult within central Queensland; Fernlees, for example, tends to have more mid-season water deficits, while Jambin has more terminal water deficits. Hence, the results of a MET in any single season would be unlikely to adequately sample the total TPE for central and southern Queensland.

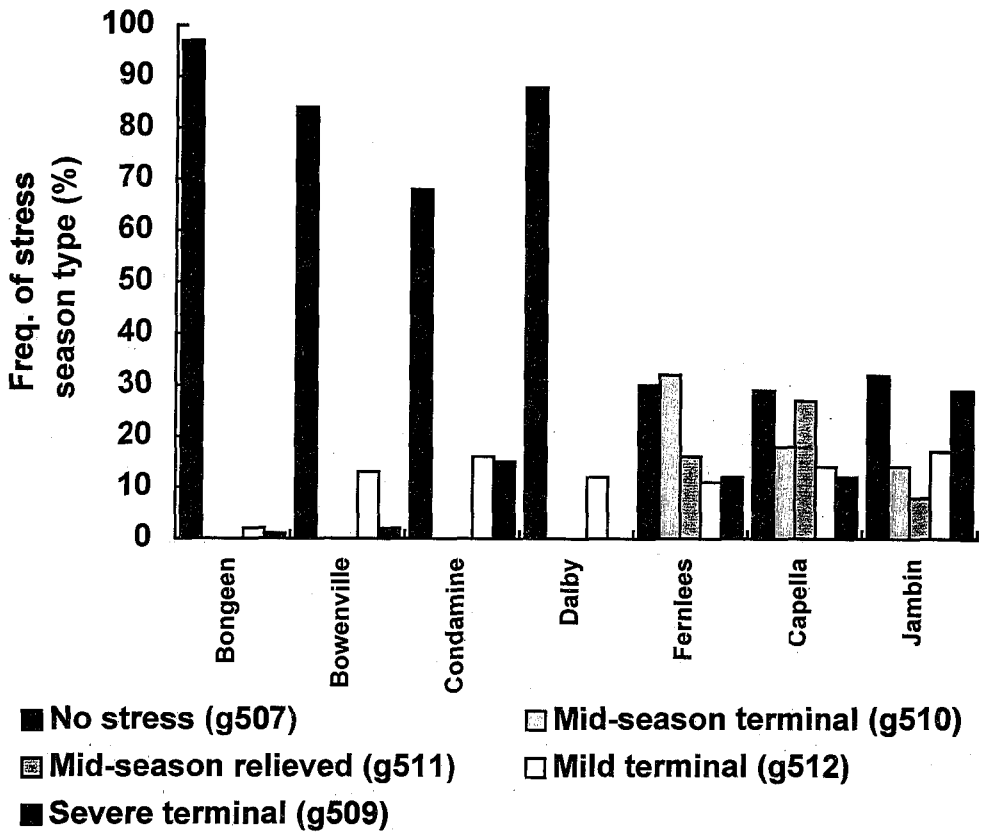


Figure 2. Frequency of water deficit season types across seven sites in Queensland's sorghum regions (Cooper and Chapman, 1996).

Cooper and Chapman (1996) also examined 17 years of METs conducted in southern and central Queensland and found that variation among sites for discrimination among cultivars was well correlated with the simulated frequency of stress seasons at any location. Assuming that the period over which the METs were conducted provided a representative sample of the possible seasons, this is strong evidence that a substantial component of the regional Gx \times E interactions for yield in sorghum is related to the occurrence of different patterns of water deficit among the regions.

Improving the Efficiency of METs

Multi-environment trials (METs) are conducted as an integral part of a plant breeding program, with the broad objective of estimating the relative performance of genotypes in the target population of environments (TPE). Much has been discussed about the impact of Gx \times E interactions in plant breeding and their analysis (see Cooper and Hammer, 1996), but generally less attention has been given to the issue of adequacy of the samples of environments obtained in METs. Where the TPE is considered to be heterogeneous with respect to the types of environments

encountered, most analyses of quantitative traits find significant and problematic crossover GxE interactions (Haldane, 1946).

Estimation of the importance of GxE interactions from METs is not independent of the sampling strategy used in conducting the METs (Cooper et al., 1996). Muchow et al. (1991) considered the limitations of METs in terms of their capacity to adequately sample the range of environments encountered in the TPE. Sampling variation results in the composition of environments included in any MET deviating from environments in the TPE. The consequence of this can be considered in terms of the genetic correlation between the performance of the genotypes in the MET and their expected performance in the TPE (Cooper et al., 1996). Where GxE interactions are large, relative to genotypic variation for average performance across environments, the consequence of the sampling variation is that the genetic correlation between the MET and TPE will fluctuate among successive METs; therefore, the realized response to selection in the TPE will fluctuate among successive METs.

A possible selection strategy to accommodate the MET sampling variation effect for a TPE is to use environmental characterization information from crop models to generate weights for individual selection environments based on their relevance to the TPE. Three pieces of information are required: 1) definition of the TPE (as discussed in the previous section) to give a measure of the types of environments encountered in the TPE and their frequency of occurrence; 2) characterization of the MET to give a measure of the types of environments sampled in the MET; and 3) environmental weights

to give an appropriate system for weighting the information from the environments sampled in the MET.

The environments sampled in the current MET can be characterized in a manner similar to that for the TPE by establishing parameters for the cropping system, obtaining the seasonal climatic data, and running the crop simulation model for that specific season. The patterns of water deficit detected from each MET environment can then be compared to the groups of patterns obtained from characterizing the TPE to determine how well the MET sample is matched with the TPE. The difference in the environmental composition between the two provides a measure of the size of the sampling variation effect for a given MET strategy.

Where there are crossover GxE interactions among the environment types identified by the crop model characterization, and where the sample of environments obtained in the MET deviates from that in the TPE, the response to selection in the TPE from selection based on the results of the MET depends on how the selection decisions are made. For example, if the objective is to improve average performance in the TPE, selection for average performance across the MET environments will have a sub-optimal genetic covariance with average performance across the TPE (Cooper et al., 1996). Weighting procedures based on a quantitative measure of the deviation between the environments sampled in a MET and the expectation for the TPE can be used to improve the match between the environmental composition in the MET and the TPE, by down-weighting the environment types that are over sampled and up-weighting the environment types that are under sampled.

There are many ways environments could be weighted to assist selection decisions. Fox and Rosielle (1982) considered weighting strategies based on the magnitude of error, pattern analysis, and canonical correlation analysis procedures in combination with a reference set of genotypes. An alternative approach is to weight environments based on their frequency of occurrence in the TPE as measured by the crop model. For example, if the frequency of an environment in the MET deviates from its frequency in the TPE, then the expected frequency of the environment in the TPE can be used as a weight for the environments in the MET. Selection decisions would then be based on the weighted mean yield across environments rather than the mean yield based on unweighted data. There are many facets to this strategy, and these are beyond the scope of the discussion that can be developed in this paper. However, using computer-based simulated selection methodologies, it has been found that weighted selection strategies perform as well as or better than selection based on unweighted MET data (M. Cooper, personal communication). The relative effectiveness of the weighted and unweighted selection strategies depends on the inheritance of the character, complexity of the GxE interactions, MET strategy, and composition of the TPE. A lot of work is necessary in this area, but preliminary observations are promising.

This approach requires access to: a) crop modelling software and capability that can be used to characterize environments in a manner relevant to the GxE interactions encountered in the TPE; b) reliable historical climatic records; and c) climatic, soil, and crop management data from the environments sampled in METs.

Sorghum simulation models are available that adequately simulate the performance of standard cultivars in water-limited environments (Hammer and Muchow, 1994). These models can easily be parameterized for new cultivars using standard field experimentation. This approach assumes water limitation is the major constraint to productivity; therefore, when another constraint (e.g., disease) interacts with water availability, caution should be exercised. A major challenge with this approach is obtaining quality historical climatic data (e.g., solar radiation, temperature, and rainfall) that encompass the spatial variation of the TPE. Furthermore, minimum data sets of soil characteristics, soil conditions at sowing, and field management operations need to be collected for each MET. Chapman and Muchow (1996) have proposed a crop-soil-climate-management database system for grain sorghum to facilitate the collection of complete datasets that can easily be linked to simulation models.

While we do not recommend this strategy as a replacement for conventional selection strategies at present, sufficient positive signals warrant its further evaluation for grain sorghum. Large GxE interactions are observed for most quantitative traits; crop modelling capability exists; water availability appears to be a major environmental factor contributing to the GxE interactions for yield; and simulated selection results suggest positive results from the weighted selection strategy. Experimental programs are underway in the field in Australia to evaluate these promising theoretical results.

Evaluating Traits For Improving Drought Resistance

Identification of major physiological or environmental factors limiting the per-

formance of existing cultivars, coupled with background physiological understanding of plant response to those limiting factors, has led to many suggestions of physiological characteristics that may be selected for by plant breeders (Donald, 1968; Ludlow and Muchow, 1990). In a recent literature survey, Jackson et al. (1996) showed that attempts to identify traits for yield improvement have been dominant in physiological research, based on the thesis that advances in crop improvement under water-limited conditions are more likely if drought resistance traits are selected in addition to yield per se.

Muchow et al. (1996a) have outlined six steps necessary for the development of germplasm containing drought resistance traits:

- 1) Identify traits that are likely to confer a yield advantage in drought environments.

- 2) Determine the extent of genetic variation in such traits.

- 3) Understand the physiological basis of genetic variation for a trait. Traits need to be assessed in appropriate genetic backgrounds, and molecular markers can assist in developing such populations.

- 4) Use simulation modelling to assess the value of the trait in a wide range of target environments.

- 5) Investigate the heritability of the trait. If heritability is sufficiently high, conventional breeding methods could be used to select for the trait, providing the trait is valuable and a practical means of screening can be found.

- 6) Seek molecular markers to improve the efficiency of trait selection if heritability is low. Drought resistance traits are generally not expressed in wetter years and therefore can only be selected for in drier years. Molecular markers would enable such traits to be selected for in all years.

Figure 3 outlines a framework for selection and evaluation of traits. If a particular trait is to improve grain yield in drought-prone environments, it must increase one or more of the following identities: amount of water transpired, transpiration efficiency (TE), or harvest index (Ludlow and Muchow, 1990). Here, we restrict our discussion to a brief treatment of the traits we feel are potentially most important: phenology, osmotic adjustment (OA), leaf area maintenance or stay-green (SG), TE, soil water and nitrogen extraction, and utilization of stem reserves for grain filling (Figure 3). A more detailed coverage is given in the recent review by Muchow et al. (1996a).

Phenology is important in adapting sorghum to drought-prone environments by matching growth duration to the available resources (Ludlow and Muchow, 1990; Muchow et al., 1996a). The association between osmotic adjustment and grain yield in drought-prone environments is not clear. While some studies found that OA was positively correlated with yield (Santamaria et al., 1990; Ludlow et al., 1990; Tangpremsri et al., 1995), others found no such correlation (Tangpremsri et al., 1991a; Krieg, 1993; Tangpremsri et al., 1995) or, in some cases, a negative correlation (Kirkham, 1988; Tangpremsri et al., 1991b). Further clarification of the physiological processes controlling OA is

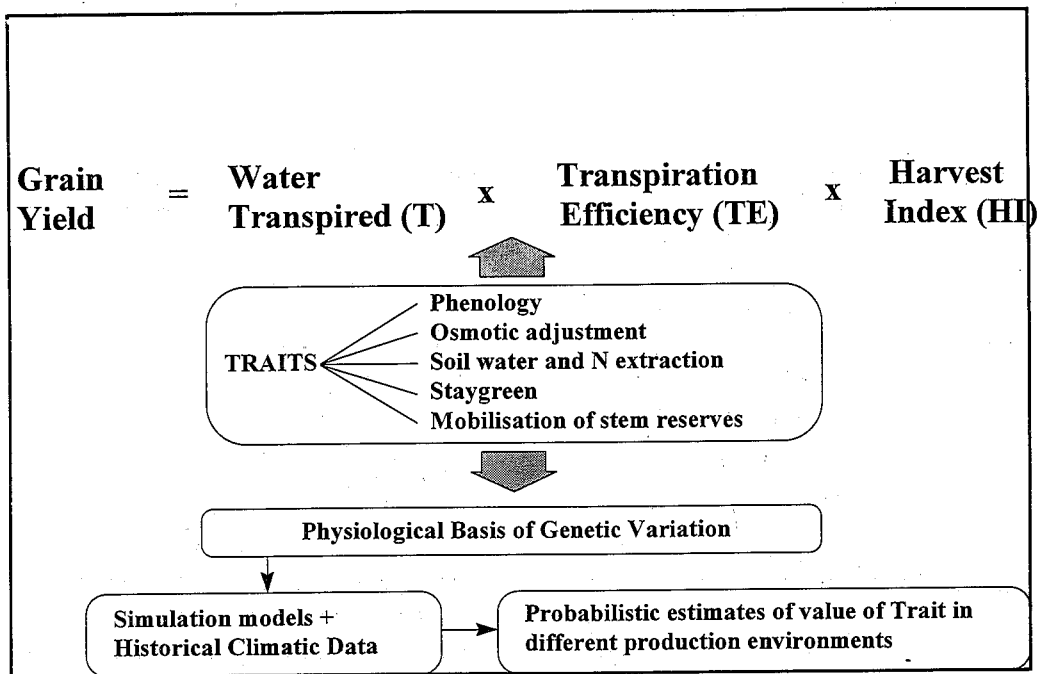


Figure 3. Framework for evaluating traits in water-limited sorghum environments.

needed before the value of this trait can be adequately assessed. It is hoped that ongoing research by Snell and Cooper (1996) will help to assess the value of this trait.

Sorghum hybrids containing the staygreen (SG) trait have been found to yield significantly more under water-limited conditions compared with hybrids not possessing this trait (Rosenow et al., 1983; Henzell et al., 1992; Borrell and Douglas, 1996). Recent research suggests that this advantage is due to maintenance of photosynthetic capacity and reduced mobilization of stem reserves to grain during the late grain-filling period, combined with lodging resistance (Borrell and Douglas, 1996). In this study, staygreen was not associated with lower harvest in-

dex as had been reported in previous studies (Rosenow et al., 1983). Further work is required to assess the extent of linkages of SG with other traits in different environments. Several studies have examined the inheritance of the SG trait (Tenkouano et al., 1993; Walulu et al., 1994; van Oosterom et al., 1996). It is difficult to select for SG because the trait is polygenic and is expressed only in drier years. Molecular markers are being developed for this trait (Tao et al., 1996) using recombinant inbred lines varying in rate of leaf senescence as a mapping population (Henzell et al., 1994).

Muchow et al. (1991) and Hammer et al. (1996a) have used simulation analysis to show that improvement in transpiration efficiency (TE) would have large benefits

in drought-prone environments. Genetic variation in TE has been observed in grain sorghum (Donatelli et al., 1992; G.L. Hammer, personal communication), but the extent of variation in TE above the value in well-adapted hybrids is relatively small. Accordingly, the scope for higher TE remains uncertain. Similarly, genetic variation in the pattern of soil water extraction (Robertson et al., 1993) and nitrogen uptake (Kamoshita et al., 1996) is small. Little progress has been made on mobilization of stem reserves to grain, beyond trait identification (Muchow et al., 1996a).

Simulation analyses provide a means to quantitatively evaluate traits in variable populations of target environments (Shorter et al., 1991; Muchow et al., 1991). Provided the physiological basis for genetic variation for a particular trait is adequately encapsulated in the model, the model can be run with historical climatic data for a specified cropping system to generate probabilistic estimates of the value of a trait in different production environments (Figure 3). Recently, Hammer et al. (1996a) simulated a MET for sorghum by introducing genetic variation for phenology, tillering, SG, and TE into the sorghum model of Hammer and Muchow (1994). They simulated ten years of experiments at three Australian sites for 24 theoretical genotypes and found that the degree of genetic variation introduced was similar to that observed among existing sorghum genotypes. While the results are specific to these environments, the analyses showed that the average response of a particular trait often was reflected in a significant advantage in a few high-yielding years, rather than superior performance in the majority of

years. The power of the simulation approach is that the value of particular traits can be evaluated in a resource-efficient manner in the TPE. This approach can be extended using optimization methodology to seek an optimal combination of plant traits and crop management, given the mix of environmental challenges in the target domain (Hammer et al., 1996a).

Using a simulation approach assumes confidence in the ability of the model to simulate the effect of a particular trait. There is no reason trait consequences cannot be simulated if the crop physiological mode of action of the trait is understood and quantified, and the crop model is sufficiently detailed to simulate the interactions with growth and development generated by expression of the trait in any particular environment. In addition, as discussed earlier, adequate long-term climatic and soil databases are required. Satisfying these "ifs" requires attention to detail in focused field experiments and examination of what constitutes "sufficient detail" in modeling. On the latter, Loomis (1993) argues that more detailed models, capable of simulating processes at a level more closely aligned to gene action, are required. Others, including Shorter et al. (1991), consider that simpler crop physiological frameworks, which are more readily aligned with plant breeders' modes of action, also are required. However, the two are not mutually exclusive, and the connection is described by Shorter et al. (1991).

There is a paucity of information on the extent of genetic variation and the physiological mode of action for many traits. Such information is essential in model

development and can be obtained only by targeted experimentation. Field work on trait mode of action for SG (Borrell and Douglas, 1996; F.R. Bidinger and A.K. Borrell, personal communication), OA (Snell and Cooper, 1996), TE (G.L. Hammer, personal communication), and nitrogen use efficiency (Kamoshita et al., 1996) is underway. Comparison of simulation of a trait with the measured impact of that trait in the field will demonstrate whether existing models are adequate for the task and whether existing assumptions about trait action are valid. For example, data from field experiments on sorghum hybrids varying in SG (Borrell and Douglas, 1996) show far greater differences than those found in the simulation analysis presented by Hammer et al. (1996a). This suggests that the mechanism associated with the SG trait involves something beyond simple maintenance of leaf area. Greater differences associated with presence of SG could be associated with greater water extraction or with changes in TE (Figure 3). The interaction between research and modeling provides a sound basis to elucidate mechanisms from the field experimentation and to extrapolate their likely worth via modelling over a far more diverse set of environments than possible via direct experimentation.

Conclusions

It is generally considered that the contribution of crop physiology to plant breeding to date has been modest (Jackson et al., 1996). However, we have entered a new era in which enhanced knowledge of both the physiology of yield accumulation in grain sorghum and the physiological

basis of genetic variation in drought resistance traits offers the potential for improving breeding efficiency in different target environments. Central to this thrust is enhanced modelling capability and improved databases. These tools can be used to characterize environments to assist multi-environment testing and to evaluate potentially useful traits. The use of such knowledge and tools requires a systems approach, with agronomists, physiologists, and breeders working together to raise sorghum yields in drought-prone environments.

A particularly exciting advance has been the characterization of the target population of environments (TPE), which offers to improve the efficiency of selection within multi-environment trials (MET) where GxE interactions are large. This has been used in developing a selection strategy to accommodate the MET sampling variation effect for a TPE where water limitation is considered to be the major variable influencing GxE interactions for yield of sorghum. The strategy is based on characterizing the types of water deficit environments and their frequency of occurrence using a sorghum simulation model, historical climatic databases, parameterization of the cropping system, and pattern analysis. This information is used to generate weights for environments that attempt to measure the relevance to the TPE of the environments sampled in the MET.

Research on drought resistance traits has advanced in recent years with particular emphasis on phenology, osmotic adjustment, transpiration efficiency and staygreen. Much more information is required on the physiological mode of ac-

tion of these traits and their likely value in different environments. Simulation models are important tools to assist in answering questions about trait actions and their value, and about the optimal mix of traits for particular environments. Considerable investment in physiological understanding is required to realize the potential of these approaches. Such strategic research on the physiology of grain sorghum is essential to realize future benefits to the sorghum industry.

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