CSIRO PUBLISHING

Australian Journal of Agricultural Research

Volume 51, 2000

A journal for the publication of original contributions
towards the understanding of an agricultural system

www.publish.csiro.au/journals/ajar

All enquiries and manuscripts should be directed to
Australian Journal of Agricultural Research
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood
Vic. 3066
Australia
Telephone: 61 3 9662 7628
Facsimile: 61 3 9662 7611
Email: jenny.fegent@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

Aust. J. Agric. Res., 2000, **51**, 223–33

Genotype by environment interactions affecting grain sorghum. III. Temporal sequences and spatial patterns in the target population of environments

S. C. Chapman[AE], *G. L. Hammer*[B], *D. G. Butler*[C], *and M. Cooper*[D]

[A] CSIRO Tropical Agriculture, Long Pocket Laboratories, 120 Meiers Rd, Indooroopilly, Qld 4068, Australia.
[B] Agricultural Production Systems Research Unit, Queensland Department of Primary Industries,
PO Box 102, Toowoomba, Qld 4350, Australia.
[C] Queensland Department of Primary Industries, PO Box 102, Toowoomba, Qld 4350, Australia.
[D] School of Land and Food, The University of Queensland, Brisbane, Qld 4072, Australia
[E] Corresponding author; email: scott.chapman@tag.csiro.au

Abstract. The variable nature of rainfall in north-eastern Australia confounds the process of selecting sorghum hybrids that are broadly adapted. This paper uses a crop simulation model to characterise the drought environment types (ET) that occur in the target population of environments (TPE) for dryland sorghum. Seventy seasons (1921–1990) of simulations of the yield of a sorghum genotype and the associated within-season sequence of a stress index were conducted for a small TPE of 6 locations and also for a large TPE of 211 locations that attempted to represent the entire sorghum region.

Previously, using the small dataset of 6 locations, pattern analysis enabled us to group seasonal stress indices from each trial into major ETs: 'low terminal stress' (ET1), severe terminal stress (ET2), and intermediate mid-season/terminal stress (ET3) in the ratio 33 : 38 : 29. When the dataset was broken into a sequence of 16 multi-environment trials (METs), each of 3 years and 6 locations, the ratios of ET1 : ET2 : ET3 differed greatly among METs, i.e. any single MET was not randomly sampling the TPE. Hence, for any MET, the average yield (GV_u) was not the same as the overall mean of the entire 70-year dataset. If the trial yields were weighted according to the ratio of ET1 : ET2 : ET3 in the overall TPE, then GV_w (s.d. = 0.13) for a single MET was much closer to the overall mean than was GV_u (0.38). For different METs, the values of GV_w were up to 30% higher or 15% lower than GV_u. Across METs, the difference between GV_u and GV_w was positively correlated ($r = 0.88$, $n = 16$, $P < 0.05$) with the frequency of ET1 ('low terminal stress') encountered within the MET and negatively correlated ($r = -0.82$) with the frequency of ET2. The value of weighting was confirmed by its ability to verify that two simulated genotypes had the same mean yield over many trials, even though they differed in their specific adaptation to the different ETs.

The large TPE consisted of more than 15 000 simulations and was classified in 2 stages (within/among locations), repeated for each of 3 soil types. In years in which the simulation sowing criteria were met, the ratios of ET1 : ET2 : ET3 were about 4 : 2 : 4, 4 : 5 : 1, and 6 : 3 : 1 in the shallow, intermediate, and deep soils, respectively. Hence, over all soil types and locations, the sorghum TPE for northern Australia consists of at least 30% each of low terminal stress (ET1) or severe terminal stress (ET2) and these environment types need to be sampled. The incidence and nature of the 'intermediate midseason/terminal stress' environment type (ET3) varies with soil type and location.

Weighting genotype performance should improve the precision of the estimate of its broadly adapted value, and be of practical use in breeding programs in these variable environments. Although the 'boundary conditions' of the TPE are not yet resolved, this paper also shows that simulation and pattern analyses can be used to determine the structure of the abiotic TPE. Taking other factors into account (e.g. soil type distribution, shire production levels, and farm profit), selection trials could be weighted to improve selection for narrow or broad adaptation, depending on the purpose of the breeding program.

Additional keywords: drought, *Sorghum bicolor*, cultivar, tropical, breeding.

10.1071/AR99022 0004-9409/00/020223

Introduction

Sorghum production in north-eastern Australia encompasses a range of soil types and rainfall regimes and, over seasons, generates a large target population of environments (TPE; Comstock 1977) for which plant breeders attempt to select for broad adaptation. Although an analysis of the temperature and rainfall regimes would suggest that the environments of the northern area (central Queensland) and southern area (southern Queensland and northern New South Wales) are 'obviously different', the implications for plant breeding and crop adaptation are difficult to quantify. As was previously found for multi-environment trials (METs) of wheat varieties (Brennan *et al.* 1981; Cooper *et al.* 1996), we determined that for sorghum, the northern and southern areas differed in the way in which they discriminated among the yields of different hybrids, i.e. rankings of hybrids changed greatly across the region (Chapman *et al.* 2000*a*).

Podlich and Cooper (1998) have demonstrated, using a genetic simulation model, that selection gain over generations can be improved by weighting the data from METs according to how representative individual trials are of the TPE. To apply these types of analyses requires estimates of the occurrence of different environments in the TPE. For many biotic stresses, the selection target (resistance or tolerance) and the geographic requirement for adaptation are relatively obvious. However, for the main abiotic limit to Australian sorghum production, drought, it has been difficult to quantify the occurrence, intensity, and importance of different patterns of stress in both on-farm trials and breeding trials that attempt to mimic on-farm conditions. Consequently, selection for drought tolerance has largely been a matter of screening in as many trials (whether progeny, test-crosses, or pre-commericals) as possible with the assumption that this degree of testing will suitably sample the range of environments.

In the two previous papers, we found that variance components for the interaction effects of genotype and environment [G (genotype)×L (location)×Y (year), G×L, G×Y] were substantial compared with that for genotypic effects. Differences in G×L that were characterised by principal component scores were related to the frequency of different environment ('stress season') types, as determined by analysis of outputs from a crop simulation model. Given knowledge of the temporal and spatial distribution of these water-limiting environment types across the region, it should be possible to improve the efficiency of utilisation of data from sorghum METs by weighting trial results to match the TPE (as Podlich and Cooper 1998 have shown elsewhere). The strategy of this approach depends on moving from a G×L×Y model (with the 'artificial' interactions of G×L, G×Y, and G×L×Y) to a G×ET model where the environment type (ET) is not 'tied' to a location or year.

Our previous simulation analysis was based on only 6 locations (Chapman *et al.* 2000*b*). One advantage of simulation models is that we can begin to test scenarios over a much greater range of seasons and locations than is physically possible. The types of questions that can be addressed by further simulation include the following. Should we select for broad adaptation (consider southern and central Queensland to be part of the same TPE) or identify cultivars that are specifically adapted to each region? Would the same genetic traits be of use in both regions? How frequently are such traits likely to be useful? As Podlich and Cooper (1998) showed, an understanding of the mixture of environment types is a critical first step in adopting a strategy of breeding for target environments utilising the weighting methodology.

In this paper we simulate the long-term value of evaluating single hybrids by weighting performance according to environment type and extend the classification of ETs to describe the TPE for water-limited environments over the entire sorghum cropping region. The discussion describes how plant-breeding programs can utilise this information to improve the efficiency of sorghum breeding for Australian dryland environments.

Materials and methods

Crop simulations

The simulations of daily sorghum growth, yield, and a stress index (relative transpiration, RT) are described by Chapman *et al.* (2000*b*). The RT index is a function of the fraction of transpirable soil water (FTSW) in the soil that is available to the roots on any day:

$$RT = 1/[1+9^{*} \exp(-23.1 * FTSW)]$$

The model, which is an updated version of that developed by Hammer and Muchow (1994), takes inputs of soil water-holding characteristics, hybrid parameters, and daily weather data and simulates growth for each occasion on which planting requirements (rainfall etc.) have been met. The model predicts biomass ($r^2 > 0.8$) and yield ($r^2 > 0.7$) quite well over a range of growing conditions. The final grain yield was output, together with the RT index, which was averaged for each 100 degree-days of thermal time [termed thermal time weeks (TTweeks)]. For the analysis of weighting, we used a subset from the results of Chapman *et al.* (2000*b*) determined for 564 trials over 6 locations and up to 100 years. A new set of simulations, described below, was generated for the spatial interpretation of stress patterns across the sorghum growing region.

Comparison of unweighted and weighted measures of genotype value

The 564 trials from 6 locations had been previously grouped (Chapman *et al.* 2000*b*) into 3 environment types: (1) low terminal stress (occurring in 33% of seasons, here termed ET1); (2) severe terminal stress (ET2) with an early-season (9%) or midseason time (29%) of onset; and (3) intermediate midseason/terminal stress (ET3) with a mid-season (9%) or late-season (20%) time of onset. (These 'ET' grouping names are also used later in the spatial classification, although it should be remembered that they do not come from the same input data). For the 6 locations, the 48 seasons of yields (1921–1968) that were common to all locations were extracted, giving a total of 287 seasons, as in several 'location years' the sowing criteria of the model were not met. Beginning in 1921 (i.e. the season 1920–21), these years were grouped into sets of 3 years to represent 16 consecutive METs, but having only a single simulated hybrid in the trial. In most seasons there were 6 locations of data, so each MET was normally 3 years by 6 locations (18 environments). Three years is a typical amount of testing that might be done on hybrids in the final stages of selection.

In each MET, each trial (‘location year’) was assigned to an environment type or group (i), and the average yield was calculated for each group within the set as Y_i. Then the unweighted genotype value (GV_u) was calculated as average yield across all locations for the 3 years. The weighted genotype value (GV_w) was computed as:

$$GV_\mathrm{w} = \sum_{i=1}^{n} Y_i \times f_i$$

where f_i is the average frequency of occurrence of group i for all 48 years of data. The values of GV_u and GV_w were compared across the 16 METs.

Apart from using the simulated grain yields (G1), a second genotype (G2) was constructed by assuming that it had a different adaptation profile to the different environment types. This was done iteratively by multiplying the simulated yields by a constant for each environment type such that G2 and G1 had the same mean yield over all 48 years of trials, but differed within environment types. The result was the yield of G2 being 5% higher than G1 in low stress environments but 10% and 4% lower than G1 in the severe and intermediate stress environments, respectively. The weighting procedure was applied as described above, and the percentage difference between the genotypes was determined for each of the 16 METs.

Simulation of the sorghum TPE

The simulation analysis described above was extended to cover the entire sorghum cropping region. A digitised map of the geographical limits of regular cropping in Australia in the late 1980s was obtained from Bureau of Rural Resources, DPIE Canberra (Hamblin and Kyneur 1993). This map had been derived from the digital version of the Atlas of Australian Resources, Vol. 6, ‘Vegetation’, produced by AUSLIG, with additional data from NSW Agriculture and Queensland Department of Primary Industries.

Using GIS software (ARC-INFO, ESRI software), the map was trimmed along shire boundaries to remove all shires for which sorghum production was negligible (<50 t/year in the shire) during the years 1990–95. This resulted in a sorghum crop cover ‘mask’ that became the base map for this analysis (Fig. 1). The single outermost boundary of this base map was then used as a filter to extract rainfall stations from a master list supplied by the APSRU systems research unit (T. Marcussen, pers. comm.). These rainfall stations are all part of the

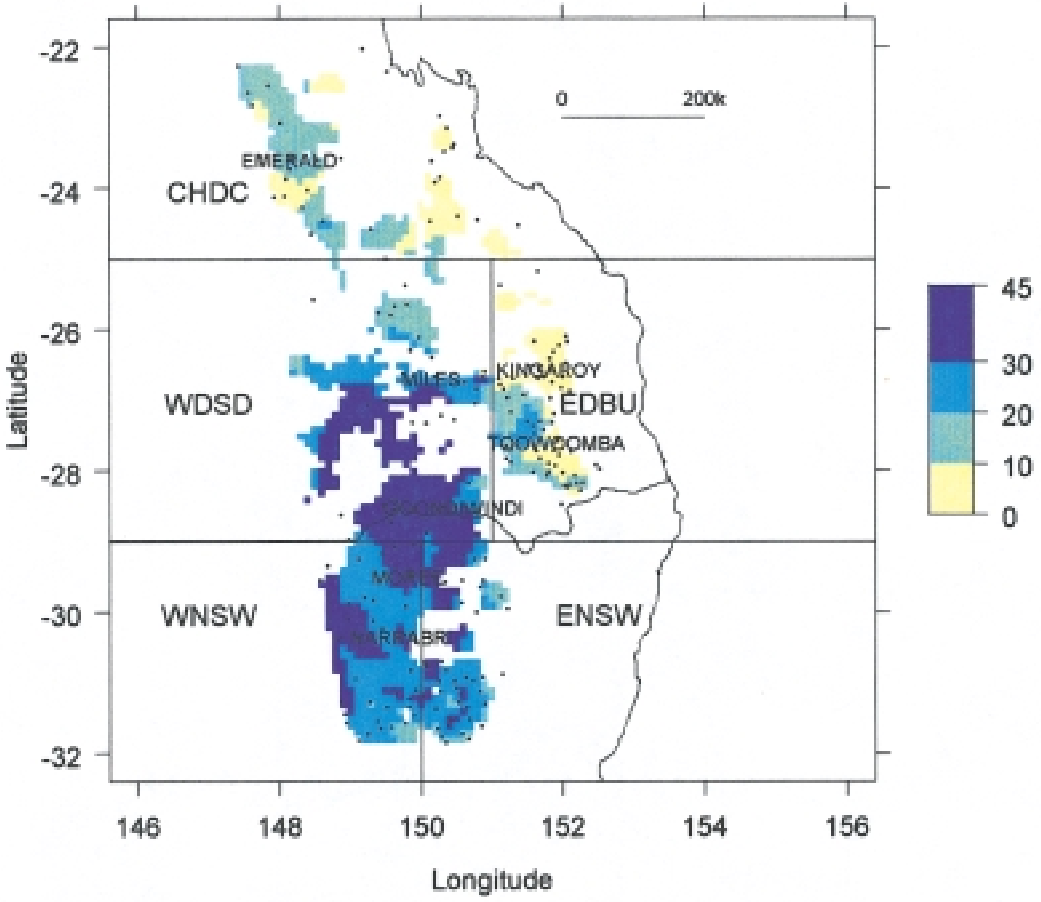

Fig. 1. Weather station locations (dots) used in the spatial analysis of the TPE, and the interpolation of the frequency of years (%) in which a crop was not planted, i.e. the simulation sowing criteria were not met. Also shown are major towns (names are centred on town location) and a simplified division of the 5 major cropping regions (Table 3): CHDC (Central Highlands/Dawson and Callide); EDBU (Eastern Darling Downs/Burnett); ENSW (eastern NSW); WDSD (western and southern Darling Downs); WNSW (western NSW).

Bureau of Meteorology network. For each of the 211 locations that fell within the base map, we then had a daily rainfall file together with daily temperature and radiation data from the nearest climatological station (Fig. 1).

For each location, simulations were generated using the same genetic parameters and starting conditions described above and by Chapman *et al.* (2000*b*), but only for the seasons from 1921 to 1990. The simulations were repeated at each location for 3 soils of differing water-holding capacity (Table 1). For each simulation, the RT index was output for each day and was averaged over each 100 degree-days (TTweeks) for the season (Chapman *et al.* 2000*b*). The last ('ragged') week was dropped from the analysis, so that all locations had the same number of weeks. Although it was considered in initial analyses, we did not attempt to group the soils together, or to map their combined effects. Soil depth maps are not detailed enough to provide an accurate picture of the variation in soil type at this large scale. Unfortunately, this will probably remain a problem and complicate decisions about which simulations to include when making classifications of environment type.

Table 1. Water-holding characteristics of simulated soil types

Soil description	Depth (cm)	Available soil water (mm)
Shallow	90	157
Intermediate	150	178
Deep	180	245

Pattern analyses of the change in RT during the season were conducted separately for each soil type using the clustering methods described by Chapman *et al.* (2000*b*). Given computer memory limitations when applying a hierarchical clustering approach to 15 000 simulations at once, the seasons were first classified by S-Plus (MathSoft Inc., Seatle, WA) routines into 20 groups (some still comprising only one season) at each location. The final pattern analysis was then applied to the resulting 4220 groups combined across 211 locations. To do this, we used the same clustering methods as for the within-location analysis, but used the PATN software (Belbin 1991) on a mainframe computer. Finally, for each soil type, we extracted the season memberships at the 3-group level and determined the frequency of seasons within a location that were members of one of the groups ('stress environment types'). The seasons within each group (and soil type) were averaged to give an RT index for the group. Across the soil types, similar names were given to the groups that had the same general form of average RT index as it changed over the season. Alternative clustering methods to the hierarchical approach might also have been suitable (e.g. as reviewed by Basford and Cooper 1998), but had not yet been tested for this type of analysis.

To produce maps of the frequency of occurrence of each season type, we used the S-Plus *interpolate* function to interpolate the data in steps of one-tenth of a degree into a 'convex hull' within the rectangular grid limited by 22°S, 146°E to –32°S, 156°E. After interpolation, the base map was used to eliminate non-cropping areas and non sorghum producing shires. A map was produced showing the frequency of years in which the systems model did not plant a crop, according to the criteria that required 30 mm of rain during a 6-day period within a planting 'calendar window' (Fig. 1).

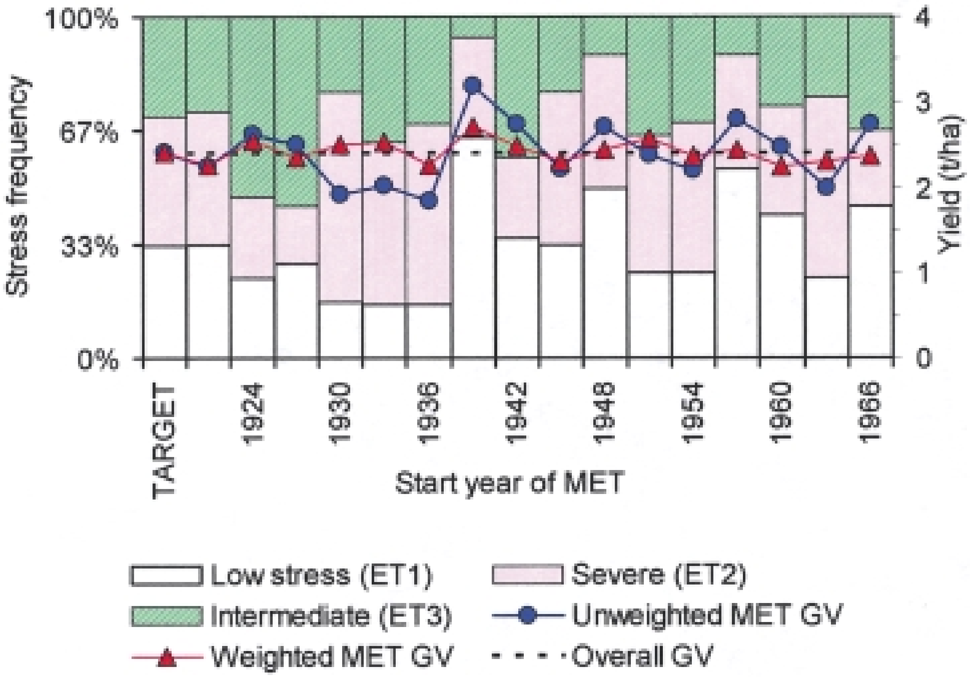

Fig. 2. For 16 consecutive simulated multi-environment trials (each of 3 years and 6 locations), the average (target) and individual distributions of 3 environment types (low terminal stress, severe terminal stress, and intermediate midseason/terminal stress); and the genotype value for each multi-environment trial either unweighted (average yield) or weighted by the average frequency of occurrence of each environment type. The left-most column is the frequency of environment types over the entire dataset ('target') and the dashed horizontal line is the genotype value.

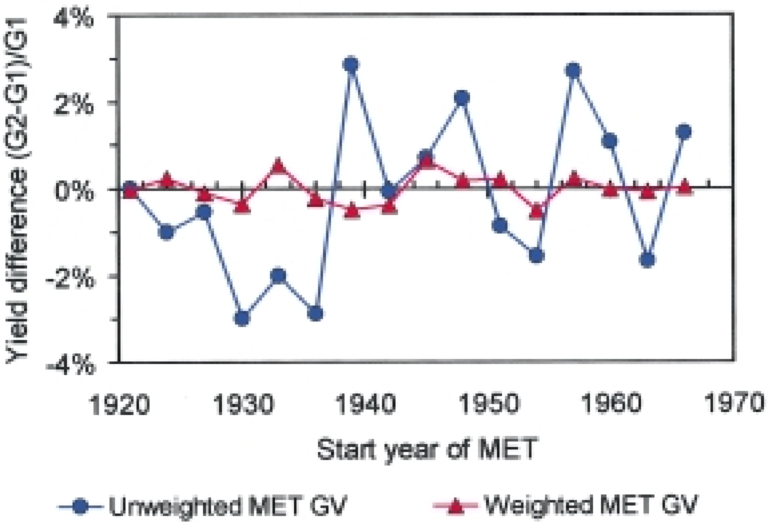

Fig. 3. In each of 16 multi-environment trials (Fig. 2), the percent difference between two simulated genotypes of the same average yield but differing in performance within different environment types (see text) when compared using unweighted and weighted genotype values.

Although interpolating the results is straightforward, it is difficult to settle on an objective method of estimating the overall frequencies of occurrence of different season types. There are two problems. Firstly, the meteorological stations are not evenly distributed over the region, so averaging the frequencies across the 211 stations introduces bias. Secondly, if weighting is to be used to account for this bias, should the basis be the area being cropped to sorghum, or the actual shire production of sorghum? We adopted the simple approach of computing the average frequencies for each soil type directly from the interpolated, masked maps. The frequencies derived therefore represent the total area currently cropped by sorghum, but with no weighting of the actual production per unit area of shires. This weighting could be derived, albeit with assumptions that may greatly change the result. Similarly, the maps could be weighted according to the potential (cf. actual) area for sorghum production.

Lines drawn on Fig. 1 also indicate 5 major regions for which stress frequencies were separately computed: CHDC (Central Highlands/Dawson Callide); EDBU (Eastern Downs/Burnett); WDSD (Western Downs/Southern Downs); ENSW (eastern NSW); WNSW (western NSW).

Results

Effects of weighted selection on genotype value

Across the 48 seasons, simulated grain yield averaged 2.41 t/ha. The 3 environment types described above were used, together with their frequencies summed for all years (the target): low terminal stress (33%), severe terminal stress (38%), and intermediate midseason/terminal stress (29%) (Fig. 2, first column). Average yields for these 3 groups across all years were 4.01, 1.00, and 2.41 t/ha, respectively.

Fig. 2 also shows, for each of the 16 consecutive METs, the proportion of each ET encountered over 3 years of testing. Comparisons with the target (first column) show that 3-year METs begun in 1930–36, 1951–54, or 1963 particularly would have experienced fewer ‘low stress’ environments than the average. In these years, the GV_u was less than the long-term mean indicated by the horizontal line. In contrast, METs begun in 1939, 1948, 1957, or 1966 would have ‘over-sampled’ the low stress ET, in comparison with the ‘target’. As would be expected, GV_u in these 4 METs was also high, up to 0.8 t/ha greater (1939) than the overall mean.

In all of the 16 METs, GV_w for a single MET was equal or closer to the overall mean than was GV_u, as is indicated by the overall lower variability of GV_w (s.d. = 0.13) compared with GV_u (0.38). Across METs, the difference between GV_u and GV_w was positively correlated ($r = 0.88$, $n = 16$, $P < 0.05$) with the frequency of the low stress ET encountered in the MET. The GV difference was negatively correlated with the frequency of occurrence of the severe stress ET ($r = –0.82$). For every 10% (absolute) by which the low stress ET was over- or under-sampled within a MET, the difference between GV_u and GV_w increased by 0.2 t/ha.

In terms of broad adaptation, the simulated METs should determine that there is no difference between genotypes G1 and G2, as their overall yield is the same. However, during the METs begun in 1930–36 and 1951–54, when the occurrence of the low stress ET was less than the overall ‘target’, the difference in GV_u between the 2 genotypes indicated that G1 was superior to G2 by up to 3% (Fig. 3). Conversely, when METs were conducted during a series of wetter years with a higher frequency of low stress environments (Fig. 2, 1939, 1948, 1957, 1960, or 1966), GV_u of G2 was superior to G1 by 1–3%. Across METs, the difference in GV_w between the 2 genotypes was more stable than the value for the difference in GV_u. In all METs, the absolute difference in GV_w between the 2 genotypes was <1%, and was consistently closer to the ‘real’ value of 0.

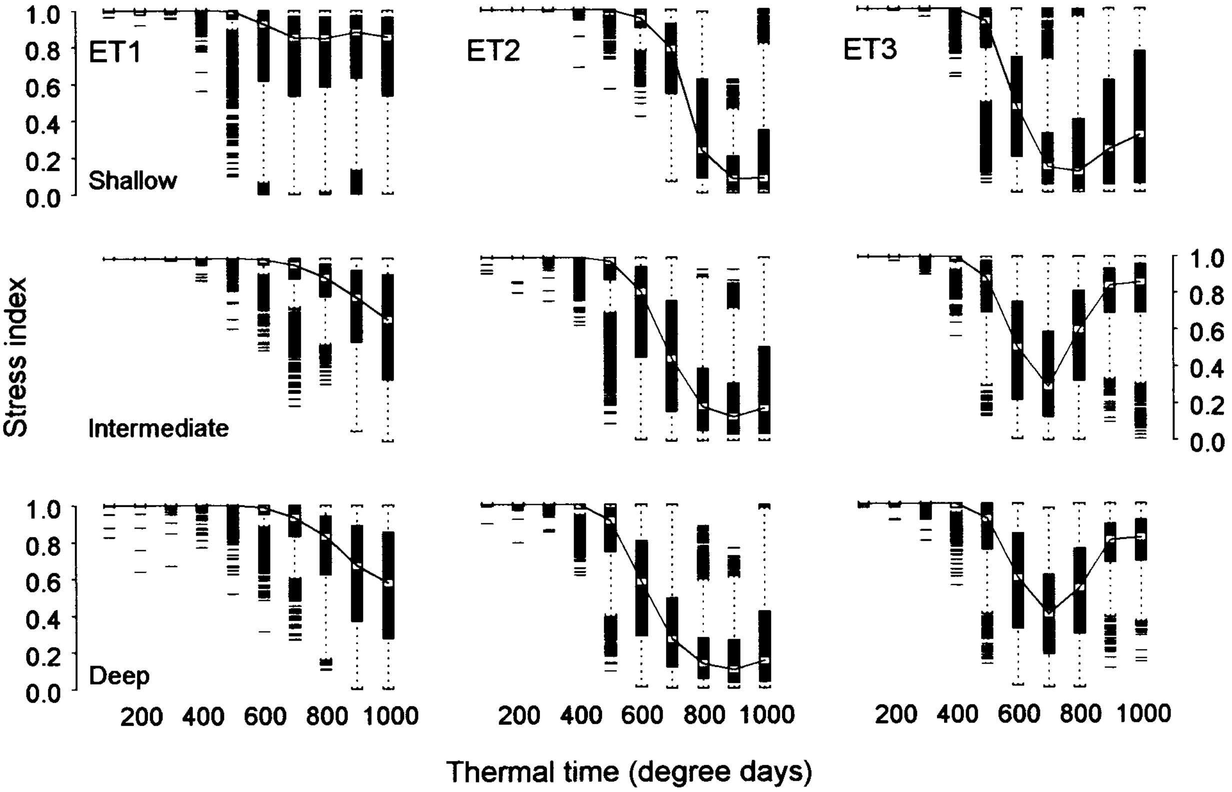

Fig. 4. For each of 3 soil types over 211 locations and 70 years, box and line (average) plots of the within-season sequence of the simulated stress (RT) index following their classification into each of 3 environment types described as 'low terminal stress' (ET1), 'severe terminal stress' (ET2), and 'intermediate midseason/terminal stress' (ET3). The centre line of each box plot is the median, and the lower and upper ends of the solid box are the first (1Q = 25%) and third (3Q = 75%) quartiles, respectively. The lower and upper ends of the dotted vertical line (bracket shape) are the minimum and maximum values, respectively, not including outliers (dashes) that are >1.5 quartile ranges (3Q–1Q) below 1Q or above 3Q. Flowering time occurred at *c*. 650 degree-days.

Spatial variation in the frequency of stress seasons

Fig. 4 shows the different seasonal stress patterns derived from simulations at 211 locations over 70 years. The line plots show the average value of stress (RT index) over the season (10 TTweeks = 1000 degree-days) for all environments within each soil type and environment type. The box plots demonstrate that there was still a substantial range in RT index within each TTweek, even after classification.

Note that the environment types for each of the soil types were derived independently, as it was not appropriate (nor possible, with our computer resources) to combine the results of the soils together. Hence, the seasons/locations that make up the 'average' RT index for a group (e.g. ET1) are not the same for each soil. Also, the RT index is a function of the fraction of transpirable soil water (FTSW) available to the roots and begins to decrease rapidly when the FTSW is below about 0.25 (Hammer and Muchow 1994). Soils that differ in depth could have the same RT index, but the 'deeper' soil would still be able to supply more water to the roots on a given day, i.e. the absolute value of the RT index is not directly comparable across soil types.

For each soil type, one of the classification groups ('low terminal stress', ET1) consisted of seasons over which the average RT index remained high until the seventh (700 degree-days) or eight TTweek, decreasing slightly to produce a terminal stress in the last weeks of the season (Fig. 4). On average, the stress in this group was more severe in deeper soils, but as mentioned above, this is at least partly a function of the independent grouping and the way that the RT index is calculated. Another of the groups (ET2) where the stress index began to decrease at about 6 or 7 TTweeks was a 'severe terminal stress'. In the intermediate and deep soils, the remaining environment type (ET3) corresponded somewhat to the 'intermediate midseason/terminal stress' of the 6-location analysis, although the midseason stress was of more severe intensity.

The frequencies of occurrence of 'unplanted years' and the 3 environment types after spatial interpolation into 0.1°×0.1° grid cells are given in Table 2. The frequency of seasons in which the model planted a crop was not greatly affected by soil type, but did vary across the region, with some regions being planted almost every year, and some in

Table 2. For three soil types, the descriptive statistics of frequencies of different environment types estimated after the interpolation of location frequency data into (0.1° × 0.1°) pixels over the entire cropping region (see Fig. 5)

The 4 values under each heading are the (min., median, mean, max.) values (%) observed over all of the pixels such that the mean values sum to 100%. In planted seasons, the ratios of mean frequencies among the 3 environment types are 36 : 22 : 42, 43 : 47 : 10, and 61 : 30 : 9 for shallow, intermediate, and deep soils, respectively.

Soil	Seasons not planted		Seasons planted	
		Low terminal stress (ET1)	Severe terminal stress (ET2)	Intermediate mid-season/terminal stress (ET3)
Shallow	2, 13, 14, 40	6, 24, 31, 76	4, 19, 20, 41	3, 41, 35, 59
Intermediate	1, 11, 13, 39	3, 27, 38, 90	5, 45, 41, 66	1, 8, 9, 21
Deep	0, 10, 13, 38	19, 46, 53, 95	1, 30, 26, 50	1, 7, 8, 17

the south and west (Fig. 1) only meeting the planting criteria in 4 years out of 10.

The mean incidence of ET1 increased with increasing depth of soil (Table 2), although the variation across the grid cells was still substantial. For all soil types, the incidence of ET1 increased from southern to northern latitudes (Fig. 5). The occurrence of ET2 was greatest in the intermediate depth soil (Table 2). For both the intermediate and deep soil types, the occurrence of this stress was more frequent in the southern regions than in the north (Fig. 5). In contrast, for a shallow soil, it was more common in the north than the south. The ET3 stress was 3 times more likely to occur in the shallow soil type than in the other soil types (Table 2) and in this soil type was more common in the southern part of the region. In both the intermediate and deep soil types, the occurrence of ET3 was <20% anywhere in the entire area.

Table 3 shows, for different soil types, the ratios of the different ETs in 'planted' years in different geographic regions. For the most common soil types within a region, the frequencies of ET1 and ET2 ranged from 20 to 70%, whereas the value for ET3 was <20%.

Discussion

Effects of weighted selection on genotype value

The results of the 16 simulated METs illustrate that even 18 trials over 3 years can still result in biased sampling for yield in a variable environment (Fig. 2). Weighting by environment types appears to be a successful method of dampening this bias (Fig. 3). If METs had been conducted in these locations to select sorghum since 1920, then simple averaging across trials would initially have developed hybrids with adaptation to a higher frequency of drought environments than the long-term average; in 5 of the 6 years from 1929–30 to 1934–35, much of this region experienced well below average rainfall (0–20 percentile). Later, between 1940 and 1970, the simulated METs encountered 2–5-year oscillations in the proportions of low stress (ET1) and drought environments, i.e. the population of environments was a moving target. Climate variability is now well appreciated as an important component of managing the cropping systems of northern Australia (e.g. Hammer *et al.* 1996). The simulation results demonstrate how the impacts of this variability are also likely to be important in the selection of cultivars by both plant breeders and producers.

Chapman *et al.* (2000*a*) observed large G×Y interactions (relative to genotype main effects) in addition to G×L and G×L×Y interactions. Large G×L effects sometimes continued over several years, while in other sequences of years G×L effects were always small (see their Figs 3 and 4). In north-eastern Australia particularly, the persistence of the El Niño Southern Oscillation (ENSO) atmospheric effects over years has a tendency to cause climate to switch between periods of drought (El Niño) and periods of greater than average rainfall (La Niña), each of which may last for several years (Nicholls 1988). Therefore, depending on the years sampled and concurrent status of the effects of ENSO, even 3–5 years of testing may sample only the lower or upper ends of the yield and stress spectrums. A further complication is that these effects are not consistent across locations, so a single season may sample all or only one of the environment types. The concept of dealing with years and locations as environments should therefore be exploited to maximise throughput of testing with as few years and locations as necessary to sample the variation.

It is particularly important to measure the impact of the high-yielding, low terminal stress ETs, because their frequency in a single MET was highly correlated with the effect of weighting in our experiment (i.e. the difference between the 2 strategies in Figs 2 and 3). Weighting selections is therefore particularly vital in sets of years when low terminal stress ETs (that are high yielding) are grossly over- or undersampled, compared with their normal occurrence of about 1 in 3 environments. Further, the advantage of the weighting strategy to identify the best broadly adapted genotypes was clear when comparing genotypes that differed in their degree of specific adaptation to the different ETs.

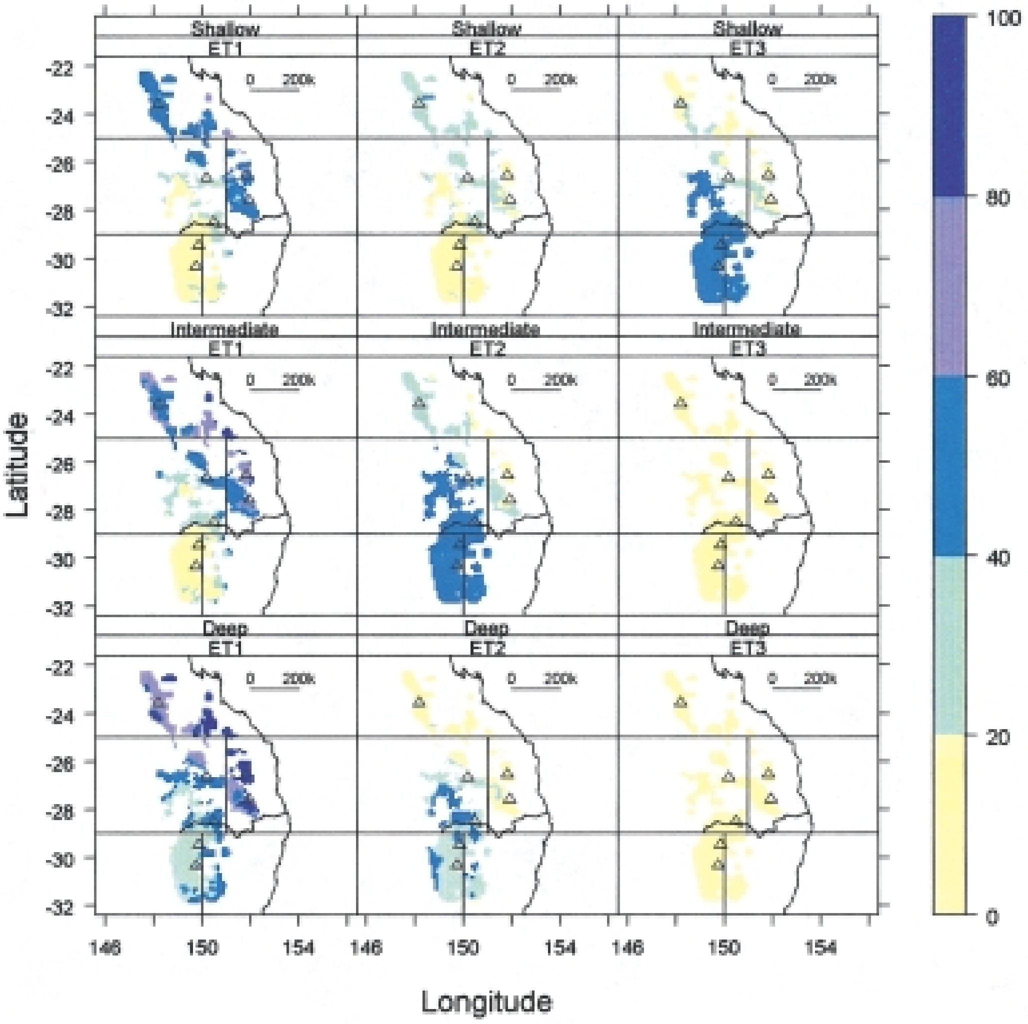

Fig. 5. The frequencies (out of 100% for each soil type) of the different environment types in Fig. 4 following spatial interpolation among stations enclosed by the sorghum growing region. Triangular symbols indicate the locations of towns named in Fig. 1.

Spatial variation in the frequency of stress seasons

The ‘low terminal stress’ environment type (ET1) corresponds to the group of the same name discussed above and by Chapman *et al.* (2000*b*) from the 6-location analysis (Fig. 4). Similarly, the ‘severe terminal stress’ (ET2) corresponded to environment type 2 in the 6-location analysis. Whereas ET3 in the shallow soil was similar in pattern to that in the other soils, there was little relief of the stress, i.e. in the shallow soil, ET2 and ET3 were essentially the same, implying that terminal drought stress is the ‘normal or average’ case for this soil type.

Apart from weather records, spatial classification is restricted by the parameters supplied to the model. For example, the frequency of unplanted years over the interpolated dataset was a just over 1 year in 10 (Table 2). As the planting rule was driven largely by the requirement for a certain amount of rainfall in a 6-day period, rather than the condition of the soil profile, there was only a small difference among the soils. Differences across the region were greater than those across the soil types. If we had specified a minimum soil water requirement (e.g. 50 mm), this may have increased differences among the soils. Note that the simulation was only of summer sorghum rotation. Opportunities for the planting of a winter crop rotation, particularly in the southern areas, would affect overall profitability and return. The flexibility of using a simulation model to characterise the TPE could therefore be expanded to include other short- and long-term management decisions of the cropping system. For the ‘planted’ years, the ratios of environment types ET1 : ET2 : ET3 were approximately 4 : 2 : 4, 4 : 5 : 1, and 6 : 3 : 1 in the shallow, intermediate, and deep soils, respectively (Table 2). Hence, the intermediate depth soil has

Table 3. Across five regions of sorghum production (as indicated in Fig. 1), and for three soil types differing in depth and water-holding capacity, the mean ratios of the frequency of simulated stress environment types (ET1 : ET2 : ET3) in years when simulation criteria for planting were met (Fig. 5)

Region		Geographic extent	Shallow	Intermediate	Deep
CHDC	Central Highlands/ Dawson/Callide	>(–25°S)	54 : 30 : 16[A]	68 : 27 : 05	83 : 12 : 05
EDBU	E Downs/Burnett	(–25°S) to (–29°S) & >151°E	55 : 23 : 22	67 : 26 : 07[A]	80 : 12 : 08
ENSW	E NSW	<(–29°S) & >150°E	25 : 18 : 57	26 : 59 : 15	50 : 38 : 12[A]
WDSD	W Downs/S Downs	(–25°S) to (–29°S) & <151°E	29 : 24 : 47	35 : 55 : 11[A]	52 : 38 : 10
WNSW	W NSW	<(–29°S) & <150°E	18 : 16 : 66	19 : 67 : 14[A]	42 : 47 : 11

[A] Indicates the major soil type depth in the region for sorghum production.

a higher incidence of ET2 (severe terminal stress) than does the deep soil. Both soils occasionally had intermediate stresses (ET3), but otherwise a low terminal stress (ET1) occurred. In a majority of years (6/10), severe terminal stresses (ET2 and, in this soil, ET3) occur in the shallow soil. Overall, the sorghum TPE for northern Australia consists of at least 30% each of low terminal stress (ET1) or severe terminal stress (ET2). Given these frequencies, crops growing in intermediate and deep soils particularly require tolerance to end-of-season stresses. In the shallow soils that prevail in the northern region, crops require tolerance to both midseason and end of season stresses.

Implications for sorghum breeding

Plant improvement programs necessarily devote substantial resources toward the development of tolerance to pests, particularly as new strains of pests develop. The success of maintenance plant breeding in the continual pyramiding of tolerance is largely hidden, but would be quickly evident if resources were diverted from these activities. Although pest-screening nurseries may be part of the selection process, selection for improved adaptation to abiotic stress occurs principally via multi-environment trials at various stages of selection.

Although dryland breeding programs in Australia practice some degree of niche breeding, the small size of the market practically requires that broad rather than narrow (geographic) adaptation be the main objective for private industry. In Australian environments, drought tolerance is assumed to be an essential characteristic. Another argument against narrow adaptation is that even the best cultivars can suffer greatly in the marketplace when they are deemed to have ‘failed’ in any one location or season, even if the expected occurrence of this environment is extremely low. As different ETs can occur in any location, it is likely to be inefficient to select or release ‘location-adapted’ cultivars, except in a few locations with highly reliable rainfall (or irrigation) and deep soils.

Given the above, and accepting that G×E for drought stress is important in determining broad adaptation of sorghum in the region, plant breeders have several options to accommodate the effect:

(1) randomly sample environments over locations and years and extend sampling where bias has apparently occurred;
(2) randomly sample environments, but classify and weight each trial in proportion to its relevance to the target population of environments;
(3) utilise specifically managed environments to ensure that the major stress season types are sampled, an approach that was used to improve drought tolerance of maize germplasm (Bolaños *et al.* 1993);
(4) combinations of the above.

Option 1 is the current approach. In a season when trial failures are high (i.e. usually ET2 environments), additional seasons of testing might be considered by a breeder. Other than this case, it is difficult to know whether sampling bias has occurred without attempting to classify the trials using weather, soil data, and a simulation model.

To be practical, methods to increase the rate of improvement in crop adaptation to physical (climate/soil) environments need to be applicable within the breeding programs. One example of this is to use ‘probe’ genotypes to detect the presence of pathogens (Cooper and Fox 1996). Another is to modify the way selections are made in METs by first classifying the environments.

For wheat, Cooper *et al.* (1996) and Podlich and Cooper (1998) have used gene simulation methodology to demonstrate over generations of recurrent selection that weighting of the occurrence of sampling environments to match their occurrence in the TPE (Option 2) should improve the rate of population improvement for broad adaptation to the TPE. The methods are based around stochastic simulations of the effects of selection on the frequency of genes that are favourable in different hypothetical environment types. Their gene model (QU-GENE) can analyse the effects of specific or random sequences of different ETs during population improvement. Our paper illustrates how sequences of different environment types can change (or persist) in the climatic record and how the frequencies of different ETs change geographically. The frequency distributions of ETs in the sorghum TPE can be input to QU-GENE to determine the best method of weighting. In a breeding program, each subsequent trial could then be characterised as it was completed, and classified to determine the ET, and the results weighted for use in selection.

The main difficulty with utilising managed environments (Option 3) to improve drought tolerance is the expense of ensuring that periods of drought occur at the right time and intensity. Generally this requires a supply of irrigation at a nursery in a seasonally arid location, together with equipment (e.g. rainout shelters) to exclude rainfall. Selection advance is possible in managed drought stress environments, but should employ advanced experimental designs and analysis to minimise experimental error and consider trait index selection where heritability for yield is greatly reduced, e.g. Bolaños *et al.* (1993). In the case of northern Australia, the inclusion of an irrigated or partially irrigated environment might also be considered necessary to ensure sampling of the higher yielding ET1 environments, as is now done for wheat in Northern Australia (Cooper *et al.* 1996).

The regional basis of the G×E interactions for sorghum yield appears to be in part associated with the different mixture of patterns of water stress encountered over seasons. In this series of papers and others investigating the effects of environment weighting on selection over generations (Podlich and Cooper 1998), there is evidence to suggest the merit of considering different types of water deficit environments as target environments. The 3 key environments for sorghum and their frequencies of occurrence are (1) low terminal stress (20–70%), (2) severe terminal stress (30–70%), and (3) intermediate midseason/terminal stress (10–60%, depending on soil type/geography). As a minimum, one needs to sample both ET1 and ET2 at a frequency of at least 30% or so, depending on the location and soil type. The precision with which frequencies need to be known for effective advance is yet to be investigated.

Although our interpretation in these papers has concentrated on the improvement of cultivars for broad adaptation, it may still be viable to develop cultivars with narrow adaptation for 2 reasons. Firstly, if drought years produce unprofitable crops, then substantial advance would be required to make them profitable. Hence, it may be better to have a cultivar that is narrowly adapted to ‘high yield’ environments by arguing that any weighting of trials should consider a set of gross margin scenarios as well as adaptation to drought. Secondly, seasonal forecasting of the probability of achieving median rainfall is becoming a valuable tool in planning on-farm management, e.g. Hammer *et al.* (1996). Therefore, forecasts of different environment types associated with variation in rainfall are likely to be possible in the future. Given this information, producers could modify the choice of cultivar according to the seasonal outlook at planting. Further simulation analysis, similar to that of Muchow *et al.* (1991), could be used to assess the utility of cultivars of differing maturity or adaptation to drought for different environment types. This would lead to a better integration of the improved cultivars with appropriate management.

Acknowledgments

We thank Greg McLean (QDPI Toowoomba) for assistance with the simulations and the reviewers of this paper for their valuable comments. This research was conducted with funding support from the Grains Research Development Corporation (GRDC) for project DAQ230.

References

Basford KE, Cooper M (1998) Genotype × environment interactions and some considerations of their implications for wheat breeding in Australia. *Australian Journal of Agricultural Research* **49**, 153–174.

Belbin L (1991) The analysis of pattern in bio-survey data. In ‘Nature conservation: cost effective biological surveys and data analysis’. Proceedings of a workshop held at Sydney, March 1988. (Eds CR Margules, MP Austin) pp. 176–190. (CSIRO: Melbourne)

Bolaños J, Edmeades GO, Martinez L (1993) Eight cycles of selection for drought tolerance in lowland tropical maize. III. Responses in drought-adaptive physiological and morphological traits. *Field Crops Research* **31**, 269–286.

Brennan PS, Byth DE, Drake DW, DeLacy IH, Butler DG (1981). Determination of the location and number of test environments for a wheat cultivar evaluation program. *Australian Journal of Agricultural Research* **32**, 189–201.

Chapman SC, Cooper M, Butler DG, Henzell RG (2000*a*) Genotype by environment interactions affecting grain sorghum. I. Characteristics that confound interpretation of hybrid yield. *Australian Journal of Agricultural Research* **51**, 197–207.

Chapman SC, Cooper M, Hammer GL, Butler DG (2000*b*) Genotype by environment interactions affecting grain sorghum. II. Frequencies of different seasonal patterns of drought stress are related to location effects on hybrid yields. *Australian Journal of Agricultural Research* **51**, 209–222.

Comstock RE (1977) Quantitative genetics and the design of breeding programs. In ‘Proceedings of the International Conference on Quantitative Genetics’. August 16–21, 1976. pp. 705–718. (Iowa State University Press: Ames, IA)

Cooper M, Brennan PS, Sheppard JA (1996) A strategy for yield improvement of wheat which accommodates large genotype by environment interactions. In ‘Plant adaptation and crop improvement’. (Eds M Cooper, GL Hammer) pp. 487–511. (CAB International: Wallingford, UK)

Cooper M, Fox PN (1996) Environmental characterisation based on probe and reference genotypes. In ‘Plant adaptation and crop improvement’. (Eds M Cooper, GL Hammer) pp. 529–548. (CAB International: Wallingford, UK)

Hamblin A, Kyneur G (1993) ‘Trends in wheat yields and soil fertility in Australia.’ (Bureau of Resource Sciences: Canberra)

Hammer GL, Holzworth DP, Stone RC (1996) The value of skill in seasonal climate forecasting to wheat crop management in a region with high climatic variability. *Australian Journal of Agricultural Research* **47**, 717–737.

Hammer GL, Muchow RC (1994) Assessing climatic risk to sorghum production in water-limited subtropical environments. I. Development and testing of a simulation model. *Field Crops Research* **36**, 221–234.

Muchow RC, Hammer GL, Carberry PS (1991) Optimising crop and cultivar selection in response to climatic risk. In ‘Proceedings of the International Symposium on Climatic Risk in Crop Production: models and management for the semiarid tropics and subtropics’. Brisbane, Australia, 2–6 July, 1990. (Eds RC Muchow, JA Bellamy) pp. 235–262. (CAB International: Wallingford, UK)

Nicholls N (1988) El Niño-Southern Oscillation and rainfall variability. *Journal of Climate* **1**, 418–421.

Podlich D, Cooper M (1998) QU-GENE: a simulation platform for quantitative analysis of genetic models. *Bioinformatics* **14**, 632–653.

Manuscript received 4 February 1999, accepted 11 October 1999