Genotype by environment interactions affecting grain sorghum. II. Frequencies of different seasonal patterns of drought stress are related to location effects on hybrid yields

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Abstract. Genotype × environment (G×E) interactions due to variation in soil moisture and rainfall complicate the interpretation of sorghum hybrid performance trials over locations (L) and years (Y). This paper aims to use pattern analysis to explain measures of the G×L interaction for yield, and whether these can, in turn, be explained using simulation models to determine the occurrence of environment types (within-season patterns of drought). The aim of this work is to simplify the analysis of G×E by explaining it in terms of interactions of genotypes with environment types (ET) that are not 'fixed' to locations and years.

In a sequential analysis of 17 seasons, 18 locations were separated into groups that tended to represent either the northern (i.e. central Queensland, CQ) or southern Queensland (SQ) regions. For a subset of 6 locations, ordination partially explained differences among locations as being related to latitude ($r = 0.88$) and rainfall ($r = –0.46$), but they were better related ($r > 0.9$) to the frequencies of 3 stress ETs as determined by long-term crop simulations. These 3 environment types were: (1) low stress (occurring in 33% of seasons); (2) severe terminal stress with an early-season (9%) or midseason time (29%) of onset; and (3) intermediate terminal stress with a midseason (9%) or late-season (20%) time of onset. Low stress ETs were more common in two SQ locations than in CQ. Stress ETs as defined by simulation models and pattern analysis had more consistent relationships with simulated yields than did the fixed descriptors of locations and years.

Sorghum hybrid trials for broad adaptation in Queensland should include locations at least from each of the 2 regions and the results should be interpreted in the context of the season in which they are conducted. To match the long-term patterns in the 6 locations of the analysis, trial yields would need to sample from at least 3 yield ranges: <1 t/ha, 1–3.5 t/ha, and >3.5 t/ha. Additional seasons of testing are likely to be required when the locations used during a season do not adequately represent the target population of environments over all locations and years.

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

Introduction

With production of 1.3 Mt in 1995–97, grain sorghum (*Sorghum bicolor* L. Moench) is the largest summer crop in dryland farming systems of subtropical north-eastern Australia (FAO 1997). Trials to choose hybrids for a production region that extends for about 1000 km north–south encounter a great diversity of environments over locations and years. These multi-environment trials (METs) detect significant genotype by environment (G×E) interaction that complicates the selection of cultivars for broad adaptation to

the region (Chapman *et al.* 2000*a*). An understanding of the effects, particularly the types of environments, acting on trials might allow breeders to accommodate or exploit this large G×E interaction to improve selection gains (Cooper and DeLacy 1994). For example, one type of 'stress environment' that has been previously identified is sorghum midge (*Stenodiplosis sorghicolor* Coquillett), for which screening nurseries are routinely used to identify resistant lines and crosses (Henzell and Hare 1996). Apart from midge, drought is a major limitation to high yields in the

region and its largely unpredictable occurrence over locations and years contributes to G×E.

Selection and screening for stress

Plant breeding has been highly successful in the selection of superior germplasm in response to biotic (pest and disease) stresses under abiotically favourable conditions. The 'presence/absence' nature of these types of environments may have contributed to this success. At a fundamental level, the relative ease of breeding for biotic stresses (in contrast to abiotic stresses) is related to the simplicity of their genetics of protection and/or plant response to a repeatable screening method. If a small number of genes is involved, then the products of these are either always present as defence [e.g. compounds that deter egg-laying by sorghum midge (Franzmann *et al.* 1996)] or produced in response to biotic attack. Although considerable research may be required to develop an appropriate screen, the response tends to discriminate repeatedly among genotypes for yield or other identifiable reactions (Henzell and Hare 1996). Similar arguments apply to the screening of germplasm in repeatable, abiotically favourable environments where the seasonal and location challenges are consistent and result in the same sets of genes being expressed.

Response mechanisms to some abiotic stresses (e.g. high soil Al) may be relatively simple to screen consistently; in this case the screen is linked to a repeatable environment attribute, the soil. However, although apparently simple mechanisms have been identified to improve adaptation to drought (Ludlow and Muchow 1990), there have been few successes in improving yield by selecting for these. Indirect selection for traits and direct selection for yield are complicated by the substantial interaction between drought and the developmental stage of the crop (Denmead and Shaw 1960). Adaptation to drought is a process that occurs over periods of weeks, not just over minutes or hours. The intensity of drought and its timing relative to crop development varies from trial to trial unless the seasonal balance of water demand and supply is exactly repeated. Even with such control, selection for drought tolerance, rather than drought avoidance, is still difficult. During the successful improvement for drought tolerance of tropical maize, researchers used indices of traits in addition to grain yield, because differences in flowering date of 2 or 3 days had substantial effects on grain yield (Fischer *et al.* 1989). These researchers had the benefit of a location with a reliable dry season, that enabled them to utilise irrigated and controlled drought conditions (Chapman *et al.* 1996). An alternative in selecting with indirect traits is to use traits such as transpiration efficiency that exhibit smaller G×E (Richards 1996).

Selection for broad adaptation to drought

For sorghum METs in Australia affected by variable water supply, Chapman *et al.* (2000*a*) found large variation across both locations (L) and years (Y), and in the magnitude of estimated components of variance for genotypic (G) and G×E effects (G×L, G×Y, and G×L×Y). This implies that broad adaptation is generally the best approach to deal with spatial and temporal variation in the occurrence of drought. Although the 3-way interaction (G×L×Y) was the largest interaction observed, the G×L variance component was still significant across years and was always greater than that for genotypic main effects in individual years. As locations are more repeatable than seasons (i.e. you can grow a trial again in the same place), pattern analysis is often used to determine the appropriate structure and number of locations used in testing (Brennan *et al.* 1981). Sequential pattern analysis of proximity matrices for locations within each year (DeLacy *et al.* 1994) attempts to identify persistent patterns among locations as they are tested over a sequence of years. Comstock (1977) described the concept of the TPE (target population of environments) as the complete set of 'types' of environments that exist across seasons within the geographical mandate of a breeding program.

In conducting METs over one or more seasons, plant breeders sample from the TPE. In the case of the temporally and spatially variable climate of the Australian sorghum region, the degree of mismatch between the MET and TPE is likely to be high. This could decrease or even reverse genetic gain (Cooper *et al.* 1996). If the results of a MET are considered as a case of 'indirect selection' then trials can be manipulated (e.g. by weighting) to maximise the correlated genetic gain in the TPE (Podlich and Cooper 1998).

Rather than using traits or specific screens to select for adaptation to drought, an alternative is to analyse yield in hybrid trials using a modification of the G, L, Y model to account for the TPE. In a MET, trials would be allocated to environment types (ET) which replace the L and Y effects. The allocation of a trial (i.e. an LY) to an appropriate ET should help to control the genotype interactions with L, Y, and L×Y. To adopt this type of weighting strategy requires a description of each ET within the TPE and its frequency of occurrence in each MET, e.g. during each season of variety testing.

Muchow *et al.* (1996) demonstrated that a crop simulation model (Hammer and Muchow 1994) could be used to characterise drought environments for sorghum. This was done, not using predictions of yield (for which most models have some limitations), but using an integrative stress index that depends more on the ability of the model to simulate biomass production and water use. These types of models are quite reliable in reproducing these effects (Hammer and Muchow 1994). Together with long-term weather records, the model was used to generate the seasonal sequence of stress experienced by simulated crops. Pattern analysis of these sequences over seasons identified different environment types, for which frequencies of occurrence could be determined at a location to describe the TPE.

An ideal test of the TPE theory to selecting for broad adaptation to variable water supply environments would be to utilise trials that have been conducted with the same genotypes over the same locations for a series of years. Using a simulation model, each trial would be classified as being a member of an ET group for which long-term frequencies of occurrence have been determined (by running the simulation with historical weather records). Selection of genotypes based on mean performance across trials would be compared with selection weighted by the long-term frequency of the ET for a given trial. Verification of the performance of these different sets of genotypes would then be compared over a long series of trials in the same locations.

This 'ideal' test is difficult to apply to a historical set of hybrid trials, given the needs of the model for information about the starting conditions of each trial. Instead, we have opted to define an appropriate set of starting conditions for each of a set of locations and to use the model to determine the long-term frequencies of environment types for each location. These frequencies can then be compared with measures from hybrid METs of similarities among locations (principal component scores) in the way in which they discriminate among hybrids. The existence of relationships between simulated ET frequencies and location PCA scores is taken to indicate that drought ET groups are a repeatable replacement for L and Y in controlling G×E during indirect selection.

The objectives of this paper are to: determine differences among testing locations in their discrimination among relative performance of different hybrids; to describe the frequency of occurrence of drought ETs in different locations (using a simulation model); and to relate the differences among locations to the frequencies of simulated environment types. In a related paper (Chapman *et al.* 2000*b*), the same simulation results are used to demonstrate the selection advantages of classifying seasons by ET rather than 'location' and to expand the analysis spatially to define the ET characteristics of the entire sorghum-growing TPE.

Materials and methods

Pattern analysis of regional trial data

Regional sorghum hybrid yield data (6681 hybrid means) from 1975 to 1991 and up to 35 locations, collected by the Queensland Department of Primary Industries (QDPI), were previously analysed (Chapman *et al.* 2000*a*) to determine the size and form of variance components for trial error, genotypic effects (G), and interaction effects associated with location (G×L), year (G×Y), and location and year (G×L×Y). The sequential pattern analysis, described below, reduced the number of locations to 18 (Table 1). The clustering and ordination procedures were developed and used by DeLacy *et al.* (1994) for wheat and Mirzawan *et al.* (1994) for sugarcane.

DeLacy *et al.* (1996) describe this procedure in detail, as applied to unbalanced data, by constructing a proximity (dissimilarity) matrix for each year of data. Using the SEQRET software (I. H. DeLacy, Plant Improvement Group, The University of Queensland, Brisbane, Australia), the genotype means for a single year were first 'environment-standardised' within locations (Fox and Rosielle 1982) to remove dominating mean environment effects and heterogeneity of phenotypic variance. A proximity matrix was created by calculating squared Euclidean distances among the locations for each season, beginning with 1974–75. The proximity matrix for each year's data was added one year at a time to form a series of sequential long-term proximity matrices. Comparisons between the same locations were averaged over years. Locations that were not compared with all other locations at least once (empty cells) within a long-term proximity matrix were dropped from the analysis, e.g. 5 locations were retained after 1 year of analysis,

Table 1.   Details of 18 locations used in the QDPI dataset for an average of 7.6 seasons

SQ, southern Queensland; CQ, central Queensland

Location	Code	Nearest weather station [A]	Region	Long.	Lat.	No. of seasons
Clermont	CL	035019	CQ	147.63	–22.83	6
Capella	CP	035016	"	148.02	–23.08	7
Fernlees	FE	035274	"	148.10	–23.87	5
Biloela	BL	039006	"	150.52	–24.40	10
Jambin	JM	039006	"	150.52	–24.40	7
Banana	BA	039003	"	150.22	–24.78	5
Monto	MT	039070	"	151.65	–25.18	3
Boondooma	BD	040177	SQ	151.43	–26.09	7
Kingaroy	KN	040112	"	151.83	–26.55	14
Condamine	CN	042023	"	150.18	–26.67	8
Warra	WR	041117	"	150.93	–26.93	10
Dalby	DB	041522	"	151.27	–27.17	11
Bongeen	BN	041008	"	151.50	–27.30	16
Bowenville	BW	041008	"	151.50	–27.30	7
Jondaryan	JN	041053	"	151.58	–27.37	5
Boonah	BH	040198	"	152.52	–27.98	3
Hermitage	HR	041044	"	152.10	–28.20	14
Goondiwindi	GD	041521	"	150.32	–28.52	6

[A] Bureau of Meteorology.

9 after 2 years, and 18 from 7 years onwards. For each of these sequential matrices, a hierarchical agglomerative cluster analysis (Ward's method) was performed to group locations.

Principal component analyses (PCA) were performed on the long-term proximity matrices for each year and are interpreted for 7 (1980–81), 12 (1985–86), and 17 (1990–91) years from the year of commencement of broad-scale testing in the QDPI program. The principal component scores at Years 7 and 12 were orthogonally rotated toward those obtained at Year 17 using the 'procrustes' function (S-Plus, MathSoft Inc., Seattle, WA). As the values of the first PCA axis are arbitrary, a procrustes rotation simply 'lines up' the base components of the different analyses, without changing their internal scores. The principal components for the 17-year analysis were correlated against various characteristics of the locations, including their latitude and average rainfall during the growing season.

To confirm that the effects of G×L, G×Y, and G×L×Y were still present in the reduced dataset of 18 locations and 17 years, the data were also analysed by the residual maximum likelihood method described by Chapman *et al.* (2000*a*). The variance components and standard errors for G×L, G×Y, and G×L×Y were thus determined.

Simulation of sorghum growth and seasonal patterns of drought stress

A sorghum crop model (Hammer and Muchow 1994) was used to simulate seasonal indices of drought stress according to the criteria given by Chapman *et al.* (1996). The model was operated within the APSIM cropping system model (McCown *et al.* 1995) and provided with inputs of soil water characteristics, cultivar parameters, and daily weather data. Apart from thermal time, leaf area index, biomass, grain yield, and other variables, the model generates a stress index (relative transpiration, RT), which is the ratio of potential transpiration by the crop to the actual transpiration that can occur given the amount of soil water available that day. The model computed the value of RT daily.

For only 6 locations spread over central (CQ) and southern Queensland (SQ), between 80 and 105 years of weather data were available (Table 2). These locations were a subset of the 18 sites for which yield data had been analysed.

Three representative soil types of different water-holding capacities were parameterised (Table 2). The soils used for SQ locations were deeper, with greater water-holding capacity, than the soils used for CQ locations. Other soil parameters required by APSIM, such as evaporation and runoff coefficients and bulk densities, were set to be the same for each soil type. The cultivar parameters used in the model caused flowering to occur at a thermal time of approximately 670 degree-days after planting and physiological maturity at 1080 degree-days. These equate to a 'medium–quick' hybrid with flowering dates of about 50–60

days after sowing in CQ locations and 60–75 days in SQ locations. Simulated maturity times are 85–90 days in CQ and 90–115 days in SQ.

The model was used to simulate the planting and growth of crops during each season of the record and estimate RT for each day. Other assumptions were that the crop was planted at 80 000 plants per hectare and that planting only took place when 30 mm of rain had been received in a 6-day period within a planting window (1 Nov.–31 Jan. for sites in CQ and 1 Oct.–15 Jan. for sites in SQ). If the sowing took place more than 45 days into the planting window, fertile tiller number, which is a genotype/environment parameter used to estimate leaf area in the model, was assumed to be 0.25 per plant. Otherwise, fertile tiller number was assumed to be 0.75 in CQ locations and 0.5 in SQ. The simulation assumed a winter fallow, so that the starting soil moisture for each sorghum crop was determined by the cropping system model running through the fallow. The first season in each site was discarded, as the rainfall record did not include the previous fallow. In another paper, we had examined a similar system while assuming that the soil water profile was filled to half of capacity prior to the sowing of each crop (Chapman *et al.* 1996).

In their analysis within 2 locations, Muchow *et al.* (1996) averaged RT over weeks to form a matrix of RT for weeks of the season (columns) for each season at a site. We modified this approach to average the daily values of RT for each 100 degree-days of thermal time to approximate calendar weeks as 'TTweeks'. Thermal time weeks are more suitable than calendar time weeks when making comparisons over a large geographical region as patterns of stress are then expressed relative to approximate stages of development, i.e. the results are not biased by the cooler, slow development experienced in spring plantings at southern locations compared with summer plantings in the north. The last 2 TTweeks of each season were removed as the RT value is less reliable in dry years when plant leaf area has been almost totally senesced.

Classification of patterns of drought stress (season types)

In contrast to Muchow *et al.* (1996) who studied patterns within locations, the analyses were applied simultaneously over the entire dataset (564 seasons). A hierarchical clustering method was used to cluster the seasons from all locations into 2–10 groups (environment types) according to how similar the RT pattern was across seasons. The process was the same as described above for the yield data, except that the data were not transformed. Analyses of variance were performed to determine how much of the variation was explained by the grouping of seasons/locations or TTweeks. The seasonal RT values were averaged for members of each group to give a sequence of RT against TTweeks for the group. Frequency tables were constructed to analyse the occurrence of these environment type groups at different locations.

Table 2.   Site and soil specifications for sorghum model simulations

Site	Weather station[A]	Weather statn location (lat., long.)	Years of record used	Rainfall (mm) (Sept.–Mar.) mean	s.d.	Soil depth (mm)	Soil available water (mm)	Simulated grain yield (t/ha) Mean	Min.	Max.
Central Queensland										
Biloela/Jambin (BL)	39006	–24.28, 150.08	1887–1991	510	166	1500	178	2.30	0.094	4.761
Capella (CP)	35016	–23.05, 148.01	1899–1991	455	172	900	157	1.88	0.247	4.272
Fernlees (FE)	35274	–23.52, 148.08	1913–1991	462	201	900	157	1.75	0.214	3.902
Southern Queensland										
Bongeen (BN)	41082	–27.43, 151.38	1887–1976	505	141	1800	245	3.63	0.676	5.585
Condamine Plains (CN)	41019	–27.42, 151.16	1887–1991	484	150	1800	245	2.28	0.119	4.612
Dalby (DB)	41522	–27.11, 151.16	1887–1991	500	138	1800	245	2.65	0.177	4.154

[A] Bureau of Meteorology.

Table 3. **From the reduced set of QDPI sorghum hybrid trials (18 locations and 17 years), variance components for effects of G (σ_g^2),**
G×L (σ_{gl}^2), G×Y (σ_{gy}^2), G×L×Y (σ_{gly}^2) and residuals (σ_e^2) and the ratio of σ_g^2 to the sum of all genotypic main and interaction components

Values in parentheses are standard errors of variance component estimates. For analyses within the seasons 1975–1991 are given the average,
minimum, and maximum values for σ_g^2, σ_{gl}^2, and the ratio $\sigma_g^2/(\sigma_g^2+\sigma_{gl}^2)$ (note that these values may be from different years)

Dataset	σ_g^2	σ_{gl}^2	σ_{gy}^2	σ_{gly}^2	σ_e^2	Ratio of σ_g^2 to $(\sigma_g^2+\sigma_{ge}^2)$
			Across all years			$\sigma_g^2/(\sigma_g^2+\sigma_{gl}^2+\sigma_{gy}^2+\sigma_{gly}^2)$
QDPI	0.0373 (0.0068)	0.0191 (0.0040)	0.0226 (0.0040)	0.2040 (0.0066)	0.2510	0.132
			Within individual years			$\sigma_g^2/(\sigma_g^2+\sigma_{gl}^2)$
Average	0.0665	0.2584	n.a.	n.a.	0.188	
Min.	0	0.1253 (0.0115)	n.a.	n.a.	0.1050	0
Max.	0.1563 (0.0622)	0.4953 (0.0528)	n.a.	n.a.	0.4974	0.430

n.a., not applicable.

For each location in the analysis, frequency distributions of the simulated yields were constructed. These were compared with distributions constructed when seasons were grouped according to environment type.

Stress frequency as related to G×L and G×Y interactions

The PCA scores from the sequential yield analysis were compared with latitude and average rainfall. The scores were also compared with the frequencies of occurrence of different stress patterns (environment types) at each location, as determined by pattern analysis of the simulations.

Results

Pattern analysis

Of the 35 initial locations, 18 were retained by the sequential pattern analysis as having sufficient comparisons with other locations over years (Table 1). As found for the original analysis of the QDPI dataset, the variance components of this subset were dominated by the 3-way interaction (σ_{gly}^2), which was about 5 times as large as σ_g^2 (Table 3). However, the variance components for both 2-way interactions (σ_{gl}^2 and σ_{gy}^2) were more than half of that for σ_g^2 and were significant, as indicated by their standard errors.

At the 2-group level the cluster analysis (Fig. 1) mostly combined the sites in their respective geographical regions (CQ and SQ, Table 1). The main exception, in group 33, was the CQ site of Banana, which grouped with SQ sites. Group 34 contained CQ sites and 3 SQ sites (Condamine, Goondiwindi, and Warra) that tend to have soils of lower water-holding capacity compared with the other SQ sites. The mean yields of Groups 33 and 34 were 5.04 and 3.22 t/ha, respectively. Further, in Group 33, the mean yield of the 'drought-tolerant' check variety, E57, was 95% of the 'potential yield' check variety, Pride, and in about 30% of trials the yield of E57 was <90% of Pride. In Group 34, the mean yield of E57 was the same as Pride and in only 13% of the trials was the yield of E57 <90% of Pride. Based on these observations, one concludes that the lower yield in Group 34, compared with Group 33, is largely due to drought.

The different symbols used in Fig. 2a show the results of the cluster analysis, truncated at the 2-group level in Fig. 1.

In single years, the first and second components from the ordination analysis together often accounted for more than 50% of the variation (data not shown). In the sequential analysis of all years, the first and second axes accounted for 12% and 11% of the variation, respectively. DeLacy *et al.* (1994) considered that even at these low percentages such findings were important where G×L interactions were shown to be significant. Those locations which are close together in the figure detect similar discrimination among the hybrids tested at the locations (i.e. they tend to rank the hybrids similarly), whereas those locations which are plotted further apart from each other were less similar in their discrimination among the hybrids. The first component was negatively correlated with location rainfall ($r = -0.56$, $P < 0.05$) and positively correlated with latitude ($r = 0.73$), whereas the second component was not correlated with either of these attributes.

In Fig. 2b, the orthogonally rotated PCAs from the sequential analyses at Years 7, 12, and 17 have been combined in a single plot. For about half of the locations, the distance between Years 7 and 17 was <0.1 PCA units, showing that the relative discrimination among genotypes at those locations was well established after about 7 years. In all but 3 locations (HR, JM, MT) the change in position between Years 7 and 12 was greater than the change between Years 12 and 17.

Simulation of grain yield and patterns of drought stress

Given that the simulations were constrained by a planting rain, without any requirement for the soil profile to be filled, the model planted a crop in all but 2 or 3 seasons at each location (data not presented). Simulated grain yields ranged from <0.1 t/ha to >5.5 t/ha and averaged 2 t/ha in CQ and 2.85 t/ha in SQ (Table 2). Fig. 3a shows the 75-year sequence of yields at Fernlees, the lowest yielding site. In only about one-third of years were the yields greater than the Australian average (1995–97) of 2.0 t/ha. The sequence of stress (RT <1.0) experienced in each of the seasons at Fernlees varied greatly (Fig. 3b) and the mean RT across all seasons was about 0.7 around flowering (650 degree-days), decreasing to 0.5 during the grain-filling period.
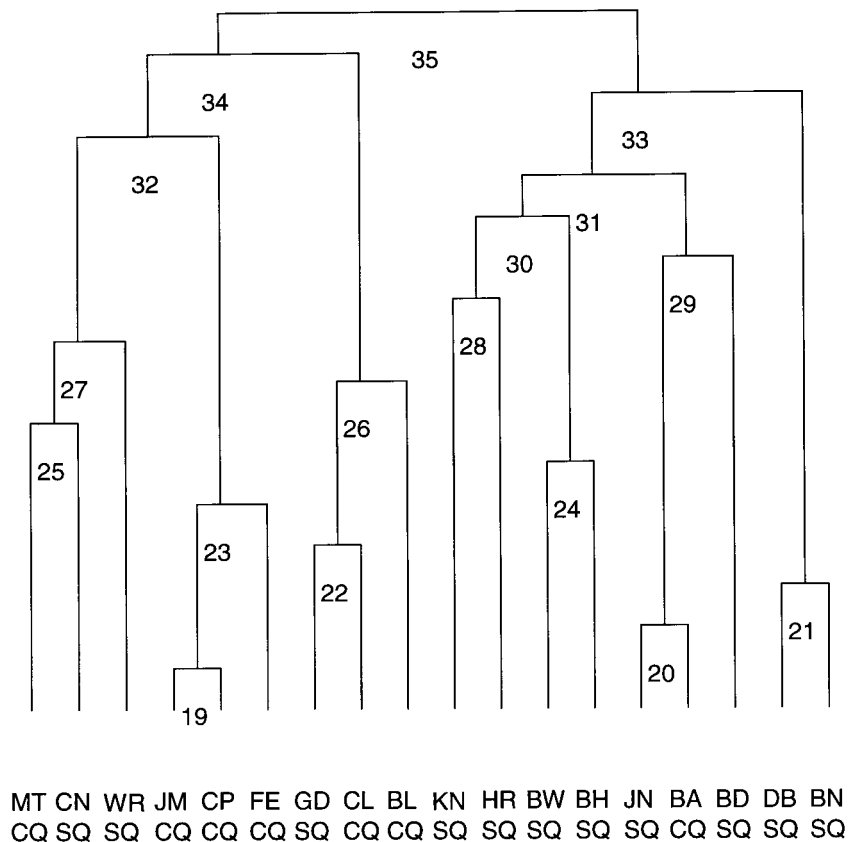
Fig. 1. Dendrogram of results of cluster analysis of 18 locations (names given in Table 1) from a proximity matrix derived from 17 sequential seasons of sorghum yield trials.

The overall frequency distribution of grain yield was somewhat bi-modal using this set of locations and years (Fig. 4*a*). At the CQ locations, the seasonal yields were distributed across the range of 0–4 t/ha, although in the majority of seasons they were <2 t/ha. A wide range of yields existed for the other locations, but whereas yields at CN (SQ) were similar in distribution to the CQ locations, yields at the other SQ locations (BN and DB) were typically higher. When the RT for each TTweek was averaged across all seasons at a location, the seasonal pattern was similar at all locations, but with lower values of RT at CQ locations and at CN (Fig. 4*c*).

Pattern analysis of TTweeks through the season

In a 2-way analysis of variance, variation among TTweeks was greater than that among seasons, with the interaction between seasons and TTweeks being greater than each main effect (Table 4). As might also appear evident from the mean data in Fig. 4*c*, the dendrogram shows that the first 5 TTweeks (pre-flowering–thermal time <600 degree-days) were fairly similar to each other in the way that they varied over seasons (Fig. 5). In this sense, the last 4 TTweeks (post-flowering–thermal time >600 degree-days) were contrasted with the pre-flowering weeks and were quite different from

each other, as judged by the high fusion points in the dendrogram. The 2-group level (the first split in the dendrogram) representing pre- and post-flowering groups explained 84% of the variation among TTweeks, whereas a 4-group classification explained 99% of the variation (data not presented). Although grouping could explain much of the variation among TTweeks, this information was only used to see which TTweeks were similar in their variation in RT values. In further analysis, the 9 TTweeks were left ungrouped so that the seasonal sequences of drought stress could be examined intact and without reordering.

Pattern analysis of seasons across TTweeks

When the 564 seasons were clustered at the 2-group level, the grouping accounted for 68% of the total SS, whereas a clustering of 10 groups explained 89% of the total SS (data not presented). At the 5-group level, the incremental SS% accounted for by grouping had begun to level off for all sources of variation (main effects, interaction, and total SS). This grouping level, which accounted for 83% of the total SS (Table 4), was accepted as a manageable number for further interpretation and one that accounted for most of the variation observed among seasons. The between-groups SS at the
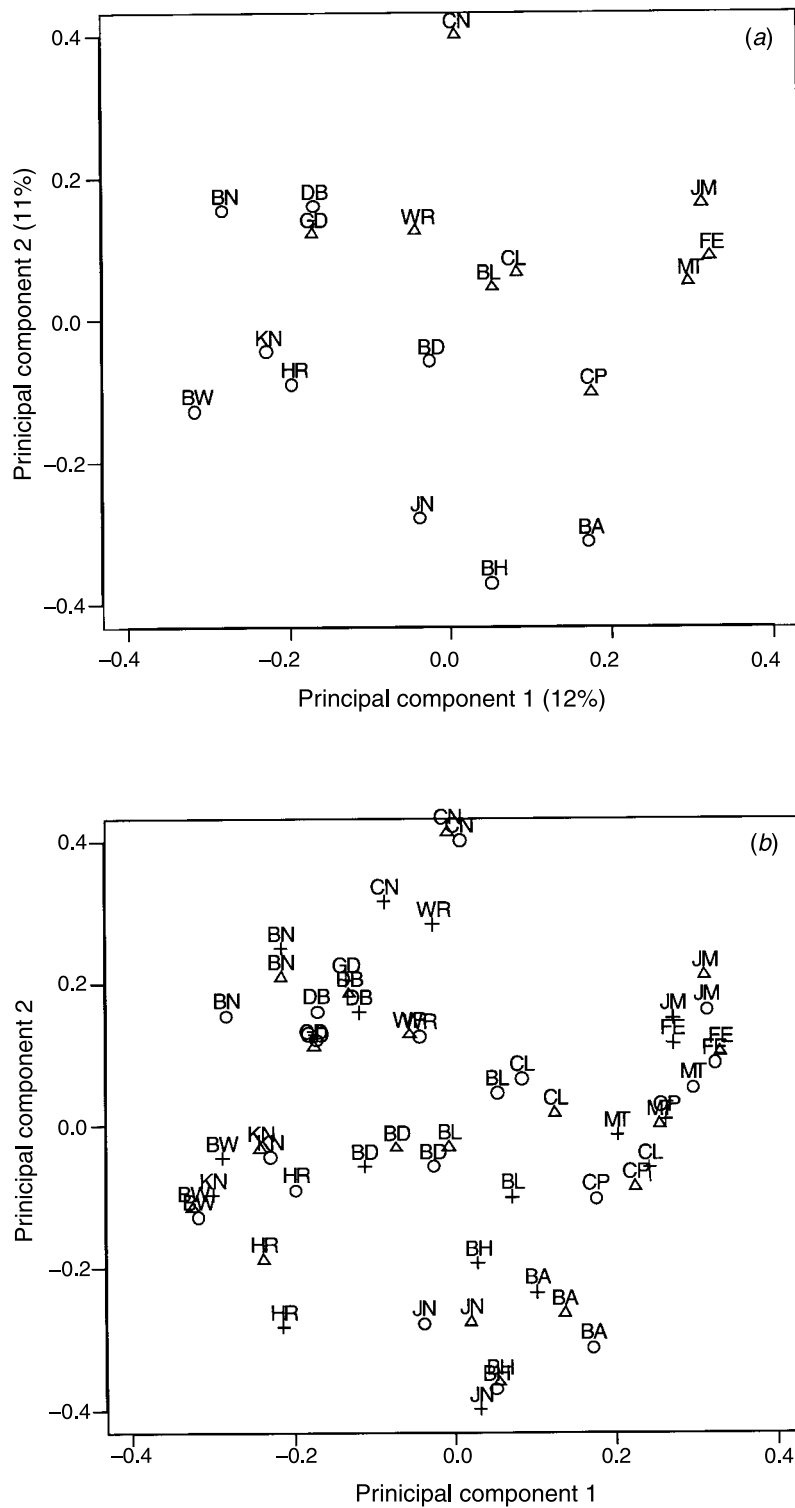
Fig. 2. (*a*) 1st and 2nd principal components of a distance matrix computed for 18 locations over 17 sequential seasons (1975–1991) of QDPI sorghum variety trials and separated at the 2-group level (triangles, Group 33; circles, Group 34) by cluster analysis. (*b*) Same components extracted after 7 (crosses), 12 (triangles), or 17 (circles) sequential seasons. See Table 1 for codes.
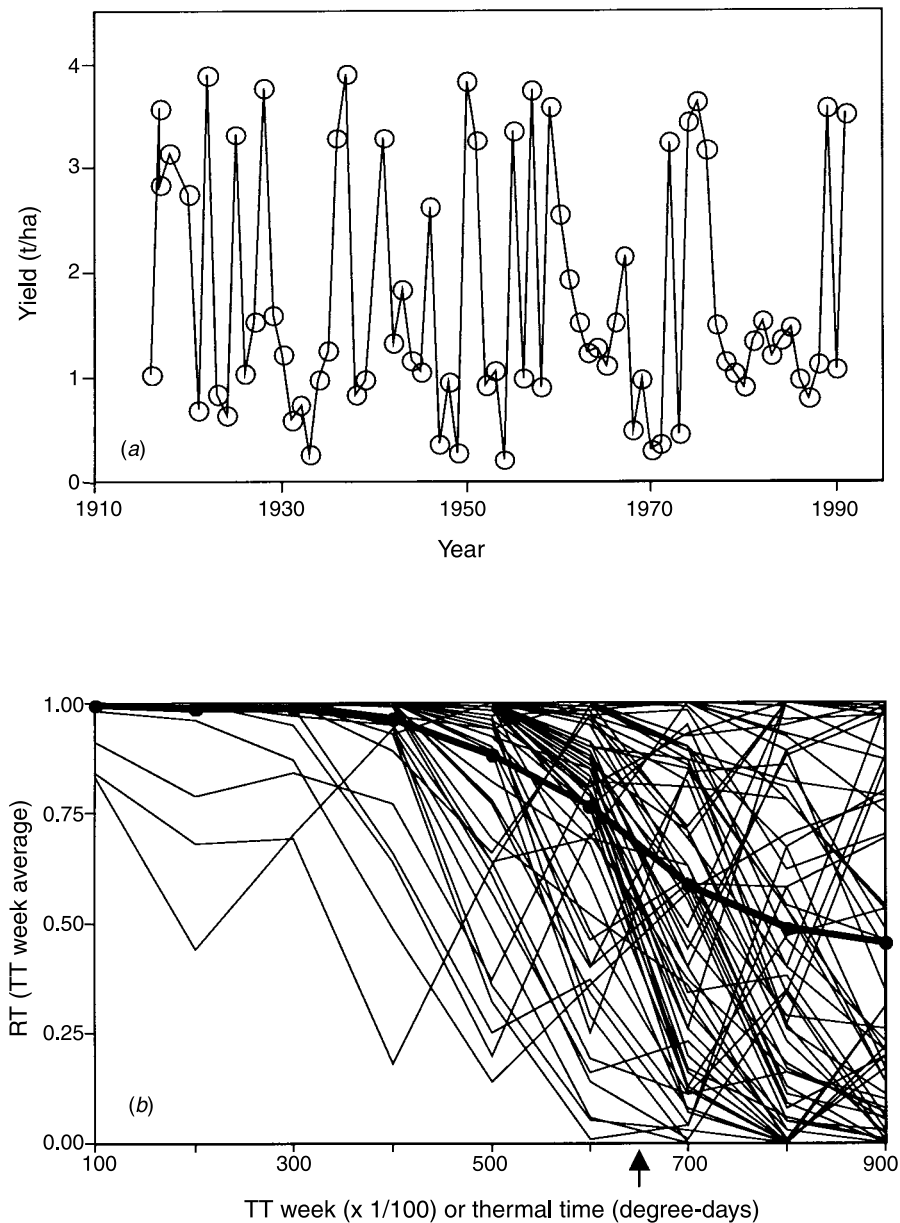
Fig. 3.   For Fernlees, CQ, (*a*) sequence of simulated yields over 75 years and (*b*) associated patterns of stress for each season as measured by relative transpiration (RT) index. Flowering occurred at about 650 degree-days, as indicated by the arrow. The bold line is the RT for each TTweek averaged over all seasons.

5-group level (dendrogram not presented) explained 86% of the SS for season main effects and 68% of the interaction between seasons and TTweeks.

For both yield and seasonal pattern of stress (Fig. 4*b*, *d*), the 5 groups (environment types) discriminated more clearly among environments than did the locations (Fig. 4*a*, *c*). Fig. 4*d* shows that in the 5-group classification, the environments making up group 543 could be described as 'low terminal stress'. Simulated yields in these types of seasons averaged 3.98 t/ha and were always >3 t/ha (Fig. 4*b*), and over all locations, these types occurred in 33% of seasons (Fig. 6, right-hand column). The lowest yields (averaging 0.53 t/ha and always <1 t/ha) were observed in the 9% of seasons comprising Group 558, which might be described as a early onset severe terminal stress (Fig. 4*b*, *d*). Another severe terminal stress with a later time of onset (Group 559) accounted for 28% of seasons, having yields always <2 t/ha, at an average of 1.16 t/ha. The final 2 types of stresses are intermediate terminal stress either during grain filling (G557) or during the
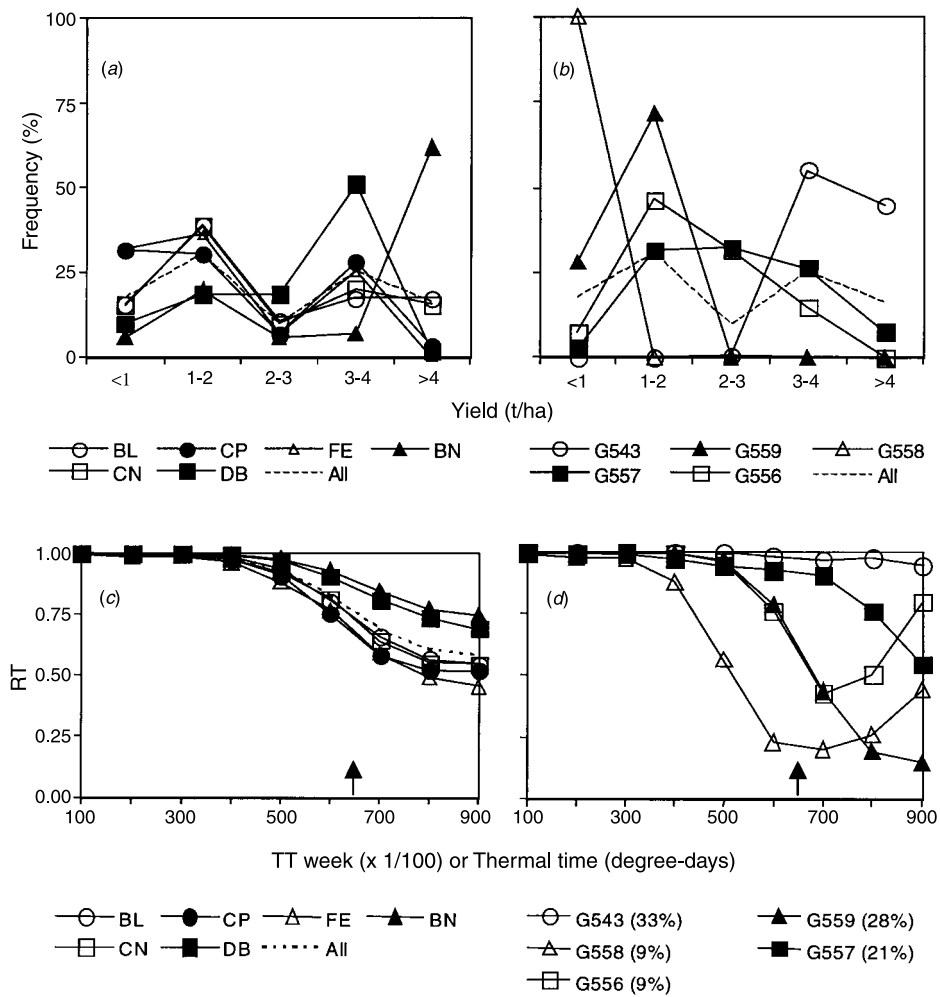
Fig. 4. For each of 6 locations (Table 2) in CQ and SQ (*a*) frequency distribution of simulated yields and (*c*) mean RT index for all seasons planted within a location. For each of 5 groups (environment types) across a total of 564 seasons in 6 locations in CQ and SQ (*b*) frequency distribution of simulated yields and (*d*) mean RT index for all seasons within a group, with % of total seasons in parentheses. Arrows indicate approximate flowering date.
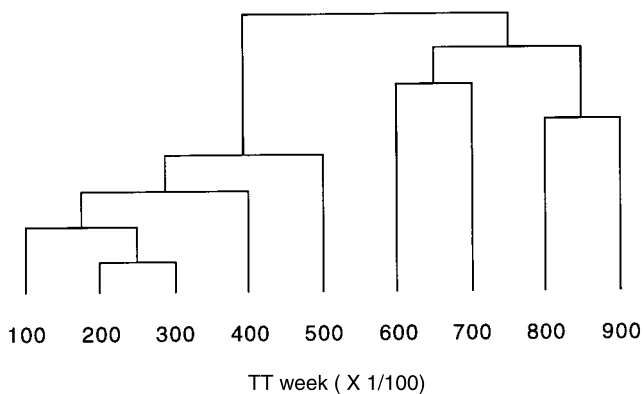

Fig. 5. Dendrogram results of hierarchical cluster analysis of 9 TT-weeks across 564 seasons from 6 locations.

period around flowering (G556). These stresses can result in a wide range of yields, depending on the actual timing and intensity of the stress period.

Distribution of stress season types within and across locations

The SQ locations of BN and DB differed from the 3 CQ locations and CN in the frequency of different season types (Fig. 6). These 2 'deep-soil' SQ locations had a higher frequency of 'low stress' type seasons (G543) together with a lower frequency of 'severe terminal stress' type seasons (G559 and G558). The frequencies at locations BL ($r = 0.93$) and CN ($r = 0.91$) were the most similar to the overall frequency distribution.

Table 4.   Two-way analysis of variance of RT value (stress index) across seasons at the 5-group level and across TTweeks (see text) at 6 locations in Queensland

Source	d.f.	SS	MSS	SS as % of total SS	SS as % of source SS
Seasons	563	93.701	0.166	23	100
Between groups	4	80.938	20. 234		86
Within groups	559	12.764	0.023		14
TTweeks	8	136.961	17.12	34	
Seasons × TTweek interaction	4504	171.741	0.038	43	100
Between season groups × TTweek	32	116.633	3.645		68
Remaining interaction	4472	55.111	0.012		32
Total SS	5075	402.403	0.079	100	100
Total SS between groups		334.531			83
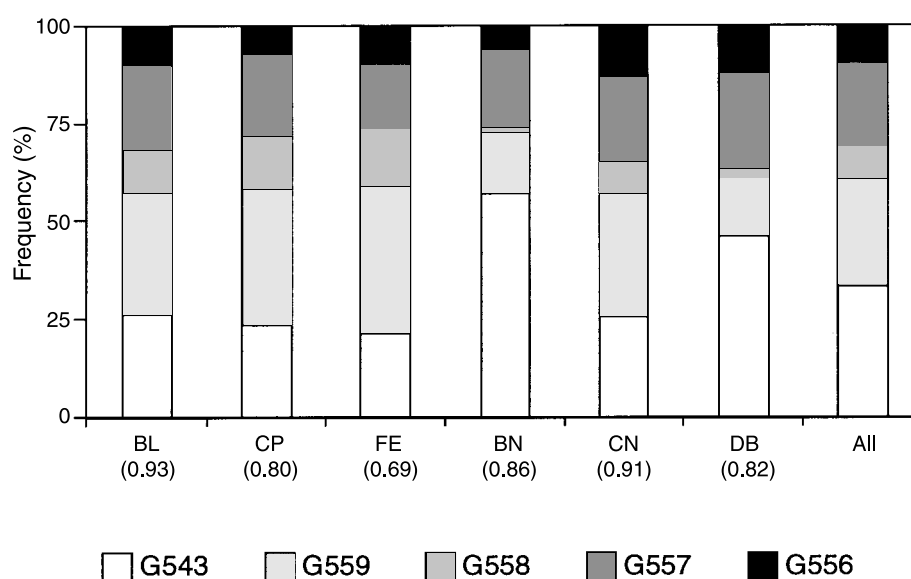
Fig. 6.   Frequency distributions of 5 'stress season' environment types within and across 6 locations in CQ (BL, CP, FE) and SQ.

Correlations between the frequency of stress season type and measures of G×E

For the 6 locations for which weather data were available, latitude ($r = 0.88$) significantly correlated ($r = 0.75$, $P < 0.05$) with the PCA1 scores. Average rainfall (Table 2) during spring and summer was poorly correlated with PCA1 scores ($r = -0.46$). Neither variable was correlated with the PCA2 scores.

Across locations, the frequency of stress season type G543 was significantly and negatively correlated with the PCA1 scores (Table 5). Stress season types G558 and G559 were positively correlated with the PCA1 scores, whereas stress season type G556 was positively correlated with PCA2 (at $P = 0.1$).

Given that stress season types G558 and G559 were both 'severe terminal stresses' (with different times of onset) that resulted in similarly low grain yields, their frequencies were combined together for each location. Over all locations, the occurrence of severe terminal stress then became 37%.

Similarly, when the groups G556 and G557 were combined to obtain total frequencies for 'mild terminal stress', the average across locations became 30%.

Fig. 7a illustrates how the frequency of low stress seasons (G543) decreases over locations when moving from SQ north to CQ locations (left to right in the figure), and correlates with differences in their pattern of discrimination among hybrids. Conversely, the incidence of severe terminal stresses increases between SQ and CQ, but with a similar correlation. Intermediate terminal stresses occur at a similar rate over all locations, although slightly more often in CN and less often in CP (Fig. 7b).

Discussion

Sequential pattern analysis of regional yield trials

Although the differentiation of locations was largely established after 7 years, there were still substantial changes in the relative positions of some locations between Years 7 and 12,

Table 5. For five different season types (Figs 4*d*, 5), the simple correlations between frequency of the season type at different locations and the first (PCA1) or second (PCA2) principal component axes for locations after sequential analysis of grain yield from 17 years of hybrid variety trials

Group	PCA1	PCA2
G543	−0.904[A]	0.122
G558	0.914[A]	−0.400
G556	0.075	0.701
G559	0.895[A]	−0.215
G557	−0.323	0.274

[A] Significant value of r is 0.75 and is indicated by ($n = 5$, $P < 0.05$).
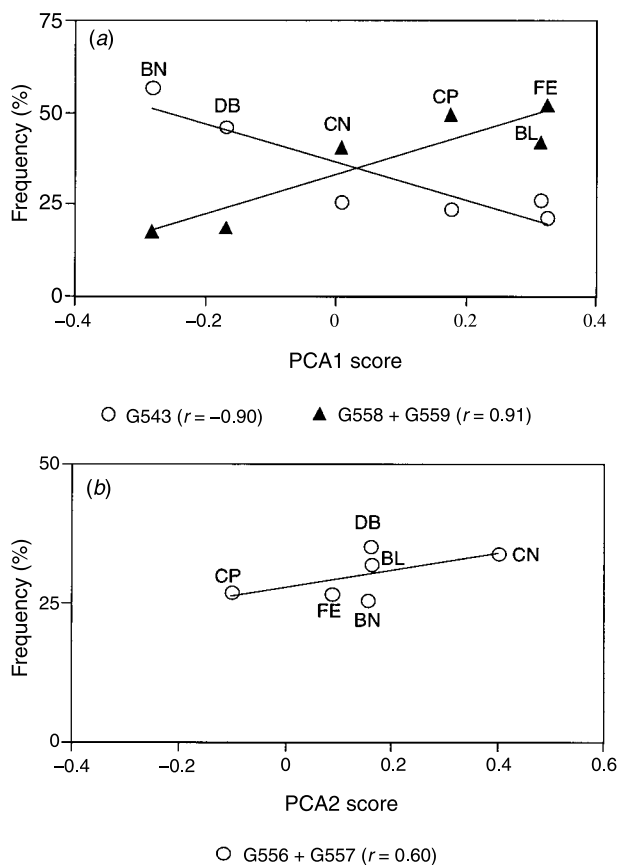

Fig. 7. Relationships between (*a*) the frequency of low stress (G543) or severe terminal stress (G558+G559) at each of 6 locations and the principal component analysis (PCA) axis 1 scores from the retrospective G×L analysis of 17 years of regional variety trials (Fig. 1*a*); and (*b*) the frequency of intermediate terminal stress (G556+G557) and PCA 2 scores from Fig. 1*a*.

particularly compared with the smaller changes between Years 12 and 17 (Fig. 2*b*). This might be expected given that the first 7 seasons (1975–1981) had generated low σ_g^2 and low h^2 (Chapman *et al.* 2000*a*), compared with either of the later two 5-year periods (1982–86 and 1987–91). A difficulty

with sequential analysis is that genetic improvement is confounded with the sequence of seasonal climate. For example, σ_g^2 may have been greater in later years due to changes in the germplasm. Repeating the procedure multiple times while using the seasons in a random order could partially overcome this problem but confounding would still exist with temporal changes in the actual germplasm diversity.

Differences in patterns of hybrid yields might arise in this way because of differential effects of phenology as well as tolerance to drought. In wet years, late-maturing hybrids tend to have the highest yields, whereas in drier years, particularly on the shallower soils in CQ, early-maturing hybrids have an advantage. Further, even in 'wet' years some locations experience 'dry' conditions, confounding the location and year effects. This would partially explain the observation of Chapman *et al.* (2000*a*) of the dominance of G×L×Y effects in the analysis of G×L across seasons and locations together. They also found that adjustment for maturity substantially reduced the G×L effect.

Drought stress season types

Over all of the simulated seasons, terminal drought stress was identified as the 'typical' condition, and existed even in the environment type Group G543, which had a high RT for most of the season (Fig. 4*d*). However, the intensity, timing of onset, and the frequency of occurrence of drought stress at different locations varied substantially (Figs 4*b*, 6). The distinction among different stresses was driven mostly by the degree of stress observed in the period from 600 degree-days onwards, i.e. from just prior to flowering (Figs 4*b*, 5). The simulation approach may underestimate the impact of stress early in the season, as the model does not account for seedling mortality due to stresses arising from high air and soil temperatures. Although a small number of seasons (<10%) experienced severe levels of drought stress early in the season, these are not clearly evident in the averaged data.

Three major stress environment types could be summarised from the 5-group analysis (Fig. 4*d*): low stress (G543), occurring in 33% of seasons (ET1); severe terminal stress with an early-season (G558, 9% of seasons) or mid-season (G559, 29%) time of onset (ET2); intermediate terminal stress with a midseason (G556, 9%) or late-season (G557, 20%) time of onset (ET3).

The incidence of ET1 was greater in 2 SQ locations than in CQ. The corresponding higher incidence of ET2 in CQ locations is associated with the lower water-holding capacities of the soils in the region and the interaction with a lower, less reliable rainfall (Table 2). Due to similarly unreliable rainfall, CN was more similar to the CQ locations than to those in SQ. At CN, both the distribution of the 5 groups of seasons (Fig. 6*b*, $r = 0.98$) and the distribution of yields (Fig. 4*a*) were almost exactly the same as those simulated at the BL location in CQ. The high correlations between the frequency distributions for BL and CN and the overall fre-

quency indicate that these 2 sites best represent the proportions of different environment types for the entire set of locations, i.e. if the number of locations in the MET was to be reduced, it would be advisable to include BL and CN as repeatable samples.

The correlation between location PCA scores and latitude indicated that differences among locations were related to geographical position, and particularly contrasted SQ and CQ. However, the correlations with stress frequency were stronger, suggesting that although the geographic effect is important, it interacts with soil type and inter-season variability. We acknowledge that relationships with other environmental parameters may explain the PCA results, but not all of these could be tested here.

The simulated grain yields can be used to illustrate the interaction effects of location and season (Fig. 4*a* and *b*). Although general yield trends are evident in a yield distribution for seasons at each location, a substantial range of yields can be generated at any location (Fig. 4*a*). However, when seasons are classified according to an environment type, rather than location, the yield distributions are much more distinct (Fig. 4*c*), particularly for the low-stress ETs (G543) and the severe terminal stress ETs (G559 and 558). High yields were only achieved in the low-stress ET, although these may occur in any location (Fig. 6). Similarly, low yields only occur in the severe terminal stress ET. The corollary of this finding is important. It follows that, given other effects (pests etc.) are controlled, yields <1.5 t/ha indicate that the crop has experienced a severe terminal stress (ET2), whereas yields of >3.5 t/ha indicate that the crop has experienced low stress (ET1). An intermediate level of stress (ET3) resulted in yields of 1–4 t/ha, although the extremes of these yield levels may also result from low or severe stress ETs. Although these comments might appear to state the obvious regarding 'stress/no-stress' environments, an appropriate interpretation of the yield levels at which these environments occur would allow plant breeders to make decisions about the relevance of the MET to their TPE. Where yields are >4 t/ha or <1 t/ha, a plant breeder would be reasonably confident of having sampled the 'low stress' and 'severe stress' ETs, respectively. Yields of 1–4 t/ha would be inconclusive without output from the simulation model to classify the trial. Further analyses of yield trials for which simulations can be made are needed to verify these findings.

Implications for selection and breeding

It has long been realised that the timing and intensity of drought stress cause different effects on crop growth and yield (e.g. Denmead and Shaw 1960). What has been lacking is a measure of how often these stresses occur. Simulation models allow the characterisation and classification of these stresses into different environment types so that as they appear during the process of variety testing, they can be accounted for in the selection for improved tolerance to drought. The use of weather data and simulation models to conduct 'real-time' classifications of ET is currently the subject of new research in the Australian northern wheat improvement program. Because we will have input data to run the models for each trial, rather than relying on historical sequences, the results of this work, compared with the sorghum research, will be closer to an 'ideal' test of the theory of weighting selection by the degree of matching between a MET and the TPE.

The frequency of occurrence of different ETs at a location has been correlated with measures of the similarity of locations in the way that they discriminate among cultivars (Fig. 7). Hence, spatial variation in the intensity, timing of onset, and the frequency of occurrence of drought stress is likely to complicate selection for broad adaptation, i.e. the assumption that a trial in any season at any location is a random sample of the testing environments is likely to be biased. If broad-based selection of cultivars is practised without regard for this sampling bias over seasons and locations, then selection could proceed toward cultivars that are poorly adapted, particularly if there are 2–10-year cycles in weather patterns (see the simulation example in Chapman *et al.* 2000*b*). The variance components for G×L for sorghum in this region have been shown to be substantially greater than the variance components for G main effects (Chapman *et al.* 2000*a*). Therefore, selection in one type of environment, say, a uniform irrigated environment, is unlikely to lead to substantial improvements in yield in other environments. Even where plant breeders select in on-farm trials, which would appear to be quite relevant to their target environments, they also inevitably practice some biased selection by abandoning low-yielding trials.

The substantial effects of G×L and G×L×Y interactions in sorghum variety trials in the variable dryland climates of northern Australia mean that random sampling of environments is likely to be an inefficient method to improve broad adaptation (Chapman *et al.* 2000*a*). Seasonal stress environment types as defined by simulation models and pattern analysis discriminate among yields better than do the effects of locations or years. Whereas this paper has considered the MET for a small number of testing locations, in a companion paper (Chapman *et al.* 2000*b*) we attempt to determine stress season ETs for the TPE by running a simulation model for the entire sorghum cropping region. That paper also considers the temporal effect of variation in the sampling of environments over long periods of sampling, and the potential impact of 'weighting' the data from different trials according to their 'representativeness'.

In the northern wheat improvement program, similar conclusions were reached regarding the north (CQ)/south (SQ) division of the region (Brennan *et al.* 1981). After adopting a new strategy in 1982 to accommodate a greater diversity of locations and increased sampling of years, the program was able to improve cultivars for wide adaptation (Brennan *et al.*

1994). Part of the program is also employing managed environments, such as irrigation, to ensure adequate sampling of the TPE (Cooper *et al.* 1995). Given the present level of information about sorghum hybrid trials, 2 guidelines to improve hybrid selection are that (1) locations should be chosen to at least represent the 3 stress environment types identified by the pattern analysis (low terminal stress, intermediate terminal stress, and severe terminal stress) with trials yielding <1 t/ha and >3.5 t/ha; and (2) METs should be continued for an extra season when trials generate hybrid differences that are not representative of the longer term effects.

Acknowledgments

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