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SELECTION FOR GRAIN YIELD IN SORGHUM UNDER MOISTURE AND NUTRIENT STRESS ENVIRONMENTS

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ABSTRACT

Crop breeders in the semi-arid tropics often confront a combination of moisture and nutrient stress in their target production environments. Stability of performance under stress conditions is, thus, a desirable goal for crop improvement. The objectives of these studies were (1) to explore the extent of genetic variability among recombinant inbred lines of sorghum *(Sorghum bicolor)* in high and low fertility as well as in irrigated and rainfed conditions, and (2) to predict and measure the correlated responses of sorghum yields when selection is exercised in either one environment or a combination of contrasting environments. We evaluated 57 unselected recombinant inbred (RI) sorghum lines. Large differences in yield, height, and maturity were detected among lines in each contrasting environment. Genetic variance and heritability estimates for each trait in each stress environment did not differ significantly from those in the corresponding non-stress environments. For improving yield under stress, indirect selection in high fertility or in the irrigated environment was less efficient than direct selection in the corresponding stress environment (low fertility or rainfed). When indirect selection involved yield combinations from low and high fertility or rainfed and irrigated conditions, at least five lines appeared among the 10 top-ranking lines of each contrasting environment. Thus, greater gain in performance over contrasting environments may be achieved by selecting for yield in more than one environment, rather than by selecting in any single environment.

Key Words: Crop improvement, genetic variance, heritability, irrigated, rainfed

RÉSUMÉ

Les reproductions de plante dans les tropiques semi-arides sont souvent confrontés à la combinaison de l'humidité et au stress des substances nutritives dans leurs environnements de productions visés. La stabilité de performance sous des conditions de stress est, ainsi, un objetif désirable pour l'amélioration de plante. Les objectifs de ces études étaient (1) d'explorer l'étendue de la variabilité génetique entre les races consanguines des recombinants de sorgho *(Sorghum bicolor)* en forte et faible fertilité ainsi que dans des conditions d'irrigation et pluies, et (2) prédire et mesurer les réponses corrélées des rendements de sorgho quand la sélection est exercée dans un seul environnement ou une combinaison contrastée d'environnements. Nous avons évalué 57 lignes consanguines des recombinants de sorgho non sélectionnées (RI). Des larges différences en rendement, hauteur et maturité étaient detectées entre les races dans chaque environnement contrasté. La variance génetique et les prévisions d'héritage pour chaque trait et chaque stress d'environnment n'ont pas différé de manière significative des correspondants en environnments non stressés. Pour améliorer le rendement sous stress, la sélection indirecte en haute fertilité ou en environnemnt irrigué étaient moins efficace que les sélection directe en environnement correspondant stressé (faible fertilité ou pluie). Quand la sélection indirecte a impliqué des combinaisons de rendements de faible et fertilité élevée ou conditions pluvieuses et irriguées, au moins cinq races ont apparu pami les 10 premiers classements des races de chaque environnement contrasté. Ainsi, un grand gain en performance au-délà des environnements contrastés peut- être atteint par sélection pour rendement dans plus d'un environnement, plutot que par sélection dans n'importe un seul environnement.

Mots Clés: Amélioration de la plante, variance génetique, en héritage, irriué, pluvieux

INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is an important food crop in the semi-arid tropics (SAT), where rainfall is generally insufficient and erratic (Rasenberg, 1984), and soil fertility status is very poor (Lal, 1987). To improve and stabilise crop production in these areas, the genetic potential of crop germplasm needs to be adjusted to available environmental resources (Kawano and Jennings, 1983).

Strategies are available for improving performance in nutrient deficient and moisture deficit soils of the SAT (Frey, 1964). One of the approaches assumes that selection of plant genotypes under optimal nutrient and moisture supply may maximise genetic gain in low input production environments. Testing the usefulness of this approach will be important both in the stress-prone SAT as well as in temperate environments where stress is infrequent but farmers often look for ways to reduce production costs (Atlin and Frey, 1989).

A review by Bramel-Cox *et al.* (1991) presented conflicting results regarding the usefulness of selection under non-stress conditions to identity genotypes for use in low input environments. The amount of genetic progress from selection for broad adaptation in both favourable and adverse production conditions diminishes as the intensity and frequency of stress increases in the unfavourable production environments (Bramel-Cox *et al.*, 1991; Zavala-Garcia *et al.*, 1992). Others have found that initial selection under limited nitrogen supply would not improve the probability of identifying crop genotypes with wide adaptation to both high and low fertility conditions (Seetharama *et al.*, 1984). These conclusions were drawn from sorghum studies which were conducted in either moisture stress (Bramel-Cox *et al.*, 1991; Zavala-Garcia *et al.*, 1992) or limited soil fertility (Seetharama *et al.*, 1984). However, crop breeders in the semi-arid tropics most frequently confront a combination of moisture and nutrient stresses in their target production environments. Therefore, evaluating breeding materials under both limited moisture and nutrient supply may increase the chance for identifying lines which are adapted to one or both stress conditions.

The breeding procedure commonly practised for handling segregating generations affects the rate of genetic progress that can be made under stress. Single plants selected from early segregating generations in nutrient deficient and moisture deficit soils may fail to maintain the same expression in subsequent progeny testing because of the inherent lack of uniformity in the intensity of these stresses in the experimental field during selection as well as because of the resultant segregation from single plants. To minimise these problems, evaluation and selection for stress tolerance may be delayed until true breeding lines are developed. The use of the single seed descent breeding method which allows rapid attainment of homozygosity may, therefore, be suitable for developing recombinant inbred (RI) lines to be tested under an array of contrasting moisture and nutrient environments. This was the subject of investigation in this study.

Therefore, the objectives of this study were: (1) to explore the extent of genetic variability among unselected single seed derived recombinant inbred (RI) lines grown in high and low fertility as well as in irrigated and rainfed conditions, and (2) to predict and measure correlated responses of yield when selection is exercised in either one environment or a combination of contrasting environments.

MATERIALS AND METHODS

Fifty-seven random RI lines of sorghum derived *via* single seed descent from the F_6 generation of a cross between two sorghum cultivars; namely, K886 and CS3541, were used as experimental materials. Cultivar K886 was an inbred line tolerant to pre-flowering drought stress, while CS3541 was chosen for susceptibility to pre-flowering drought stress and its good general combining ability and production of high yield potential hybrids under stress-free conditions. The responses of these two sorghum inbred lines to limited nutrient supply was unknown.

The 57 RI lines, the two parents, and three checks with tolerance to either pre- or post-flowering drought stress were grown at Lubbock under rainfed and irrigated conditions in 1990 and 1991. When sorghum is grown under rainfed conditions at Lubbock, it normally experiences pre-flowering drought stress. In the irrigated experiment, supplementary irrigation was applied from planting to flowering, whenever it was deemed necessary. The same sets of lines were also planted at Lafayette under high and low fertility treatments in 1990 and 1991. In each year, the low fertility experiment was planted in the field which received no fertiliser for over 35 years. The high fertility experiment received 150 kg N, 40 kg P, and 50 kg K per hectare.

Genotypes were arranged in a randomised completed block design and were replicated four times in each test environment (rainfed, irrigated, low-and high-fertility). Because of limited seed supply, however, only 44 and 54 inbred lines were common to the two years at Lafayette and Lubbock, respectively. Each line was planted in a single row of 3 to 5 m long spaced 76 cm apart. The experiments were planted either in late May or in early June of each year.

All plots were harvested at maturity and grain yield was measured as the weight of threshed grain from a plot expressed in kg ha^{-1} Days to flowering were recorded as the number of days from planting to the date when 50% of the plants in a plot were shedding pollen. Plant height was measured as the distance from the soil surface to the tip of the panicles in each plot.

Analyses of variance combined over years were computed for each contrasting environment from standardised data. The raw data of each trait within each environment and year was standardised, with a block mean of zero and standard deviation of one (Fox and Rosielle, 1982). This was done to remove the effects of large differences in scale on comparison of variances and predicted gains from selection between stress and non-stress environments.

Inbred lines and years were considered to be random effects. Genetic variances were estimated from mean squares among RI lines and their interaction with year in the analysis of variance. Standard errors of the genetic variances were calculated using the method of Anderson and Bancroft (1952). The heritability of each contrasting environment was calculated on an entry-mean basis as a ratio of genotypic variance to phenotypic variance for each trait. The standard errors for heritabilities were computed according to the method of Hallauer and Miranda (1988).

Genetic covariance between stress and non-stress environments for each trait was calculated using the method of Atlin and Frey (1989). The genetic correlation between two contrasting environments for yield, plant height, and days to flowering was estimated by using the formula of Falconer (1989). Standard errors for the genetic correlations were computed according to the method of Mode and Robinson (1959). The magnitude of gain from selection in a non-stress environment which was expected to be expressed in a stress environment was predicted using the formula of Falconer (1989) given below:

$$CR_s = i\sigma_s h_s h_{ns} r_g,$$

where:

CR_s = correlated response in stress environments to selection in non stress environments
i = selection intensity
σ_s = square root of phenotypic variance under stress
r_g = genetic correlation between stress and non stress environment
h_s = square root of heritability in stress environments
h_{ns} = square root of heritability in non stress environments

Simple correlations among the three agronomic traits were calculated for all test environments.

A rank summation index was used to optimise genetic gain in a single environment or two contrasting environments. The index scores for the lines within each contrasting environment were calculated as the sum of ranks of the line mean yields in the two years. Index scores for a combination of two contrasting environments were also computed as:

RSI = Rank (90 yield-stress) + Rank (91 yield-stress) + Rank (90 yield-non-stress) + Rank (91 yield-non-stress).

The actual response of indirect *versus* direct selection was measured by comparing the mean performance of the top-ranking 10 lines which were selected in a single environment or a combination of environments with the mean response of the same set of lines selected in a single environment. The mean of the selected lines in a single environment or a combination of environments was expressed as a percentage of the overall mean of all the random lines which were tested in each response environment. Because year to year variation is inherently high in stress-prone production environments, a selection scheme that takes advantage of genotype by year interaction may prove useful. A rank summation index which assigned equal weights to the two years in each environment as well as in a combination of contrasting environments was used to evaluate the actual yield advances from indirect and direct selections.

RESULTS AND DISCUSSION

Yields of all RI lines, their parents, and checks in the low fertility environment were significantly ($P \leq 0.05$) smaller than those in high fertility environment (Table 1). Low soil fertility reduced yields of all genotypes to 46% of the high fertility environment. The overall mean yield of all genotypes in the rainfed environment was reduced to 69% of the irrigated environment. Grain yields under irrigation were unexpectedly low because of the limited irrigation water supply. The recombinant inbred lines, their parents, and checks did not differ significantly ($P > 0.05$) for grain yields in each contrasting environment (data not shown). Soil fertility as a factor did not differ significantly ($P > 0.05$) for plant heights of the inbred lines, their parents, and checks. By contrast, plants from each group grew significantly taller in the irrigated than in the rainfed environment. The differences in mean days to flowering between high and low fertility and between rainfed and irrigated environments were not significant (Table 1).

TABLE 1. Mean grain yields, days to flowering, and plant height of single-seed derived F_6 lines, their parents, and inbred checks grown under high and low fertility as well as rainfed and irrigated conditions*

Environment	Recombinant inbred lines			Parent	Check
	Min	Max	Mean	Mean	Mean
Grain yield (Mg ha^{-1})					
Low fertility	1.44	4.84	2.84a**	3.96a	2.67a
High fertility	3.42	9.16	6.46b	7.72b	6.44b
Rainfed	1.08	2.94	1.94a	2.34a	1.96a
Irrigated	1.25	4.64	2.94b	3.23b	2.92b
Plant height (cm)					
Low fertility	68	184	124a	106a	109a
High fertility	65	194	126a	108a	113a
Rainfed	60	158	98a	87a	80a
Irrigated	64	192	123b	108b	102b
Days to flowering					
Low fertility	68	92	76a	76a	76a
High fertility	70	85	76a	75a	74a
Rainfed	58	69	64a	63a	62a
Irrigated	56	72	66b	66a	63a

*Pooled data, obtained over a 2 year period.

**Means within a column followed by the same letter were not significantly different at P=0.05 level using t-test

Mean yield of the highest yielding RI line was more than twice that of the lowest yielding recombinant inbred line in each test environment (Table 1). In spite of such large differences in grain yield, the genetic variance in high fertility environment was not significant because of large year x line interaction (Table 2). Since the 1991 cropping season was dry at Lafayette, it could contribute to the large year x line interaction. The genetic variance for grain yield in each stress environment did not differ from the corresponding non-stress environment based on standard errors. Furthermore, line x year interaction for grain yield in each stress environment was either comparable to or significantly smaller than that in the corresponding non-stress environment (Table 2).

Although the genetic variances for plant height and days to flowering in non-stress environments were slightly higher than those in the respective stress environments, the differences were not significant statistically (P>0.05) different. Heritability estimates for each trait in each contrasting environment followed a similar trend as the genetic variance estimates (Table 2).

Blum *et al.* (1989) demonstrated that plant height and days to flowering had marked effects on productivity when sorghum was grown under drought stress. In our studies, however, the correlation of these two traits with grain yields were very low (r<0.04) in both stress and non-stress environments (Table 3). Genetic correlation between low and high fertility environments for grain yield did not differ significantly from zero

TABLE 2. Components of variance and heritability estimates for grain yield, plant height, days to flowering of recombinant inbred lines for contrasting test environments

Environments	Gen. var	G x E var	Heritability
Grain yield			
Low fertility	0.18±0.08**	0.14±0.07**	0.60±0.26
High fertility	0.04±0.10	0.51±0.13**	0.18±0.44
Rainfed	0.16±0.08*	0.21±0.08**	0.54±0.28
Irrigated	0.24±0.09**	0.18±0.09**	0.59±0.24
Plant height			
Low fertility	0.83±0.19**	0.09±0.02**	0.96±0.22
High fertility	0.86±0.19**	0.05±0.02**	0.97±0.21
Rainfed	0.71±0.17**	0.11±0.03**	0.93±0.22
Irrigated	0.89±0.19**	0.05±0.02**	0.97±0.21
Days to flowering			
Low fertility	0.67±0.15**	0.04±0.02*	0.94±0.21
High fertility	0.59±0.16**	0.24±0.06**	0.88±0.23
Rainfed	0.49±0.13**	0.13±0.05**	0.86±0.23
Irrigated	0.81±0.18**	0.07±0.03**	0.94±0.21

*, ** Significantly different from zero at P=0.05, and P=0.01 levels, respectively

TABLE 3. Correlation coefficients among grain yield, plant height and days to flowering inlow and high fertility as well as in rainfed and irrigated environments

Trait combinations	Test environments			
	Low	High	Rainfed	Irrigated
Yield with height	0.35**	0.27*	0.02	-0.02
Yield with flowering	-0.21*	0.01	-0.09	0.12
Height with flowering	-0.31**	-0.24*	-0.39**	-0.24*

*, ** Significantly different from zero at P=0.05, and P=0.01 levels, respectively

(Table 4). Although the genetic correlation between grain yields in rainfed and irrigated environments (r_g=0.66) was more than two times as large as its standard error, it was not very high either. Genetic correlation between grain yields in rainfed and low fertility environments was close to one. These results suggested that yield responses of the RI lines in the two sets of contrasting environments, soil fertility and moisture regime, were controlled by different sets of alleles. This is in agreement with earlier studies (Atlin and Frey, 1990). By contrast, the performances of inbred lines under rainfed and low fertility environments were similar. Genetic correlations between contrasting environments for plant height and days to flowering were significant and high (Table 4).

Predicted gain from indirect selection for grain yield in each non-stress environment (high fertility and irrigated) was smaller than the predicted gain from direct selection in the corresponding stress environment (low fertility and rainfed), as indicated by the relative efficiency value of <1.0 (Table 5). Indirect selection for grain yields under rainfed condition was found to be as efficient as direct selection under low soil fertility. Indirect selection for plant height and days to flowering in each non-stress environment produced as large a response in the respective stress environment as direct selection in the stress environment.

Indirect selection in low fertility environment was less effective for improving grain yield under high fertility environment than direct selection in high fertility environment (Table 6). In contrast, the yield advances under low fertility environment resulting from indirect selection in high fertility environment was nearly as high as that from direct selection in low fertility environment. Selection based on the rank summation, which included both low and high fertility environments, increased yields significantly in these two contrasting environments. When the index involved rainfed and low fertility environments, yield increases of the selected lines was greater in low fertility environment than in high fertility environment. Selection in the rainfed environment improved yields significantly ($P \leq 0.05$) in both rainfed and irrigated environments. On the other hand, indirect selection in the irrigated environment failed to improve yields under rainfed condition. Indirect selection for increased yields based on the rank summation which involved both irrigated and rainfed environments or rainfed and low fertility conditions were nearly as good as the corresponding direct selections made in irrigated and rainfed environments (Table 6).

To a breeder who is interested in developing inbred lines, the number of superior lines which are common in the two contrasting environments is of great importance. Of the best 10 lines

TABLE 4. Genetic correlations between contrasting environments for grain yield, plant height, and days to flowering

Pairs of environments	Genetic correlations		
	Yield	Plant height	Days to floweing
High and low fertility	1.41±1.46	1.02±0.02	0.97±0.03
Irrigated and rainfed	0.66±0.28	0.99±0.01	0.91±0.05
Rainfed and low fertility	0.93±0.28	0.99±0.01	0.74±0.09

TABLE 5. The ration of predicted response from indirect selection in non-stress environment to the response from direct selection in a stress environment (relative efficiency of indirect vs direct selection

Selection environment	Response environment	Ratio of indirect to direct selection		
		Grain yield	Plant height	Days to flowering
High fertility	Low fertility	0.77	1.03	0.94
Irrigated	Rainfed	0.69	1.01	0.95
Rainfed	Low fertility	-0.98	1.01	0.77

selected under low fertility and rainfed conditions using the rank summation, five lines were also present in the top-ranking lines in high fertility and two lines were also among the top-ranking lines under irrigated environments (Table 7). When the rank summation involved two contrasting environments, between six and eight of the best 10 lines were common in both stressful and non-stressful conditions. It is interesting to note that selection based on the rank summation calculated from rainfed and low fertility environments identified at least five of the top-ranking 10 lines in both stressful and non-stressful conditions.

As sorghum is largely produced in nutrient and moisture deficit soils in the semi-arid tropics, it is necessary to evaluate the genetic potential of breeding materials to withstand these two stresses. Although, a limited number of recombinant inbred lines were included in our studies, large differences in grain yield among these lines were found in low fertility and rainfed environments. Thus, the cross segregated for genes controlling productivity in both nutrient deficient and moisture deficit soils. The variation in grain yield was not correlated with the variation in plant height and days to flowering, indicating that it should be possible to identify high yielding lines specifically adapted to nutrient- and moisture- limited environments in different maturity and height backgrounds.

One of the arguments for selecting in a favourable environment, even if improved performance is sought for a stress environment, is that the former permits greater genetic variance among lines with smaller year to year fluctuation in genotypic performance than the latter (Blum, 1988; Frey, 1964; Srivastava *et al.*, 1983). The genetic and line x year interaction variance estimates for grain yields in the high fertility and irrigated environments of our studies did not indicate such trends. In fact, genetic variances for grain yield in these two non-stressful conditions did not differ significantly ($P>0.05$) from those in the corresponding stress conditions. The magnitude of line x year interaction for grain yields in each non-stress environment (high fertility or irrigated) was either comparable to or greater than that in the respective stress environment (low fertility or rainfed). Even if the genetic variance under non-stress condition was larger than the genetic variance under stress condition, the differences for grain yields observed in the absence of stress might be largely unrelated to the differences observed in the presence of severe stress (Ceccarelli, 1987). Variation in productivity of genotypes observed in the presence of drought stress may arise from differences in

TABLE 6. Mean grain yield of the best 10 lines selected in a single environment or a combination of environments by using the rank summation index which was expressed as a percentage of the overall mean of all the random lines tested in each response environment.

Selection environment	Response environment	
	Low fertility	High fertility
Low fertility	135**	111
High fertility	126**	125**
High + low fertility	130**	122**
Rainfed + low fertility	132**	113**
	Rainfed	Irrigated
Dryland	131**	124**
Irrigated	93	142**
Irrigated + rainfed	126**	134**
Rainfed + low fertility	128**	129**

**Significantly higher than the overall mean of all the inbred lines (100%) at P=0.01 level using LSD

TABLE 7. The number of top-ranking 10 recombinant inbred lines selected by the rank summation index from either a single environment or a combination of environments which were present in the top-ranking 10 lines of each contrasting response environment

Selection environment	Response environment	
	Low fertility	High fertility
Low fertility	10	5
High fertility	5	10
High + low fertility	7	8
Rainfed + low fertility	7	5
	Rainfed	Irrigated
Rainfed	10	2
Irrigated	2	10
Irrigated + rainfed	6	6
Rainfed + low fertility	7	5

anatomical, morphological, and physiological features (Blum *et al.*, 1989; Ludlow and Muchow, 1990). Furthermore, variation in the yielding ability of genotypes in the presence of nutrient stress may be mediated by differences in nutrient uptake, partioning of the nutrients into the grain, and nutrient use efficiency (Muruli and Paulsen, 1981; Clark, 1982). Therefore, detecting differences among genotypes for responses to stress by means of such complex traits of adaptation will be difficult when stress is absent (Srivastava *et al.*, 1983).

Frey (1964) used the relative values of heritabilities in stress *versus* non-stress conditions to predict progress from selection. Because the heritability for each non-stress environment did not differ significantly from the heritability for the corresponding stress environment in these studies, it was difficult to use this criterion to predict the rate of progress from indirect selection in non-stress environment that could be expressed in a stress environment. Others also found no relationship between heritability estimates and the level of productivity of test environments (Ceccarelli, 1989; Zavala-Garcia *et al.*, 1992). Ceccarelli (1989) pointed out that the difference in magnitude of heritabilities between stress and non-stress conditions would be less important than the extent to which differences expressed in one environment would be maintained when the same set of genotypes were planted in another environment.

Indirect selection for increased yield under high fertility or irrigated environment was found to be less efficient than direct selection in the corresponding stress environment (low fertility or rainfed). However, selection in each non-stress environment based on the rank summation index scores identified lines which did well in the respective stress environment. Since the genetic correlation was an overall inverse measure of the genotype x environment interaction of the entire set of lines, some genotypes could interact very little with contrasting environments notwithstanding the presence of a low genetic correlation (Atlin and Frey, 1990).

Heterogeneity within lines derived from early segregating generations may partly contribute to their broad adaptation to a range of contrasting environments (Frey, 1964; Shabana *et al.*, 1980). As the recombinant inbred lines included in our studies were derived from the F_6 generation, however, heterogeneity within lines would be minimal at this level of inbreeding. Thus, other mechanisms may confer broad adaptation of the recombinant inbred lines. Since adaptation resulting from heterogeneity within lines cannot be fixed (Frey, 1964; Shabana *et al.*, 1980), the use of recombinant inbred lines which are homogeneous may facilitate the transfer of genes for wide adaptation intact from parents to their progenies.

Indirect selection for superior genotypes using a combination of low and high fertility or rainfed and irrigated conditions identified at least six of the top-ranking 10 lines in each contrasting environment. Even when rainfed and low fertility environments were included in the rank summation, at least half of the best 10 lines did very well in both low and high fertility as well as in rainfed and irrigated environments. These results indicated that greater gain in performance over contrasting environments may be achieved by selecting for yield in more than one environment, rather than by selecting in any single environment.

Our results suggested that selection for yield in moisture- and nutrient- stress environments should be done directly in those environments. However, the development of separate breeding programmes for moisture and nutrient stress environments will be difficult and expensive. A more realistic approach would be to screen breeding materials in plots which combine both drought and nutrient stress. Srivastava *et al.* (1983) provided enough evidence from selection experiments which were conducted in low fertility-dry farming conditions that supported this approach. The strong genetic correlation between rainfed and low fertility environments for yield and the common occurrence of inbred lines which were top-ranking in both rainfed and low fertility conditions in our studies provides additional support to this approach. To achieve greater gain in performance in these two stress conditions, incorporating parents with good performance under low input levels in crosses will be needed. Because favourable growing seasons are occasionally encountered in sorghum production environments alternating selection in moisture and nutrient stress with selection in favourable conditions may permit the identification of lines which are adapted to both stressful and non-stressful conditions (Cercceralli, 1989).

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