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Assessment of groundnut cultivars for end-of-season drought tolerance in a Sahelian environment

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SUMMARY

A 2-year study (1990 and 1991) was conducted at the ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) Sahelian Centre, near Niamey, Niger, to select groundnut cultivars tolerant to drought and to examine selection techniques. Thirty-six cultivars known to vary in yield potential were grown under rainfed and irrigated conditions. Crop growth rate (C) and partitioning co-efficient (*p*) were estimated from phenological and final harvest data. The correlation between years was greater for partitioning than for pod yield (implying a higher heritability for *p* than for yield). Tolerance as determined by a drought susceptibility index for pod yield (S_Y), crop growth rate (S_C) and partitioning (S_p) to reproductive sinks showed thirteen cultivars as drought tolerant for either C or *p* or for both. The Sahelian cultivars 796, 55–437 and TS 32–1 were the most consistent for drought tolerance. Partitioning was the most important yield component affecting yield variation among cultivars.

INTRODUCTION

Groundnut (*Arachis hypogaea* L.) is grown as a rainfed crop in the Sahelian zone of west Africa. During the crop season, rainfall is poorly distributed and shows great variation, with frequent dry spells of 8–25 days during the beginning and towards the end of the crop season (Sivakumar 1991). In addition, the growing season is short, beginning in June and ending in September (Sivakumar 1988). Thus, groundnut grown in the Sahel often experiences water deficits during the pod-filling phase, which usually coincides with the end of the rainy season. In addition, soils have a low organic matter and water-holding capacity. These conditions make water supply a major environmental factor limiting the yield of groundnut in the Sahel (Virmani & Singh 1986). The development of groundnut cultivars that are better able to resist the effects of reduced water supply during the pod addition and filling growth stages would help to stabilize yield. However, selection for resistance to drought has proved to be difficult because of inadequate and costly techniques and the absence of clearly defined environmental stress patterns.

Comparative studies of the effects of drought occurring at different stages of growth in groundnut have shown that terminal drought (i.e. during pod-filling) had the greatest impact on yield (Nageswara Rao *et al.* 1985), and that varietal differences in drought sensitivity to terminal drought were strongly correlated with yield under non-stressed conditions in a selection of varieties (Nageswara Rao *et al.* 1989).

There are many morphological, physiological and biochemical traits that may contribute to the improved performance of drought-affected crops (Ludlow & Muchow 1988), including groundnut (Harris *et al.* 1988; Matthews *et al.* 1988; Wright *et al.* 1991). High yield under drought stress could be a result of an escape mechanism rather than stress tolerance (Fischer & Maurer 1978). Because the drought resistance of plant genotypes is defined in multiple and often complex ways, simple tests for drought tolerance appropriate for selection purposes have not been developed adequately. Therefore many plant breeders rely on yield performance under stress as a major selection criterion for tolerance. A drought stress index (S), which provides a measure of stress resistance, based on minimization of yield under dry compared to moist conditions rather than solely on yield level under dry conditions, has been used to characterize wheat genotypes (Clarke *et al.* 1984; Bruckner & Frohberg 1987).

The yield of any crop is a product of crop growth rate (C), the partitioning of assimilates to reproductive

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Table 1. *Drought susceptibility indices for pod yield* (S_Y), *crop growth rate* (S_C) *and partitioning* (S_p) *of 36 groundnut cultivars grown in West Africa in 1990 and 1991*

	1990			1991		
Cultivar	Pods (S_Y)	Crop growth rate (S_C)	Partitioning (S_p)	Pods (S_Y)	Crop growth rate (S_C)	Partitioning (S_p)
1. ICGV SM 86725	1·10	0·88	1·06	1·60	1·27	3·68
2. ICGV SM 83005	1·06	0·76	1·41	1·55	1·40	2·92
3. ICGV SM 83011	1·08	0·80	1·27	1·45	0·80	3·30
4. ICGV SM 85039	0·98	0·63	1·22	1·41	0·63	3·07
5. ICGV SM 85043	0·81	0·66	0·77	0·38	−0·28	−0·02
6. ICGV SM 86051	1·16	0·97	0·88	1·68	2·25	3·01
7. ICGV SM 86052	1·03	0·65	1·62	1·43	1·60	2·06
8. ICGV SM 85002	1·21	0·91	1·69	1·50	2·12	1·10
9. ICGV SM 85764	1·11	0·66	1·76	1·57	1·54	2·33
10. ICGM 197	1·02	0·63	1·33	1·10	1·05	0·46
11. ICGM 336	1·13	1·02	1·73	1·03	−0·24	2·64
12. ICGM 614	1·21	0·89	1·83	1·60	2·06	2·05
13. ICGM 623	1·20	0·65	2·19	1·62	1·65	3·48
14. ICGM 631	1·23	1·04	2·06	1·08	1·33	0·21
15. ICGV 87156	0·86	0·78	0·37	0·38	−0·36	−0·07
16. ICGV 87157	1·05	0·83	1·35	1·42	1·62	2·07
17. ICGV 87160	0·94	0·75	0·68	0·04	0·40	−1·80
18. ICGV 87185	0·99	0·60	0·56	0·71	0·67	0·20
19. ICGV 86024	0·92	0·36	0·99	1·42	1·69	1·89
20. ICGV 86548	1·13	0·90	1·25	1·47	1·51	2·11
21. ICG 1260	1·12	0·96	0·99	0·64	0·76	−0·55
22. ICG 2140	0·89	0·73	0·74	0·30	0·36	−1·36
23. ICG 2229	0·83	0·72	0·24	−0·13	0·16	−2·40
24. ICG 2327	1·15	0·75	1·69	1·13	0·31	2·43
25. ICG 8361	0·94	0·71	0·56	0·51	0·72	−0·82
26. ICGV SM 83701	1·05	0·44	1·57	1·34	1·14	2·45
27. ICGV SM 83709	0·95	0·80	0·84	0·65	0·96	−0·79
28. ICGV SM 86066	0·82	0·86	−0·18	−0·08	−0·83	−0·53
29. ICGV 86168	0·85	0·68	0·63	0·82	1·09	0·42
30. ICGV 87078	1·02	0·86	0·41	0·21	0·28	−1·51
31. ICGV 87086	0·88	0·73	0·52	−0·17	−0·48	−1·38
32. ICGV 87087	1·05	0·83	0·93	1·26	1·73	0·33
33. 55–437	0·44	0·38	0·33	0·91	1·28	−0·29
34. 28–206	1·15	0·84	1·76	1·37	2·04	−0·15
35. TS 32–1	0·95	0·75	0·33	0·63	0·80	0·03
36. 796	0·64	0·57	0·15	−0·24	−1·20	−0·38

sinks (p) and the duration of the crop's reproductive phase (D_r) (Duncan *et al.* 1978). The C and p components of the model for yield determination described by Duncan *et al.* (1978) are often determined through growth analysis based on destructive sampling. Williams & Saxena (1991) and Williams (1992) demonstrated that final harvest data in combination with phenological observations can provide good estimates of C and p without extensive destructive growth analysis. While the model is simple, and caution needs to be exercised in its use, it allows interpretation of differences in yield in a more mechanistic manner than is possible from the original data. The rate C is determined by resource capture and efficiency, while variations in p are determined by another set of physiological factors. With stress indices for the components of the model, it should be possible to identify those genotypes that have performed well under drought conditions for one or other of the factors contributing to yield during drought. Then, in the long term, complementary attributes can be combined through hybridization and selection. The possibility of being able to identify and combine major 'families' of plant reactions to drought could simplify the process of breeding for this difficult problem. The application of this technique to selection in plant breeding is as yet unproven.

The objectives of this study were to characterize a set of groundnut cultivars for drought tolerance using stress indices for pod yield, crop growth rate and partitioning response and to determine their relationship.

MATERIALS AND METHODS

Thirty-six genetically diverse cultivars of groundnut (Table 1) were tested under rainfed and irrigated conditions in 1990 and 1991 at the ICRISAT Sahelian Centre research farm near Niamey, Niger. The soil type was sandy siliceous, isohyperthermic psammentic paleustalf, low in organic matter content and water-holding capacity.

Cultivars 55–437, 796 and TS 32–1 are standard cultivars widely grown in the Sahel, while 28–206 is a local variety grown in higher rainfall zones of West Africa. Cultivars with the prefix 'ICG' and 'ICGM' are germplasm lines and those with the prefix 'ICGV' and/or 'SM' are advanced breeding lines of diverse pedigrees developed by ICRISAT in India and Malawi.

Groundnut was sown on 24 July in 1990 and on 26 July in 1991, about one month after the rains had begun. The objective of late sowing was to have the crop mature when there was little likelihood of rain. The experiment was divided into two parts, each having the 36 cultivars arranged in a 6 × 6 lattice design with four replications. The two parts were 10 m apart. A basal application of 18 kg P_2O_5/ha in the form of single superphosphate was made before sowing. Seed was sown by hand in plots of five rows, 0·5 m apart and 3 m long. One part of the experiment was rainfed and the other part was irrigated until maturity after the rains had stopped (Fig. 1). In 1991, rainfall in September was very low and two supplementary irrigations, each of 40 mm of water, were given to both rainfed and irrigated parts weekly until the end of September, and thereafter a 40 mm irrigation per week was given only to the irrigated part until maturity. In 1990, overhead sprinkler irrigation was used, while in the 1991 season a linear movement irrigation system was used. All plots were monitored for the date at which 50% of the plants had commenced flowering. The beginning of the pod-filling phase was taken as 15 days after the date of 50% flowering for each cultivar.

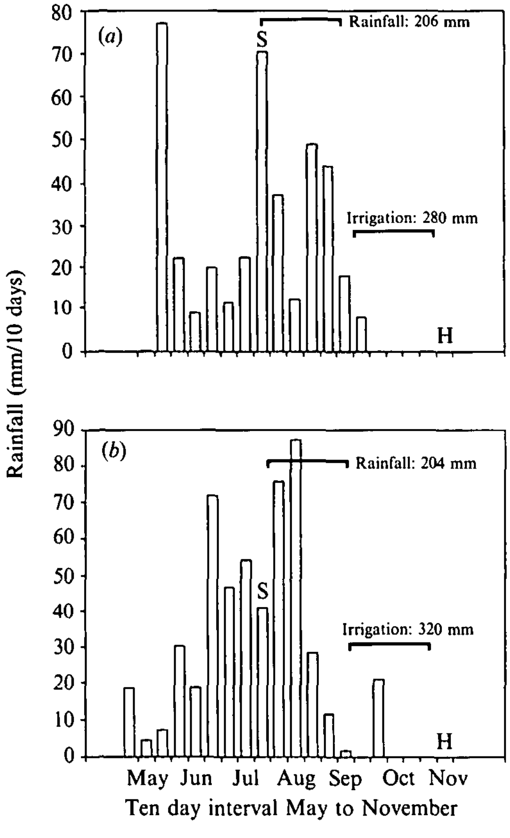

Fig. 1. Rainfall (mm/10 days) from May to November in (*a*) 1990 and (*b*) 1991, in the Sahelian zone of West Africa. S denotes date of sowing, H denotes date of harvest.

The experiment was harvested between 13 and 19 November in 1990 and between 7 and 12 November in 1991 when at least 50% of the developed pods were mature as determined by the blackening of the internal shell wall (Williams & Drexler 1981). All five rows in each plot were harvested. The dry mass of haulms and the dry mass of pods were measured after air drying to constant weight and threshing percentage was determined from a 200 g sample of pods from each plot as the ratio of seed weight:pod weight.

The crop growth rate (C) and partitioning coefficient (*p*) were estimated from phenological and final harvest data using the methods of Williams (1992) after adjusting for the higher energy of pods (Duncan *et al.* 1978):

$$\text{CGR} = \text{Haulm yield} + (\text{Pod yield} \times 1{\cdot}65)/\text{T}_\text{T} \quad [1]$$

$$\text{PGR} = (\text{Pod yield} \times 1{\cdot}65)/(\text{T}_\text{T} - \text{T}_\text{V} - 15) \quad [2]$$

$$p = \text{PGR}/\text{CGR} \quad [3]$$

where CGR is crop growth rate (C), PGR is pod growth rate and *p* is the partitioning coefficient, T_T is the number of days from sowing to harvest, and T_V is the duration from sowing to 50% flowering. The drought susceptibility indices based on pod yield (S_Y), crop growth rate (S_C) and partitioning (S_p) were calculated for each cultivar as the reduction in the trait from irrigated to rainfed conditions relative to the mean of all cultivars (Fischer & Maurer 1978). This index (using yield as an example) is expressed as:

$$\text{S} = (1 - \text{Y}/\text{Y}_\text{w})/(1 - \text{X}/\text{X}_\text{w}) \quad [4]$$

where Y is yield under rainfed conditions, Y_w is yield under irrigated conditions and X and X_w represent averages over all cultivars under rainfed and irrigated conditions, respectively. The term $(1 - X/X_w)$ is defined as 'stress intensity' (D). S values $< 1·0$ indicate low susceptibility, while S values of zero or less indicate no effect of drought on yield. The relationships between pod yield, C and p were examined using regression analysis.

Initially, standard analyses of variance were conducted separately for each irrigation treatment in each year. After this, all data were combined in a 'multi-site' analysis over both years and both irrigation treatments.

RESULTS AND DISCUSSION

Year, drought and cultivar effects

With the exception of days to maturity and reproductive duration, there was a significant ($P < 0·05$) reduction in all the analysed variables due to drought stress (Table 2). In 1990, average pod yield was 0·24 t/ha in the rainfed treatment and 1·01 t/ha in the irrigated treatment. In 1991, average pod yields were 0·25 and 0·53 t/ha in the rainfed and irrigated treatments, respectively. In 1990, seed mass averaged 42 g/100 seeds in the irrigated treatment and 29 g/100 seeds in the rainfed treatment. Mean 100-seed mass was much lower in the irrigated treatment in 1991 (32 g) than in 1990, while it was similar in the rainfed treatment over both years. The decrease in C for rainfed crops in both years indicated a sensitivity of general crop growth to water deficit. Drought stress reduced total dry matter at maturity in proportions roughly similar to the reduction in pod yield in both years (Table 2). Differences among cultivars for partitioning were greater in the rainfed than in the irrigated conditions (as indicated by the wide range of means).

In 1990, ICGM 614 (No. 12), ICGV 87185 (No. 18) and ICGV 87087 (No. 32) produced the highest mean pod yields in the irrigated conditions but not in the

Table 2. *Range and means of phenological and yield characteristics of 36 groundnut cultivars grown under irrigated and rainfed conditions in West Africa, 1990 and 1991*

	1990					
	Irrigated			Rainfed		
Traits	Range	Mean	S.E.	Range	Mean	S.E.
Days to maturity	103–118	110	2·2	*	111	—
Duration of reproductive phase (days)	75–91	83	2·2	79–84	83	0·5
Pod yield (t/ha)	0·51–1·37	1·01	0·139	0·06–0·47	0·24	0·054
Crop growth rate (t/ha per day)	0·012–0·033	0·02	0·003	0·003–0·013	0·01	0·001
Total dry matter (t/ha)	0·91–2·80	1·95	0·276	0·27–1·26	0·69	0·124
100-seed mass (g)	30–67	42·0	1·61	13·7–42·6	29·0	3·48
Shelling (%)	30–74	61·0	1·97	10–59	35·0	5·30
Partitioning coefficient	0·66–0·97	0·86	0·030	0·28–0·95	0·59	0·041
	1991					
Days to maturity	*	109	—	*	109	—
Duration of reproductive phase (days)	78–86	84	0·4	72–81	79	0·382
Pod yield (t/ha)	0·25–0·86	0·53	0·158	0·07–0·63	0·25	0·060
Crop growth rate (t/ha per day)	0·010–0·030	0·02	0·003	0·006–0·021	0·013	0·002
Total dry matter (t/ha)	0·94–2·89	1·64	0·274	0·54–2·04	1·22	0·205
100-seed mass (g)	25–41	32·0	2·54	22–36	29·0	2·05
Shelling (%)	13–58	37·0	4·10	22–55	39·0	3·50
Partitioning coefficient	0·36–1·01	0·56	0·107	0·16–0·90	0·46	0·64

* Harvested on the same day.

S.E., Effective standard error for each of the 36 adjusted cultivar means.

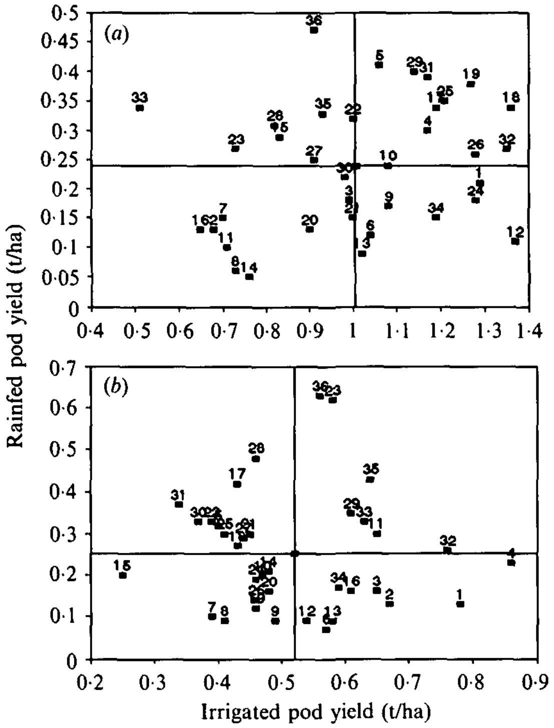

Fig. 2. Mean pod yield (t/ha) of groundnut in irrigated and rainfed treatments in (*a*) 1990 and (*b*) 1991. Numbers refer to individual cultivars (see Table 1).

rainfed conditions (Fig. 2). Only ICGV 87087 maintained its position in the top-yielding irrigated cultivars in 1991. Cultivar 796 (No. 36) gave the highest yield in the rainfed conditions in 1990 and was above average in both conditions in 1991 (Fig. 2). Ten cultivars in 1990 and seven in 1991 produced above average pod yield in both rainfed and irrigated conditions with only ICGV 86168 (No. 29) and ICGV 87087 (No. 32) achieving this in both years (Fig. 2). These results showed that for yield there are strong genotype × environment interactions due to seasonal differences in rainfall preceding the treatment. This also confirms the general observation by Nageswara Rao *et al.* (1989), that high yield potential in unstressed conditions correlates with drought susceptibility.

The estimation of C using final biomass gives an indication of the seasonal differences in crop resource use and resource-use efficiency imposed by the treatments. There was a significant ($P < 0{\cdot}01$) year effect for partitioning (p) and pod yield but not for C, which was almost the same in both years (Table 2). However, the method does not take into account differences in the distribution of that growth within the season. In this experiment, it would have been useful to have obtained estimates of C during the drought phase by measuring water use directly, although this would have been difficult for such a large number of cultivars.

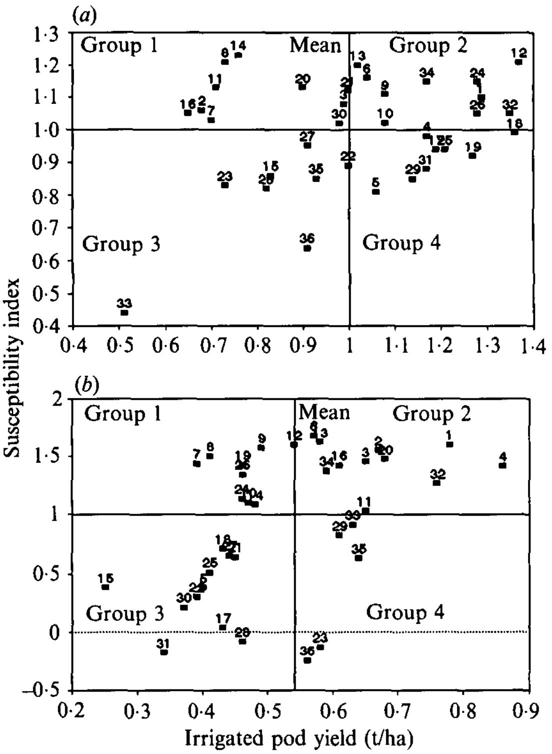

Fig. 3. Classification of groundnut cultivars based on pod yield (t/ha) in the irrigated treatment and drought susceptibility index in (*a*) 1990 and (*b*) 1991. Numbers refer to individual cultivars (see Table 1).

The within-season pattern of water availability may have interacted with the method of estimation of partitioning. This could occur because the growth of pods depends largely on photosynthesis. The shortage of resources for photosynthesis during this phase should thus have a larger effect on the pod growth rate than on the overall (seasonal) C value. Thus, while the methodology is unable to provide an absolute value of p, it provides estimates by which the relative performance of genotypes can be assessed. On average across varieties, partitioning was higher in the dry year (1990) than in the wet year (1991), confirming this hypothesis (Table 2).

In both irrigated and rainfed treatments, the correlation coefficient for cultivar pod yield between years was small ($r = 0{\cdot}48$ and $-0{\cdot}072$). Similarly C values for cultivars were not correlated between years. In contrast the correlation coefficient obtained for partitioning in the rainfed treatment between years was large ($r = 0{\cdot}84$, D.F. 34) while in the irrigated treatment, the correlation coefficient was very small

($r = -0{\cdot}114$). These results indicate that partitioning in dry conditions is a more reliable selection criterion for the identification of cultivars tolerant to end-of-season drought than is yield.

Stress susceptibility indices

The stress indices provide a measure of tolerance based on the minimization of yield loss under stress conditions rather than on yield performance *per se*. Except for cultivar 796, which showed superior performance in rainfed conditions in both years, drought-tolerant cultivars did not have outstanding yields in the irrigated treatment. One such example was cultivar 55–347 (No. 33). However, such cultivars could be used in breeding programmes as sources of stress resistance.

The susceptibility indices for yield and the model components over the 2 years indicated that, out of the 36 cultivars, 13 were relatively drought tolerant (i.e. cultivar Nos. 5, 15, 17, 18, 22, 23, 25, 27, 28, 31, 33, 35 and 36). Cultivars were classified into four groups according to their susceptibility index and yield of pods in the irrigated treatment (Fig. 3). Group 1 had below average pod yield and low drought resistance ($S > 1{\cdot}0$). Group 2 comprised cultivars with above average yield and low resistance to drought and thus performed well in irrigated conditions only. Group 3 comprised cultivars with below average yield which were tolerant to drought ($S < 1{\cdot}0$), performing well in rainfed conditions only. Group 4 contained cultivars with above average yield and with $S < 1{\cdot}0$, which thus yielded well in both rainfed and irrigated conditions. Most of the cultivars in Groups 1 and 2 were those with ICGV SM or ICG SM classifications and 28–206 (No. 34).

The Sahelian cultivars 796 (No. 36), 55–437 (No. 33) and TS 32–1 (No. 35) can be considered to be specifically adapted to dry conditions. This is consistent with previous results of Gautreau (1982) and Greenberg *et al.* (1992) and thus the technique used here in evaluating groundnut cultivars for end-of-season drought resulted in reasonable consistency for cultivar drought tolerance. The greater susceptibility rating of the cultivars with the prefixes ICGV SM and ICGM, as well as 28–206, is not surprising since they have been developed in and are more adapted to higher rainfall zones. Although they are of longer duration than the Sahelian lines, drought escape (whereby cultivars reach physiological maturity before the onset of stress) did not appear to be a major factor influencing tolerance ratings as there was no significant correlation between reproductive duration and pod yields in either irrigation treatment. However, for partitioning, there was evidence of escape being a determinant of varietal response, as the duration of the reproductive phase was correlated ($r = 0{\cdot}39$; $P = 0{\cdot}001$, $n = 144$) with partitioning in only the rainfed treatment; but this measure of phenology only accounted for *c.* 15% of the variation.

Relationships between pod yield, crop growth rate and partitioning

In 1990, C was not significantly correlated ($r = 0{\cdot}37$) with pod yield in the irrigated treatment, but accounted for 63% of the variation in the final pod yield in the rainfed treatment. In 1991, C accounted for 47% of the variation in pod yield in the rainfed treatment. This effect is attributed to the effect of variations in environmental resource capture rather than to genotypic effects, because the correlation was not consistent for cultivars across years.

In 1990, pod yield and p were not significantly associated in the irrigated conditions, but p accounted for 53% of the variation in pod yield in the rainfed treatment. In 1991, pod yield was significantly ($P < 0{\cdot}01$) correlated with p in both rainfed ($r = 0{\cdot}85$) and irrigated ($r = 0{\cdot}73$) conditions. These differences in relative significance of C and p in the drought responses in the 2 years are probably due to differences in rainfall (i.e. 20 mm in October 1991; Fig. 1) during the stress phase.

Separating the effects of drought into the components of a yield determination model should allow improved selection for drought responses. Cultivars which have an advantage in resource capture or efficiency of water use may be expected to have superior maintenance of C. On the other hand, cultivars with a superior maintenance of partitioning in the presence of drought probably utilize a different set of mechanisms (e.g. escape, tolerance) to achieve their advantage.

Values of C and p under drought stress were significantly ($P < 0{\cdot}01$) correlated with (S_Y) in both years. The correlation coefficients were respectively $-0{\cdot}70$ and $-0{\cdot}44$ in 1990 and $-0{\cdot}61$ and $-0{\cdot}79$ in 1991. This suggested that, in both years, resource capture and utilization contributed significantly to drought tolerance, but the contribution of p to drought tolerance was more environmentally/seasonally sensitive. However, the correlations of S_Y, S_C and S_p for varietal performance between the 2 years were weak but showed that C is a powerful contributor to stress tolerance within years. These contributions are probably due to environmental effects and are of little value in selection. This suggests that the use of the stress index of Fischer & Maurer (1978) can be improved for selection purposes by applying it to determinants of yield.

Genetic improvement in any crop requires the identification of relevant physiological traits as selection criteria and testing to verify the value of such selection for improvement of stress tolerance. Our results suggest scope for indirect selection for yield under dryland conditions by selecting for partitioning.

Partitioning was a major component contributing to good performance of cultivars under rainfed conditions.

Stress susceptibility indices identified genotypes that could not be identified on the basis of actual performance *per se* due to low yield. However, because of the integrative effect of the methods used, cultivars exhibiting extreme stress tolerance or susceptibility should be investigated more extensively to identify the component mechanisms contributing to stress tolerance or susceptibility. Used together, susceptibility indices provided a better understanding of the yield components contributing to good or poor performance under rainfed conditions than did actual yield performance alone. Examination of yield components has been used to determine the timing of critical stress and to relate sensitivities of a range of crop genotypes (Hanson & Nelsen 1980). Comparable analysis of susceptibility to stress using susceptibility indices of yield components has been determined in other crops, particularly wheat (*Triticum aestivum*) (Bruckner & Frohberg 1987). The approach here advances these ideas in that the effects of stress are evaluated on processes determining response rather than on the end result of that process. The apparent improvement of heritability for drought responses for components of the model is an important advance in the methodology for breeding drought-resistant varieties.

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