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Evaluation of groundnut genotypes for heat tolerance under field conditions in a Sahelian environment using a simple physiological model for yield

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SUMMARY

Heat tolerance of groundnut (*Arachis hypogaea* L.) was evaluated under field conditions using physiological traits identified in a yield model [crop growth rate (C), reproductive duration (D_r) and partitioning (p)]. In 1991, 625 diverse genotypes were initially screened under irrigation during the hottest months (February to May). Subsequent tests consisted of 16 contrasting genotypes selected based on a combination of high pod yield and partitioning coefficient of $> 0{\cdot}50$. Large variation was observed among the 625 genotypes for pod yield and physiological traits. C was a powerful factor influencing pod yield. Eight genotypes combining high pod yield and a partitioning coefficient greater than 0·6 were identified. These included two released cultivars (55–437 and 796) in the Sahel. Correlations between seasons were significant for p ($r = 0{\cdot}84$), but non-significant for pod yield ($r = 0{\cdot}40$), C ($r = 0{\cdot}39$), and D_r (0·36). Date of sowing and genotypes had significant effects on pod yield and C, but were slight on p and D_r. Pod yield of most genotypes declined by more than 50 % when flowering and pod formation occurred when maximum temperatures averaged 40 °C. The results revealed that estimates of p would be a more reliable selection criterion for identification of genotypes tolerant to heat than yield. Further research is suggested to maximize crop growth rate and partitioning of genotypes growing under supra-optimal temperatures.

INTRODUCTION

The groundnut is an important oil, food and fodder crop which plays a significant role in the agriculture economy of countries of semi-arid tropics. In the Sahel, only one crop is produced in the short rainy season (June–October) which is characterized by poorly distributed rainfall with frequent dry spells of 8–25 days at the beginning and towards the end of the crop season (Sivakumar 1991). It is, however, possible to grow two crops in a year by exploiting the long dry season (November–May) under irrigation. This should result in increased groundnut production, thus contributing to alleviation of poverty. It should also facilitate rapid generation advance of breeding populations leading to faster progress in crop improvement. The dry season is characterized by a cool, dry period starting mid-November through February when night temperatures are below optimum for groundnut, followed by a rapid transition to a hot dry period when temperatures are above optimum until May. In a study involving a limited number of groundnut genotypes during the dry season in Niger, observed responses were attributed to temperature differences during pod-filling phase on partitioning (Ntare *et al.* 1998). However, no systematic investigation and exploitation of variations in groundnut varietal tolerance to high temperatures has been conducted in the Sahel.

Groundnut is sensitive to temperature with the optimum temperature for most processes being between 27 and 30 °C (De Beer 1963). It has been shown that irrigated groundnut for the dry season should be sown in November to allow the crop to develop under relatively cool temperatures that maximize pod yield (Ntare *et al.* 1998). Varieties grown by farmers in the Sahel yield well in the hot months prior to the onset of the rains and this has been attributed to their ability to maintain partitioning to pods in above normal temperatures (Greenberg *et al.* 1992, Ndunguru *et al.* 1995). Thus, we believe that

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temperature tolerance is an important component of drought resistance and a necessary attribute for varieties destined for the Sahel. By providing adequate nutrients and water to groundnuts growing in very hot months, genotypes with the necessary heat tolerance can be identified without the confounding effects of moisture stress. However, the growth of groundnut in the Sahel is extremely variable and selection based on yield alone is difficult (Ntare & Williams 1998).

Yield of groundnut is a product of crop growth rate (C), the partitioning of assimilates to reproductive sinks (p) and the duration of the crop's reproductive phase (D_r) (Duncan *et al.* 1978). Thus,

$$Y_{pod} = pCD_r \quad [1]$$

This yield model provides a framework for understanding yield variation in variable environments. The model components integrate many physiological processes. While a full understanding of these processes is desirable, much can be achieved by working with integrated parameters rather than yield only. Crop growth rate is determined by resource capture and efficiency (Duncan *et al.* 1978), variations in D_r are largely by temperature (Ong *et al.* 1986) and p variations are determined by another set of physiological factors. 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 with original data.

The C and p components of the model are often determined through growth analysis based on destructive sampling. This would not be economically feasible for a large number of genotypes. Williams & Saxena (1991) demonstrated that final harvest data in combination with phenological observations can provide good estimates of C and p without extensive growth analysis. The application of this methodology has been demonstrated in groundnut (Nigam *et al.* 1994; Ndunguru *et al.* 1995; Ntare & Williams 1998).

The objectives of this study were to assess the variation for tolerance to high temperature of diverse groundnut genotypes under field conditions and determine the response to varying temperature regimes during the dry season.

MATERIALS AND METHODS

A series of trials was conducted under irrigation during the dry season from 1991 to 1994 at the ICRISAT Sahelian Centre research farm (13° 29′ N, 2° 10′ E; 221 m above sea level) in Niger. Soils are Psammentic Paleustalfs (sandy, siliceous, isohyperthermic) with low pH, low inherent soil fertility and low organic matter content. No rainfall was received during the experiments. The 10-day mean maximum and minimum air temperatures from a meteorological station 500 m from the experimental fields are presented in Table 1.

Experiment 1: Genotype screening

The experiment in 1991 consisted of 625 genotypes, including 300 advanced breeding lines from ICRISAT programmes in India and Malawi, 300 germplasm lines originating from primary and secondary centres of diversity; and 25 released cultivars in India and Africa. Seeds obtained from the breeding and released lines in 1990 rainy season sowings were used. For the germplasm line, seeds from a regeneration planting in the same season were used. Seed lots from a common source were used to minimize variation caused by the seed production in different environments. The genotypes were laid out in a 25×25-lattice design with three replications. Prior to sowing, 46 kg/ha P_2O_5 was applied as diammonium phosphate. Plot size was 4 rows of 2 m long and seeds were sown on 7 March 1991 on ridges 50 cm apart and 10 cm within the ridges. Adequate amount of water (40 mm per week) was provided by a linear movement irrigation system.

Plots were regularly observed to decide the date at which 50% of the plants started flowering. At flowering 400 kg/ha of gypsum was applied to ensure that calcium was available for pod filling. The beginning of the pod development was taken as 15 days after (the date of) 50% flowering as earlier observed for most groundnut genotypes at this location. Maturity was determined by randomly picking a few pods from border plants and examining the internal pod wall. Mature pods are indicated by the blackening of the internal pod wall (Williams & Drexler 1981). At harvest, all plants in a plot were hand-lifted. The pods were separated from the vegetative parts (haulms) along with some roots that came up with the pods on lifting. Both the pods and the haulms were dried in the sun until constant weight. The dried pods and vegetative weights were added to calculate the final harvest biomass. Crop growth rate (C, kg/ha per day), pod growth rate (R, kg/ha per day) and partitioning (p, proportion of dry matter partitioned into pods) were estimated by modifying the non-destructive methodology described by Williams & Saxena (1991) using observations on time to flowering, and physiological maturity and pod and haulm yields at the final harvest. Pod dry matter was multiplied by a correction factor of 1·65 (Bell *et al.* 1992) to adjust for the differences in energy requirement for producing vegetative *v.* pod dry matter. C and R were computed as:

$$C = (HWT + (PWT \times 1{\cdot}65))/T_2 \quad [2]$$

$$R = (PWT \times 1{\cdot}65)/(T_2 - T_1 - 15) \quad [3]$$

and

$$p = R/C \quad [4]$$

where HWT is the haulm weight, PWT is the pod weight, T_2 is the number of days from sowing to

Table 1. *Mean maximum and minimum temperatures during the experiments*

	10-day average temperature (°C)					
	1–10		11–20		21–30	
Year/Month	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum
1991						
February	36·1	18·5	39·0	22·4	39·9	23·1
March	38·3	23·7	38·0	23·3	41·3	25·7
April	41·0	24·7	41·3	27·6	41·6	28·3
May	38·4	27·4	37·5	26·8	34·2	24·2
1992						
February	33·8	18·1	34·4	19·2	35·5	18·7
March	37·6	21·6	38·3	22·4	39·24	24·1
April	41·4	26·8	40·2	25·6	41·4	25·8
May	40·4	27·3	38·8	27·0	39·0	26·7
1993/94						
November	37·4	24·3	39·3	22·7	39·6	23·7
December	35·2	20·1	32·2	16·7	31·0	15·7
January	30·9	15·8	31·3	15·9	34·1	18·6
February	31·9	16·9	36·9	25·2	35·9	19·3
March	38·4	21·2	40·1	23·7	42·4	24·9
April	40·1	25·3	41·9	26·9	42·3	28·1
May	40·2	26·5	41·4	28·9	40·0	27·7

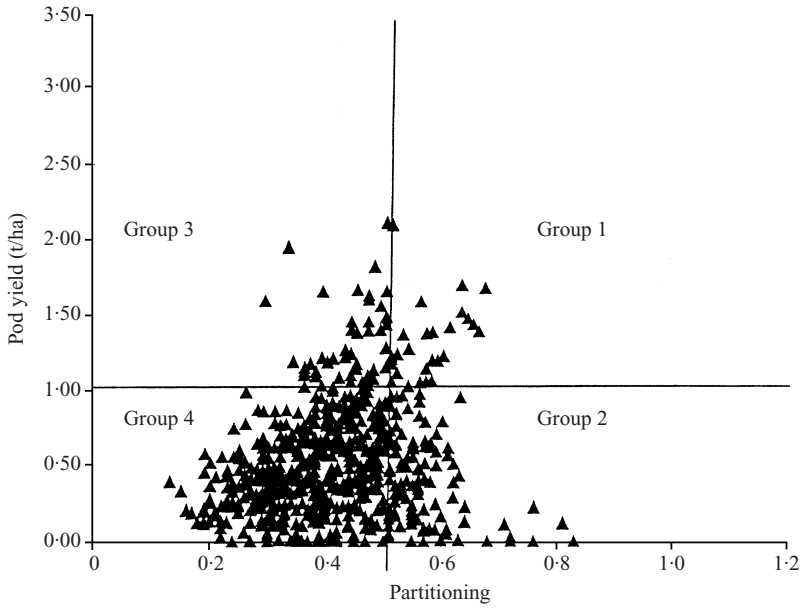

Fig. 1. Classification of 625 groundnut genotypes based on pod yield (t/ha) and partitioning (proportion of dry matter partitioned into reproductive sinks) in 1991.

harvest, T_1 is the number of days from sowing to flowering, and 15 is the number of days between flowering and the start of pod expansion.

Data were analysed using GENSTAT statistical procedures. Due to a large variation in the number of plants harvested in Expt 1, yield data were not normally distributed and required a square root transformation. The genotypes were classified into four groups (Fig. 1) based on a combination of pod yield ($> 1{\cdot}0$ t/ha) and partitioning ($> 0{\cdot}50$). A

Table 2. *Ranges, means and distribution of characters measured on 625 groundnut lines in the screening experiment 1991*

Variable	Minimum	Maximum	Mean	Distribution
Days to flower	27	47	32·74	Normal
Days to harvest	119	148	133·3	Normal
Plants harvested	1	69	24·6	Normal
Haulm weight (t/ha)	0·008	11·8	1·99	Skewed
Pod weight (t/ha)	0·003	4·8	0·555	Skewed
Crop growth rate (kg/ha/day)	4	39	17	Skewed
Partitioning coefficient	0·0260	1·10	0·480	Normal
Reproductive duration (days)	63	104	85·6	Normal

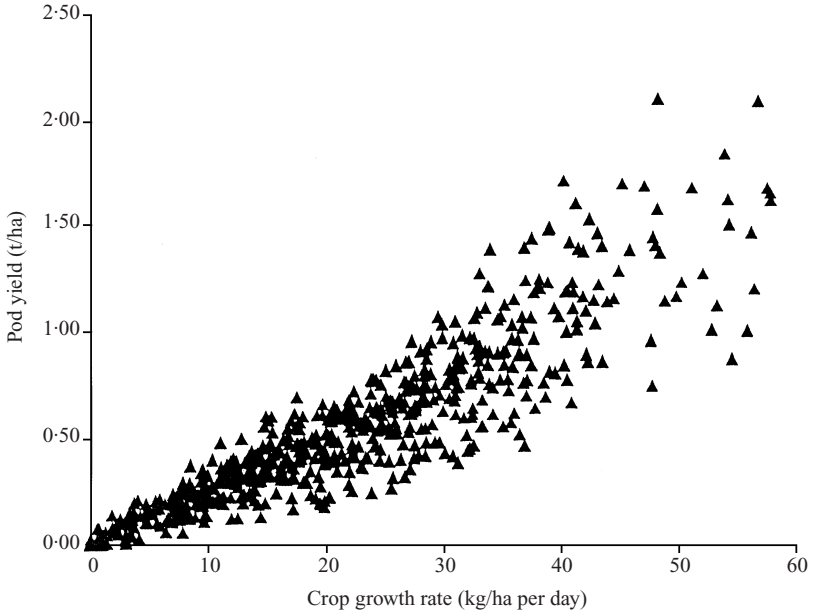

Fig. 2. Relationship between pod yield (t/ha) and crop growth rate (kg/ha per day) in 625 groundnut genotypes.

genotype with pod yield of > 1 t/ha was considered high yielding in this environment. The partitioning coefficient of 0·50 was close to the average of the experiment. Thus genotypes in group 1 were those with high pod yield and above average partitioning, group 2 included those genotypes with above average partitioning but low pod yield, group 3 contained those with high yield but below average partitioning and group 4 were genotypes with low pod yield and below average partitioning. From each group, four genotypes were selected for further testing.

Experiment 2: Evaluation of selected genotypes

The 16 genotypes selected from the previous season were sown on 15 February 1992 in a randomized complete block design with four replications. The plot size was 4 rows 4 m long and seeds were sown on ridges 0·75 m apart and 0·10 m within the ridge. Cultural practices and data recording were as in Expt 1. The data were subjected to standard analysis of variance using GENSTAT statistical procedures.

Experiment 3: Genotype × sowing date responses

To examine the possible genotype by temperature interactions, a date of sowing experiment was conducted using 10 of the 16 genotypes in Expt 2. The choice of these genotypes was based on the availability of enough seed. The genotypes were sown at four different dates (5 and 26 November, 17 December 1993 and 26 January 1994). A randomized complete block with treatments in a split-plot pattern was used, with sowing dates as main plots and genotypes as subplots with four replications. Subplots were four rows 5 m long with inter- and intra-row spacing of 0·75 m

and 0·10 m respectively. Irrigation, cultural practices and data collection were as in the other experiments. Statistical analysis was done using GENSTAT.

RESULTS

Experiment 1

Variation in characters measured was substantial (Table 2). Most genotypes produced pods ranging from 0·2 and 0·5 t/ha and only a few produced above 1·0 t/ha (Fig. 1). Despite the wide variation in yields, the large size of the experiment produced a standard error, which was able to show significant differences in the transformed pod yield between genotypes. However, this was confounded by the large variation in the number of plants per plot (Table 2), and on the yield alone the data could not determine whether a variety yielded poorly because of its plant population or its genotypic attributes.

By computing the model parameters contributing to yield and analysed separately C was a powerful factor influencing pod yield (Fig. 2). Although there were differences in crop growth rates between genotype, these were partly a reflection of differences in plant stand at harvest and plant number was a significant covariate in the yields. When pod yield was analysed with crop growth rate as a covariate, the frequency distribution changed and the coefficient of variation was reduced from 36 to 18% (Table 3). Partitioning data were normally distributed, and significant differences between genotypes were also found. Most genotypes partitioned 0·40 to 0·60. A negligible percentage partitioned less than 0·2 and

Table 3. *Distribution of sums of squares between factors and covariate in the analysis of variance*

Source	D.F.	Square root pod yield	Partitioning	D.F	Square root pod with C as covariate
Replication	2	2·144	0·499	2	2·144
Covariate	—	—	—	1	51·700
Genotypes	624	119·318	33·400	623	28·989
Residual	1208	68·810	21·677	1208	17·108
CV%		36	28		18

Table 4. *Pod yield* (*t/ha*), *partitioning*, *crop growth rate*, *CGR* (*kg/ha per day*) *and reproductive duration* (*days*) *of 16 contrasting genotypes in 1991 and 1992*

	Pod yield		Partitioning		CGR		Reproductive duration	
Genotype	1991	1992	1991	1992	1991	1992	1991	1992
High/high								
MF-47	1·68	0·60	0·67	0·53	44·8	24·3	95	86
55-437	1·47	0·71	0·64	0·55	38·5	23·9	95	84
796	1·43	0·69	0·65	0·60	37·1	21·4	96	84
ICGV 88461	1·70	0·66	0·63	0·53	39·8	20·6	108	98
High/low								
ICGV-SM 86775	1·67	0·55	0·45	0·47	46·7	21·7	103	99
ICG 1697	1·60	0·47	0·47	0·43	53·9	21·1	75	65
IBPGR42	1·94	0·55	0·33	0·28	83·4	43·9	96	86
ICG 9819	1·58	0·57	0·48	0·51	20·2	27·9	94	84
Low/high								
ICG 1622	0·62	0·34	0·55	0·65	20·6	13·5	92	84
ICG 1236	0·39	0·71	0·56	0·56	12·3	37·0	95	86
ICG 2058	0·54	0·51	0·54	0·56	17·5	23·2	93	84
ICGV 85033	0·42	0·18	0·51	0·62	20·6	9·7	89	76
Low/low								
ICGV 87303	0·67	0·99	0·38	0·34	27·8	53·1	97	84
CS 11	0·42	0·10	0·41	0·33	18·2	8·9	74	64
ICG 7899	0·55	0·24	0·40	0·37	23·2	25·0	92	85
ICG1576	0·57	0·38	0·38	0·40	22·7	24·5	78	63
S.E. (1208 D.F. in 1991 and 48 D.F. in 1992)	0·235	0·045	0·065	0·006	7·82	4·85	4·0	3·9
Means	0·55	0·52	0·41	0·51	21·47	24·40	77	78

Table 5. *Effect of genotype and date of flowering and reproductive duration of 10 groundnut genotypes in 1993/94*

Genotype	Days to flower					Days to maturity				
	5 Nov	26 Nov	17 Dec	26 Jan	Mean (genotype)	5 Nov	26 Nov	17 Dec	26 Jan	Mean (genotype)
MF-47	33	40	46	41	40	113	104	115	98	108
55-437	34	40	46	41	40	116	111	115	105	112
796	31	41	42	38	38	113	102	115	103	108
ICGV 88461	38	44	53	47	46	130	130	141	121	131
ICGV-SM 86775	45	47	52	45	47	139	139	139	133	138
ICG 9819	33	41	46	42	40	118	130	134	114	124
ICG 1622	33	41	45	42	41	118	114	111	105	112
ICG 2058	33	40	46	42	40	113	109	115	103	110
ICGV 87303	35	45	45	43	44	137	143	141	121	136
ICG 1576	33	41	45	43	40	123	123	122	124	123
Mean (dates)	35	42	47	43	42	122	121	125	113	120
	s.e. between dates 0·28 (9 d.f.), between genotypes 0·43 (9 d.f.), genotypes × dates 0·86 (108 d.f.)					s.e. between dates 2·2 (9 d.f.), between genotypes 1·9 (9 d.f.), genotypes × dates 3·9 (108 d.f)				

Table 6. *Effect of genotype and sowing date on pod yield and partitioning in 10 groundnut cultivars*

Genotype	Pod yield					Partitioning				
	5 Nov	26 Nov	17 Dec	26 Jan	Mean (genotype)	5 Nov	26 Nov	17 Dec	26 Jan	Mean (genotype)
MF-47	2·57	2·49	1·73	1·32	2·03	0·82	0·97	1·03	0·80	0·90
55-437	2·29	2·15	1·71	1·04	1·80	0·73	0·93	0·85	0·76	0·84
796	2·37	2·48	1·80	10·8	1·93	0·76	0·95	0·90	0·82	0·86
ICGV 88461	2·56	2·31	1·55	1·52	1·99	0·75	0·72	0·97	0·80	0·81
ICGV-SM 86775	1·79	2·24	1·83	0·65	1·63	0·76	0·72	0·87	0·51	0·72
ICG 9819	1·07	1·15	0·95	0·91	1·02	0·48	0·54	0·69	0·62	0·59
ICG 1622	2·32	1·94	1·71	1·42	1·85	0·64	0·86	0·90	0·88	0·82
ICG 2058	2·76	2·45	1·23	1·34	1·85	0·81	0·94	0·93	0·85	0·88
ICGV 87303	2·17	2·11	1·15	0·64	1·52	0·65	0·68	0·67	0·42	0·60
ICG 1576	2·14	1·69	1·39	0·85	1·52	0·59	0·63	0·66	0·63	0·63
Mean (dates)	2·20	2·10	1·51	1·08	1·72	0·70	0·79	0·86	0·71	0·76
	s.e. between dates 0·190 (9 d.f.), between genotypes 0·120 (9 d.f.), genotypes × dates 0·240 (108 d.f.)					s.e. between dates 0·029 (9 d.f.), between genotypes 0·022 (9 d.f.), genotypes × dates 0·043 (108 d.f.)				

there were some that partitioned above 0·80. Several genotypes with low yield were found to have high partitioning. The p was only poorly related to plant stand and the differences between genotypes have been attributed mostly to genotype effects. Reproductive duration ranged from 63 to 104 physiological days.

The impact of the use of the physiological model in the interpretation of the data is provided by examining the effects of selecting on yield alone, compared to that of involving partitioning and yield (Fig. 1). Genotypes in group 1 were considered high yielding with above average partitioning. This group included genotypes such as 796, 55-437, 4-2-12-7, 4-4-4-20, MF 47 and ICGV 88461. Group 2 are genotypes with low pod yield and high partitioning. This group consisted mainly of germplasm lines, but none of which originated from West Africa. These lines would have been discarded based on yield alone. Group 3 represents genotypes with high pod yield but low partitioning. This included a mixture of germplasm (e.g. ICG 1697 and IBPGR 42) and breeding lines (e.g. ICGV MS 86775 and ICGV 88427). Genotypes in group 4 were considered low yielding with below average partitioning. Such genotypes would require no further investigation.

Experiment 2

The performance of the 16 genotypes is presented in Table 4. Pod yield was lower and variable in 1992 compared to the previous season. The correlation between seasons was not significant for pod yield ($r =$ 0·40; D.F. 14), C ($r = 0{\cdot}30$; D.F. 14), and D_r (0·36, D.F. 14). When p of the genotypes in 1992 was compared with the 1991 values there was a significant correlation ($r = 0{\cdot}84$, $P = 0{\cdot}001$), indicating that the ranking of genotypes was fairly similar in both seasons.

Experiment 3

Maximum and minimum temperatures during the experiment are shown in Table 1. Cool night temperatures characterize December and January. All genotypes took a shorter time to flower when sown in early November (Table 5). Genotypes ICGV 88461 and ICGV-SM 86775 took longest to flower. Days to maturity ranged from 108 to 138. Groundnut sown at the end of January averaged 113 days to maturity, while sowing in November and December averaged 122 and 125 days respectively.

Both sowing dates and genotypes had a significant ($P < 0{\cdot}01$) effect on pod yield (Table 6). Pod yield of most cultivars declined by more than 50% from sowing in November to end of January. The interaction of cultivars with sowing date was not significant. Crop growth rate followed a similar trend, showing a decline from 51·0 kg/ha per day in the November sowing to 38·0 kg/ha per day in late January sowing. However genotypes differed in the magnitude of both pod yield and crop growth rate decline as sowing was delayed till the end of January. For example the pod yield decline ranged from 15% for ICG 9819 to 71% for ICGV 97303. Partitioning was slightly affected by sowing date but was highest when sowing was done in December.

DISCUSSION

The large variation in crop growth rate, partitioning and pod yield in Expt 1 indicated genetic differences among genotypes in their adaptation to high temperatures. Although the genotypes used in this study differed in maturity, escape (where a genotype would escape high temperature periods) did not appear to be a major factor influencing classification of genotypes. The trial was designed to ensure that flowering and pod initiation in all genotypes occurred during the hottest months (March and April). In addition the correlation between reproductive duration and pod yield was not significant.

The classification of genotypes into four groups demonstrated the impact of the physiological model in the selection of genotypes. The released cultivars (796 and 55-437) in group 1 are considered to be specifically adapted to dry conditions and thus tolerant to high temperatures. Heat tolerance of cultivar 55-437 was also reported by Wheeler *et al.* (1997). Genotypes in group 2 would have been discarded on the basis of their low pod yield. Their high partitioning however, suggests that such genotypes would require further investigation. The majority of the genotypes in group 3 probably derive their high yield from better radiation interception. The possible existence of genotypes that may have better radiation-use-efficiency would justify further investigation of the genotypes. The extreme genotypes in this group are of interest because they apparently achieved high yield by exploiting mechanisms different from those common to most genotypes. Such genotypes had superior growth rates under these adverse conditions and suggest the possibility of combining superior p and C under high temperature conditions. Crossing between parental lines from group 2 and 3 would achieve this.

The significant inter-year correlation for partitioning in Expt 2 indicated stability of p across seasons and would be a more reliable selection criterion for identification of groundnut genotypes tolerant to heat than is yield. Although the methodology is unable to provide an accurate value for p, it provides estimates by which the relative performance of genotypes can be assessed. Partitioning is positively correlated with yield under high temperature and water deficit field conditions (Greenberg *et al.* 1992; Ndunguru *et al.* 1995). It also appears to be a good indicator of high

temperature stress in the experiments reported here. These results suggest partitioning as a screening tool for development of heat-tolerant genotypes, especially in the Sahelian environment, where conditions are not generally ideal for groundnut growth.

Results from the date of sowing experiment indicate that temperature has a significant effect on the phenology and productivity of groundnuts. This is consistent with results reported by Ntare *et al.* (1998). The delayed flowering in late November and December sowings may be partly due to low night temperatures during this period. This temperature effect was, however, beneficial in that it resulted in higher growth rates. The reduced pod yield and growth rates were associated with high temperature during flowering (end of January sowing) relative to sowing in early November. In the latter case flowering occurred when diurnal temperatures were on the cooler side in December (Table 1). Pod yield of genotypes was reduced by 50%. Flowering and pod formation of groundnuts sown in January coincides with supra-optimal temperatures in March and April and reduces early reproductive yield in both cultivars. Average maximum/minimum temperatures of 40/23 °C characterized this period. These are in agreement with those of Ketring (1984) who reported that 35/22 °C reduced the number of pegs by 33% relative to 30/22 °C. Similarly Vara Prasad *et al.* (1999) reported a 50% reduction in pod yield at 38/22 °C relative to 28/22 °C under controlled conditions.

This study reveals that estimates of p can facilitate the determination of the relative performance of genotypes under high temperatures. This supports the assumption that in the harsh Sahelian environment, the majority of environmental effects are expressed through variations in C, while the majority of genetic effects are expressed as p. Further research on this aspect is of considerable significance not only in crop modelling, but also in developing methodology for selecting genotypes for adaptation to variable temperatures.

The results of this study have implications for groundnut breeding programmes in the Sahel. It is possible to grow three generations in one year by exploiting the cool and hot months of the dry season under irrigation. This should bring about faster progress in breeding, but would apply selection pressure for high temperature tolerance.

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