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Response of peanut genotypes to mid-season moisture stress: phenological, morpho-physiological, and yield traits

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Abstract. Nine peanut genotypes were evaluated in two seasons under irrigated and simulated mid-season drought conditions to investigate the influence of water stress on some phenological, morpho-physiological, and yield traits. Analysis of variance revealed significant genotypic differences for all the traits studied. Water saturation deficit and epicuticular wax load increased in response to water stress and age of the crop, while specific leaf area decreased with water stress and age of the crop. In general, correlations of water saturation deficit (WSD), epicuticular wax load (EWL), and specific leaf area (SLA) with yield traits were fairly weak. WSD in the early stage under irrigated conditions was found to be positively associated with pod yield under water stress; EWL in the early stage was negatively associated with harvest index (HI) under stress. Although significant and negative correlations of SLA were found only when it was recorded in the early stage under stress and the later stage under irrigated conditions with HI and pod yield (PY), both under irrigated conditions, the trends of its associations showed that SLA had rather weak and negative correlations with PY and HI both under irrigated and stress conditions. Genotypes that accumulated flowers sooner after initiation showed less yield reduction. The negative association between HI under stress and its reduction deems HI under moisture stress an important criterion of selection for drought tolerance in peanut.

Additional keywords: drought tolerance, epicuticular wax load, harvest index, specific leaf area, water saturation deficit, pod yield.

Introduction

In tropical, subtropical, and warm temperate regions of the world, where peanut (*Arachis hypogaea* L.) is grown, drought is one of the prevalent yield-reducing abiotic stress factors as rainfall in these regions, particularly at the time of pod formation and its development, is erratic in most years and temperatures are high. The inherent capacity of peanut to moderately sustain drought renders it to be grown largely under rain-dependent conditions, especially by the resource-poor farmers, resulting in low productivity. This situation warrants enhanced impetus in breeding peanut varieties that would yield satisfactorily under water-limited conditions, or in other words, tolerant to drought.

Drought tolerance in peanut can be enhanced by improvement in soil water extraction capability (Wright and Nageswara Rao 1994), or in water-use efficiency (WUE), or both (Hebbar *et al*. 1994). It has been hypothesised that improving WUE would be the best strategy to cope with occurrence of intermittent droughts. Indeed, previous research intended to enhance the drought tolerance of peanut has led to the selection of transpiration efficiency (TE) as an important component trait of WUE and designated it as a major source of yield variation under drought stress (Nageswara Rao and Wright 1994; Wright *et al*. 1994). The growing need to find non-destructive and less laborious methods of selection for improved TE, has led to the identification of surrogate traits that are closely related to TE, such as specific leaf area (SLA) (Nageswara Rao and Wright 1994; Wright *et al*. 1994), carbon isotope discrimination ($\Delta^{13}C$) (Hubick *et al*. 1986; Wright *et al*. 1994), SPAD Chlorophyll Meter Reading (SCMR) (Nageswara Rao *et al*. 2001; Bindu Madhava *et al*. 2003), and specific leaf nitrogen (SLN) (Nageswara Rao *et al*. 2001; Sheshshayee *et al*. 2006). Also, the subsequent finding of low SLA genotypes with greater photosynthetic capacity per unit leaf area (Nageswara Rao *et al*. 1995) further strengthened the proposition of using leaf thickness (low SLA) as a selection criterion for enhancing TE in peanut. SLA is an inexpensive and easy to measure trait, often used for screening for improved drought resistance in peanut (Nageswara Rao *et al*. 2000), and is significantly negatively correlated with SCMR (Nigam and Aruna 2008).

The epicuticular wax acts as the first protective barrier that regulates non-stomatal water loss. It is now well established that epicuticular wax helps leaves in retention of water (Jordan *et al*. 1984) by minimising cuticular transpiration (Jefferson *et al*. 1989; Premachandra *et al*. 1992). Higher levels of leaf epicuticular wax have been shown to be associated with seedling drought tolerance in *Eragrostis lahmanniana* Nees (Wright and

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Dobrenz 1973), with relative drought tolerance in oat (*Avena sativa* L.) cultivars (Bengston *et al.* 1978), and with greater WUE in wheat (*Triticum aestivum* L.) (Johnson *et al.* 1983). In peanut, Samdur *et al.* (2003) reported genotypic differences for epicuticular wax as well as its increase with crop age.

Partitioning of assimilates as measured through harvest index (HI) has the greatest effect on pod yield in peanut (Duncan *et al.* 1978). Low to moderate variation has been reported for HI in peanut (Dhopte and Zade 1981; Murty *et al.* 1983; Velu and Gopalkrishnan 1985; Sharma and Varshney 1995). However, the influence of water-deficit stress, if any, on the HI of peanut, is not very well understood.

Peanut, being an indeterminate legume, tends to have longer flowering duration, thereby producing flowers in high number. However, reproductive efficiency of peanut in converting flowers into mature pods is much lower (Coffelt *et al.* 1989; Lal *et al.* 1998). Furthermore, days to flower initiation and duration for accumulation of first 25 flowers in a genotype have been suggested as component traits of early maturity in peanut (Upadhyaya and Nigam 1994). Therefore, study of these two traits of early maturity and also determinants of reproductive efficiency in relation to drought stress, becomes imperative.

Although aforementioned morpho-physiological adaptations that impart drought tolerance to crop plants are known, a comprehensive understanding of the relative contributions of various factors that enhance drought tolerance in peanut is lacking. Similarly, the response of peanut plants with respect to traits under controlled conditions of irrigation and with stress over years has not been examined, although several studies have reported the effect of drought on SLA, water saturation deficit (WSD), yield, or related traits.

Although several studies have examined the effects of SLA, SCMR on WUE, and alterations in yield components on final yield under field conditions, few have simultaneously examined what happens under controlled conditions of irrigation and water stress over several years. The aim of this work was to study the effect of mid-season drought on WSD, epicuticular wax load (EWL), SLA, flowering pattern, and yield traits in different peanut genotypes under irrigated and water stress conditions, and to examine their inter-relationships.

Materials and methods

Trials were conducted for 2 years (2002 and 2003) in the post-rainy season (February–June) at the experimental farm of the Directorate of Groundnut Research (DGR) (formerly National Research Centre for Groundnut), Junagadh, India (21°31′N, 70°36′E; alt. 61 m). The soil was a Vertisol Ustochropt (pH 7.5) with low organic matter, available nitrogen, and phosphorus contents.

A cultivator was used for land preparation. With the help of a furrow-opener, furrows were opened at 45-cm spacing, deep enough to allow the placement of seed at 50 mm depth. Before sowing, fertiliser (25 N : 50 P : 0 K) was applied in furrows (37.5 g/m^2). Sowing was done manually in the second week of February every year, maintaining a population density of 22 plants/m^2.

The genotypes grown were 6 improved lines (PBS 11023, PBS 11049, PBS 12115, PBS 21042, PBS 21050, and Code 9) with good agronomic traits developed at DGR, one germplasm line (NCAc 17090) originating in Peru, and 2 commercial varieties (J 11 and GG 2) popular in the region. Code 9 is an inter-specific derivative of *Arachis hypogaea* × *A. cardinasii*. The variety GG 2 is known to have tolerance to drought.

The plants were grown in a field, which was divided into 2 areas (irrigated and water stress conditions) separated by a 3-m-wide central corridor. The irrigated plots (controls) were regularly irrigated at 7–8 day intervals. The water stress plots were irrigated at regular 7–8 day intervals up to 40 days after sowing (DAS), irrigation discontinued up to 75 DAS, followed by resumption of regular irrigation to simulate mid-season water stress. The simulated water stress period (40–75 DAS) corresponded to peg and pod formation, and the pod development stage of the crop. Individual genotypes were grown in 6 rows each of 3 m length arranged in 3 replications in both the irrigated and water stress plots. Within the replication, each genotype was distributed randomly. Every genotype occupied an area of 8.1 m^2 in each replication.

Observations on SLA, WSD, and EWL were recorded at two stages, i.e. at 55 DAS (stage I) and 75 DAS (stage II, before relieving the plants of water-deficit stress). The second fully opened leaf from the apex of the main stem of the 5 randomly selected plants in each replication in both the control and water stress plots was sampled in the morning (08:00–09:30 hours). Leaf area of these leaves was measured with a LI3100 leaf area meter (LI-COR Inc., Lincoln, NE, USA). Leaves were then oven-dried at 60°C for 72 h and weighed. Specific leaf area (cm^2/g) was calculated as the ratio of leaf area to leaf dry weight. Three leaflets each from the 3rd to 5th (top to bottom) leaves were collected from 10 different plants of a genotype from each treatment and used immediately for determination of WSD (%) and EWL (mg/dm^2). Five plants randomly selected at maturity were used to record biological yield (BY, g/plant) and workout HI (%) based on pod yield (PY, g/plant). Harvest index was calculated by dividing PY by total BY and expressed as percentage. Pod yield of each genotype was recorded on 4 rows and converted into kg/ha. The border rows of the plots were not considered for any sampling.

From the lamina of each leaflet (excluding the midrib), 10-mm-diameter discs were obtained with a leaf punch and then 30 such leaf discs were used for determination of EWL by the colourimetric method (Ebercon *et al.* 1977). The moisture status of leaves was determined by the method of Barrs (1968) and expressed as WSD, which was calculated as follows:

$$\text{WSD}(\%) = [(\text{turgid weight} - \text{initial weight})/(\text{turgid weight} - \text{dry weight})] \times 100$$

where initial weight is the weight of leaves at the time of sampling in the field, turgid weight is the weight of leaves recorded 6 h after immersion of these leaves in water (so as to allow all the cells to acquire full turgidity), and dry weight is the weight of leaves dried in the oven at 60°C for 72 h.

To estimate days to flower initiation (DFI), number of days between the sowing date and the time at which 50% of the plants on a plot basis had initiated flowering was counted. Observations on the days for accumulation of 25 flowers from appearance of the first flower (DF_{25}) were recorded on the 5 randomly selected plants in each genotype and replication in the control as well as water stress plots.

At the time of sampling of leaves, soil samples from the upper layer (0–0.15 m) and lower layer (0.15–0.30 m) were also taken from each treatment for determination of gravimetric soil moisture content. Observations on daily maximum and minimum temperatures and relative humidity during the experiment were also recorded and averaged over standard weeks.

Statistical analysis of the experimental data was performed as outlined by Gomez and Gomez (1984) for variance analysis. Pearson correlation coefficients were calculated to examine relationships among the phenological, morpho-physiological and yield traits. Mean comparisons were carried out to estimate differences between years, treatments, and genotypes, using Duncan's test or l.s.d. values.

Results

Soil moisture content

Moisture content averaged across the upper and lower layers of the soil under irrigated and water stress conditions at stage I and stage II recorded in the growing seasons of 2002 and 2003 is shown in Table 1. It was observed that irrigated plots in 2002 had moisture contents of 18.8% (stage I) and 15.7% (stage II) and the corresponding values for the water stress plots were 7.6% and 6.7%, respectively. In 2003 a similar pattern was found, but the moisture content remained slightly higher in both the control and stressed plots than in the previous year. Control plots recorded moisture contents of 22.1% (stage I) and 21.0% (stage II) and the corresponding values for the water stress plots were 12.9% and 10.7%, respectively (Table 1).

Weather parameters

The minimum temperature in 2002 ranged from 13.1 to 27.6°C and the maximum temperature was between 29.2 and 44.8°C (Fig. 1*a*). During 2003, the minimum and maximum temperatures ranged from 14.8 to 26.6°C and from 32.7 to 43.2°C, respectively. The maximum temperature in 2002 was recorded during the 18th standard week and in 2003 it was recorded during the 17th week. The relative humidity in 2002 varied between 12 and 44% (min.) and 40 and 83% (max.). In 2003, the corresponding values were 5 and 43% (min.) and 32 and 83% (max.). Humidity varied much more widely in 2003 than in 2002 (Fig. 1*b*).

Table 1. Moisture content of soil, and morpho-physiological traits (averaged over genotypes) under irrigated and water stress conditions
WSD, Water saturation deficit; EWL, epicuticular wax load; SLA, specific leaf area

	Stage I			Stage II		
	Irrigated	Stress	Difference	Irrigated	Stress	Difference
			Soil moisture (%)			
2002	18.77	7.64	11.13	15.65	6.74	8.91
2003	22.05	12.90	9.15	21.00	10.70	10.30
			WSD (%)			
2002	3.78	8.80	5.02	5.57	11.19	5.62
2003	2.90	7.08	4.18	6.34	12.57	6.23
Mean	3.34	7.94	4.60	5.96	11.88	5.92
			EWL (mg/dm^2)			
2002	2.49	3.12	0.63	2.59	3.13	0.54
2003	1.56	1.97	0.41	2.09	2.31	0.22
Mean	2.03	2.55	0.52	2.34	2.72	0.38
			SLA (cm^2/g)			
2002	128.2	117.9	10.3	114.8	104.7	10.1
2003	129.8	118.1	11.7	116.1	113.3	2.8
Mean	129.0	118.0	11.0	115.5	109.0	6.45

Analysis of variance

Analysis of variance of data pooled over 2 years revealed that, except for DFI, expression of all the traits under irrigated conditions was significantly ($P<0.01$) different from what was observed under water stress. Significant ($P<0.01$) variation due to stage of the crop was observed in all 3 morpho-physiological traits (EWL, SLA, and WSD). Except for yield traits (PY, BY, and HI), differences due to years were significant for all traits studied ($P<0.01$). Significant ($P<0.01$) variations due to interactions between different sources of variation (year, irrigation treatments, growth stages, and genotypes) were also observed (Table 2).

Phenological traits

The DFI is depicted in Fig. 2*a*. Mean values of DFI for each genotype were obtained across the replications, irrigation

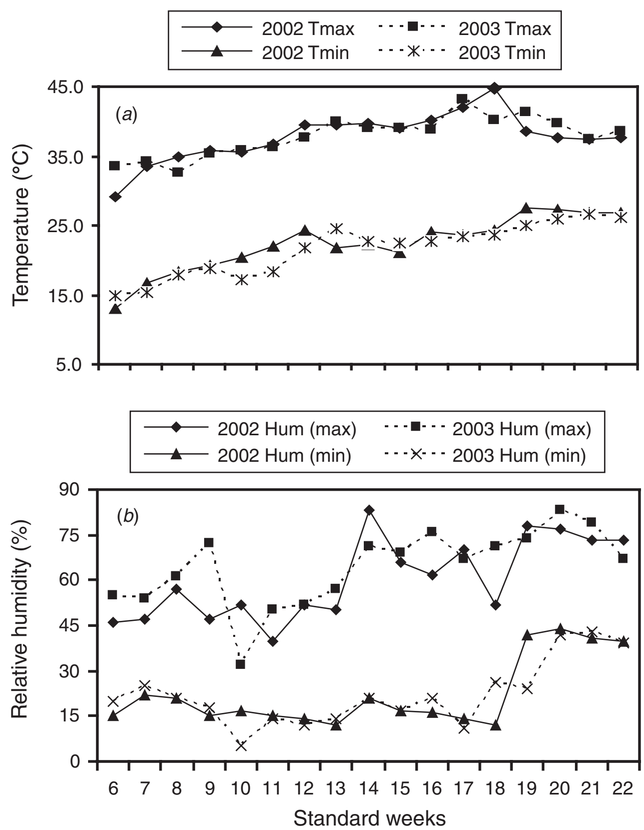

Fig. 1. (*a*) Daily maximum and minimum temperature averaged over standard weeks for the 2002 and 2003 growing seasons. (*b*) Daily maximum and minimum relative humidity averaged over standard weeks for the 2002 and 2003 growing seasons.

Table 2. Analysis of variance for phenological, morpho-physiological, and yield traits for the pooled data

d.f., Degrees of freedom; WSD, water saturation deficit; EWL, epicuticular wax load; SLA, specific leaf area; DFI, days to flower initiation; DF_{25}, days to accumulation of 25 flowers after flower initiation; PY, pod yield; BY, biological yield; HI, harvest index. $^{**}P < 0.01$; n. s., not significant at $P = 0.01$

Source of variation	d.f.	Mean sum of squares							
		WSD (%)	EWL (mg/dm^2) ($10^{-2} \times N$)	SLA (cm^2/g)	DFI	DF_{25}	PY (kg/ha)	BY (g/plant)	HI (%)
Replication	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Irrigation treatments (E)	1	1497.0**	1085**	1800**	n.s.	3**	52 745 405**	4263**	3137**
Growth stages (S)	1	579.0**	315**	3909**	–	–	–	–	–
E × S	1	n.s.	n.s.	1263**	–	–	–	–	–
Year (Y)	1	0.7**	4311**	4300**	n.s.	n.s.	n.s.	n.s.	n.s.
E × Y	1	n.s.	n.s.	1471**	n.s.	94.54**	232**	n.s.	3**
S × Y	1	76.0**	125**	99**	–	–	–	–	–
E × S × Y	1	7.0**	2**	n.s.	–	–	–	–	–
Genotypes (G)	8	18.8**	43**	2152**	42**	11.7**	1 373 268**	65**	392**
E × G	8	n.s.	4**	n.s.	n.s.	3.8**.	n.s.	13**	n.s.
S × G	8	19.5**	3**	111**	–	–	–	–	–
E × S × G	8	n.s.	n.s.	n.s.	–	–	–	–	–
Y × G	8	22.3**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
E × Y × G	8	n.s.	3**	n.s.	n.s.	2.14**	n.s.	10**	n.s.
S × Y × G	8	n.s.	4**	165**	–	–	–	–	–
E × S × Y × G	8	n.s.	n.s.	146**	–	–	–	–	–

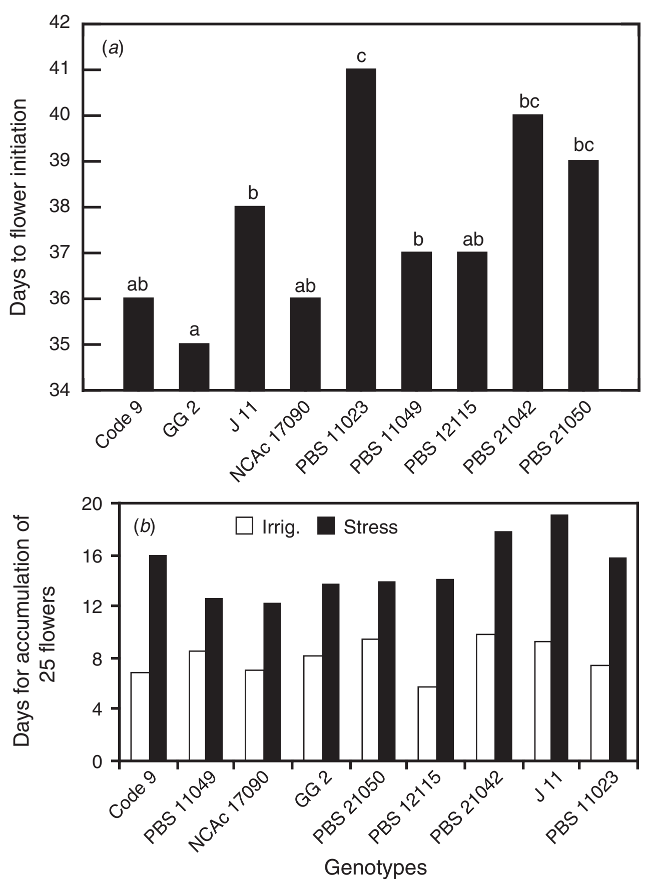

Fig. 2. (*a*) Days required for flower initiation in 9 peanut genotypes. Genotypes with the same letter are not significantly different at $P = 0.05$ (Duncan's test). The number of days are means of 2 years across irrigation treatments. (*b*) Days required for accumulation of 25 flowers in 9 peanut genotypes under irrigated and water stress conditions. The number of days is means of 2 years.

treatments (control and water stress) and years because all 3 sources of variation were not found to be significant for this trait, although there was significant genotypic variation ($P < 0.01$). Differences between the earliest (GG 2) and the latest (PBS 11023) genotypes were 6 days. Duncan's test revealed that GG 2, the earliest to initiate flowering, was on par with NCAc 17090 and Code 9, whereas PBS 11023, the latest in flower initiation, was on par with PBS 21042 and PBS 21050.

The DF_{25} under irrigated and water stress conditions was calculated for each genotype (Fig. 2*b*). Differences due to genotypes ($P < 0.001$) and irrigation treatments ($P < 0.05$) were highly significant. Since differences between years were not significant for this trait the values were taken as mean across years. Genotypes PBS 12115, NCAc 17090, and Code 9 were the earliest flowering genotypes under irrigated conditions, whereas under water stress, NCAc 17090 was the earliest followed by PBS 11049, PBS 12115, GG 2, and PBS 21050.

Morpho-physiological traits

Mean values obtained for morpho-physiological traits (WSD, EWL, and SLA) across genotypes at stage I and stage II under irrigated and water stress conditions in the growing seasons of 2002 and 2003 are given in Table 1. The WSD in the leaves was significantly higher under stress compared with the irrigated crop, and it increased significantly with increase in age of the crop in both years, indicating that the crop was actually experiencing water-deficit stress. Similar trends were observed for EWL, which increased in response to water stress and also with increase in age of the crop (Table 1). In the case of SLA, the pattern of its response to water stress and age of crop was opposite to that observed for WSD and EWL. Specific leaf area in genotypes decreased in response to water stress and age of crop (Table 1).

Water saturation deficit (WSD)

The WSD differed significantly with genotype and was in the range of 5.84 (PBS 11023) to 8.03% (GG 2), averaged over seasons and stages. The WSD increased significantly from 5.64 to 8.92% with increasing age of the crop. WSD was higher in 2002 (7.33%) than in 2003 (7.22%), this difference being significant. The imposition of water stress caused a significant increase in WSD from 4.65 (irrigated) to 9.91% (stress) (Table 3). This increase in WSD due to moisture stress was observed in all genotypes at both stages. Increase in WSD with age of the crop was also observed in all genotypes under both irrigated and stress conditions. However, in the case of Code 9 and PBS 11049 the increase observed from stage I to stage II under stress was only marginal (Table 4).

Table 3. Mean values of nine peanut genotypes for morpho-physiological and yield traits pooled over seasons and stages under irrigated and water stress conditions

WSD, Water saturation deficit; EWL, epicuticular wax load; SLA, specific leaf area; PY, pod yield; BY, biological yield; HI, harvest index. Means followed by the same letter are not significantly different at $P < 0.05$ (Duncan's test)

Source of variation	WSD (%)	EWL (mg/dm^2)	SLA (cm^2/g)	PY (kg/ha)	BY (g/plant)	HI (%)
Genotypes						
Code 9	7.71b	2.31a	100.75a	1894c	28.5b	30.6b
GG 2	8.03b	2.40ab	121.25c	1926c	25.8ab	29.4b
PBS 11023	5.84a	2.51b	124.00cd	1680bc	32.7c	22.4ab
PBS 12115	7.05ab	2.27a	120.50c	1665bc	28.6b	28.8b
NCAc 17090	7.52b	2.38ab	131.25d	1131ab	27.7ab	26.5b
J 11	6.97ab	2.28a	124.50cd	1062a	26.2ab	24.4ab
PBS 21050	6.58ab	2.62b	114.75b	1411b	24.9ab	21.2a
PBS 11049	7.9b	2.34a	109.25b	1946c	25.8ab	30.7b
PBS 21042	7.92b	2.59b	114.50b	1562bc	24.0a	25.6ab
Mean	7.28	2.41	117.86	1586	27.1	26.6
CD (5%)	1.521	0.131	7.42	346.2	4.07	5.14
Age of the crop						
Stage I	5.64a	2.29a	123.50b			
Stage II	8.92b	2.53b	112.22a			
Mean	7.28	2.41	117.86			
CD (5%)	0.717	0.063	3.49			
Year of experimentation						
2002	7.33b	2.86b	116.40a	1556a	25.12a	26.8a
2003	7.22a	1.96a	119.33b	1616a	29.10a	26.4a
Mean	7.275	2.41	117.86	1586	27.11	26.6
CD (5%)	0.09	0.063	2.89	176.1	4.03	5.74
Irrigation treatments						
Irrigated	4.65a	2.19a	122.23b	2184b	32.72b	31.5b
Stress	9.91b	2.64b	113.50a	988a	21.50a	21.7a
Mean	7.275	2.41	117.86	1586	27.11	26.6
CD (5%)	0.09	0.063	2.89	161.9	1.99	1.74

Table 4. Yield traits of peanut (averaged over genotypes) in irrigated (Irrig.) and water stress conditions

PY, Pod yield; BY, biological yield; HI, harvest index. Values in parentheses indicate reduction (%) in stress compared with irrigated conditions

Year	PY (kg/ha)		BY (g/plant)		HI (%)	
	Irrig.	Stress	Irrig.	Stress	Irrig.	Stress
2002	2165	947 (56.26)	30.33	19.9 (34.38)	31.15	22.5 (8.65)
2003	2203	1029 (53.29)	35.1	23.1 (34.19)	31.90	20.9 (11.00)

Epicuticular wax load (EWL)

The EWL differed significantly with genotype and was in the range of 2.27 (PBS 12115) to 2.62 mg/dm^2 (PBS 21050). The EWL increased significantly from 2.29 (stage I) to 2.53 (stage II) mg/dm^2 with increasing age of the crop and was higher in 2002 than in 2003 irrespective of the irrigation treatments. The imposition of water stress caused a significant increase in EWL from 2.19 (irrigated) to 2.64 mg/dm^2 (stress) (Table 3). This increase in EWL due to imposition of moisture stress and with age of the crop (irrespective of the irrigation treatments) was observed in all genotypes. However, in the case of two genotypes there was either a slight decrease (2.85 to 2.75 mg/dm^2) or no change in EWL from stage I to stage II (in PBS 11023 and PBS 12115, respectively) under stress conditions (Table 4).

Specific leaf area (SLA)

The SLA differed significantly with genotype. Minimum SLA was observed in Code 9 (100.75 cm^2/g) and maximum in NCAc 17090 (131.25 cm^2/g). It decreased significantly with increasing age of the crop (stage I to stage II) and there was a significant difference between years. The SLA also decreased significantly due to water stress from 122.23 (irrigated) to 113.50 cm^2/g (stress) (Table 3). All genotypes recorded lower SLA under water stress than under irrigated conditions at stage I as well as at stage II and also with age of the crop, irrespective of irrigated or stress conditions, except genotype PBS 21042 where no change was observed under irrigated conditions with increase in age, and the corresponding change observed under stress conditions was only marginal (Table 4).

Yield traits

Pod yield (PY)

The PY differed significantly among genotypes and it varied from 1062 (J 11) to 1946 kg/ha (PBS 11049). Although mean PY across irrigation treatments and genotypes was higher in 2003 (1616 kg/ha) than in 2002 (1556 kg/ha), these differences due to year were not significant. The imposition of water stress caused a significant decline in PY from 2184 (irrigated) to 988 kg/ha (stress) (Table 3). Reduction in PY was observed in all genotypes, although its magnitude differed among genotypes. The highest reduction of ~68% in PY was observed in PBS 11023, from 2536 kg/ha (irrigated) to 823 kg/ha (stress) (Table 4). This was followed by Code 9 (60%) and J 11 (58%). The least reduction in PY due to imposition of water stress was observed in PBS 11049 (39%) followed by NCAc 17090 (46%) and GG 2 (49%). The percentage change in PY due to imposition of moisture stress varied only slightly (3%) between the two growing seasons (Table 5).

Biological yield (BY)

The BY differed significantly among genotypes and it varied from 24 (PBS 21042) to 33 g/plant (PBS 11023) and was significantly higher in 2003 (29 g/plant) than in 2002 (25 g/plant). The imposition of water stress caused a significant reduction in BY from 33 (irrigated) to 22 g/plant (stress). Seasonal variations observed for BY were not significant, although highly significant differences were

Table 5. Morpho-physiological and yield traits of peanut genotypes under irrigated (Irrig.) and stress conditions
WSD, Water saturation deficit; EWL, epicuticular wax load; SLA, specific leaf area; PY, pod yield; BY, biological yield; HI, harvest index; I, stage I; II, stage II

Genotypes and irrigation treatments		WSD (%)		EWL (mg/dm^2)		SLA (cm^2/g)		PY (kg/ha)	BY (g/plant)	HI (%)
		I	II	I	II	I	II			
Code 9	Irrig.	2.73	5.85	1.91	2.22	112	97	2706	33	36
	Stress	11.10	11.14	2.38	2.71	100	94	1081	25	25
	Mean	6.92	8.50	2.15	2.47	106	96	1894	29	31
GG 2	Irrig.	5.37	6.78	2.11	2.26	136	116	2553	30	37
	Stress	7.80	12.17	2.50	2.73	120	113	1299	22	22
	Mean	6.59	9.48	2.31	2.50	128	115	1926	26	29
PBS 11023	Irrig.	2.73	4.92	2.05	2.37	133	118	2536	38	30
	Stress	4.65	11.06	2.85	2.75	131	114	823	27	15
	Mean	3.69	7.99	2.45	2.56	132	116	1680	33	22
PBS 12115	Irrig.	3.10	8.30	1.79	2.26	140	116	2330	34	35
	Stress	5.91	10.88	2.52	2.52	115	111	1000	23	22
	Mean	4.51	9.59	2.16	2.39	128	114	1665	29	29
NCAc 17090	Irrig.	3.24	6.17	2.08	2.35	141	126	1468	33	27
	Stress	6.03	14.63	2.46	2.64	136	122	794	22	26
	Mean	4.64	10.40	2.27	2.50	139	124	1131	28	27
J 11	Irrig.	2.92	6.39	1.95	2.26	131	121	1490	32	27
	Stress	6.36	12.19	2.39	2.53	129	117	633	21	21
	Mean	4.64	9.29	2.17	2.40	130	119	1062	130	24
PBS 21050	Irrig.	2.94	3.80	2.20	2.58	128	111	1966	31	28
	Stress	9.03	10.54	2.73	2.98	117	103	856	19	15
	Mean	5.99	7.17	2.47	2.78	123	107	1411	25	21
PBS 11049	Irrig.	4.37	5.72	1.97	2.34	116	110	2417	33	32
	Stress	10.63	10.87	2.42	2.61	108	103	1474	19	29
	Mean	7.50	8.30	2.20	2.48	112	107	1946	26	31
PBS 21042	Irrig.	2.62	5.68	2.22	2.44	124	124	2192	31	32
	Stress	9.97	13.42	2.70	3.01	106	104	932	17	20
	Mean	6.30	9.55	2.46	2.73	115	114	1562	24	26
Grand mean	Irrig.	3.34	5.96	2.03	2.34	129	115	2184	33	32
	Stress	7.94	11.88	2.55	2.72	118	109	988	22	22

noticed between irrigated and stressed conditions within each season (Table 3). The reduction was observed in all genotypes, but its magnitude differed among genotypes (Table 4). The lowest reduction was recorded in Code 9 (24%), followed by GG 2 (27%) and PBS 11023 (29%). PBS 21042 registered the highest reduction (45%), followed by PBS 11049 (42%) and PBS 21050 (39%). The BY recorded in 2003 was higher than in 2002 under both irrigated and stress conditions, but reduction (34%) due to imposition of water stress was similar in both years (Table 5).

Harvest index (HI)

The HI also differed significantly among genotypes and it varied from 21.2 (PBS 21050) to 30.7% (PBS 11049). There was no effect of growing season on HI as the mean values obtained in 2002 (26.4%) and 2003 (26.8%) were statistically on par. However, imposition of water stress caused a significant drop in HI from 31.5 (irrigated) to 21.7% (stress) (Table 3). Change in HI was observed in all genotypes; however, its magnitude varied among genotypes (Table 4). The least difference was recorded in NCAc 17090 (1) followed by PBS 11049 (3) and J 11 (6). GG 2 and PBS 11023 recorded the highest difference (15). Although season did not contribute much to the variation in HI, the difference between HI obtained under irrigated and water stress conditions was more pronounced in 2003 (11) than in 2002 (8.65) (Table 5).

Relationship among phenological, morpho-physiological, and yield traits

Pearson's correlations of morpho-physiological traits (SLA, EWL, and WSD), studied between irrigation treatments and stages for a trait and among these traits, showed significant and positive correlations at stage I ($r = 0.78$, $P < 0.01$) and stage II ($r = 0.81$, $P < 0.01$), between the SLA recorded under irrigated and stress conditions. Between stages, positive and significant correlations were observed for SLA under irrigated ($r = 0.71$, $P < 0.01$) and stress ($r = 0.87$, $P < 0.01$) conditions, and for SLA observed at stage I under stress conditions and SLA observed under irrigated ($r = 0.67$, $P < 0.01$) and stress conditions ($r = 0.93$, $P < 0.01$) at stage II (Table 6). Similar associations were observed for EWL. However, in the case of WSD, such associations were not significant. When these correlations were studied among three morpho-physiological traits of the study, EWL at stage I under irrigated conditions was negatively and significantly associated with WSD observed under irrigated conditions at stage II ($r = -0.68$, $P < 0.05$).

Table 6. Correlation coefficients among morpho-physiological traits at stage I and II under irrigated and stress conditions

WSD, Water saturation deficit; EWL, epicuticular wax load; SLA, specific leaf area; I, irrigated; S, stress; Stg, stage. *$P < 0.05$; **$P < 0.01$

Trait	SLA-I-StgI	SLA-S-StgI	SLA-I-StgII	SLA-S-StgII	EWL-I-StgI	EWL-S-StgI	EWL-I-StgII	EWL-S-StgII	WSD-I-StgI	WSD-S-StgI	WSD-I-StgII
SLA-S-Stg1	0.78**										
SLA-I-Stg2	0.71*	0.67*									
SLA-S-Stg2	0.87**	0.93**	0.81**								
EWL-I-Stg1	0.01	0.11	0.35	0.01							
EWL-S-Stg1	0.20	0.18	0.27	0.03	0.55						
EWL-I-Stg2	–0.01	0.04	0.21	–0.13	0.75*	0.69*					
EWL-S-Stg2	–0.24	–0.29	0.02	–0.41	0.85**	0.67*	0.77**				
WSD-I-Stg1	0.11	0.00	–0.04	0.14	0.04	–0.33	–0.27	–0.22			
WSD-S-Stg1	–0.60	–0.43	–0.12	–0.50	0.32	0.06	0.58	0.44	–0.36		
WSD-I-Stg2	0.39	0.00	0.16	0.31	–0.68*	–0.53	–0.77**	–0.69*	0.26	–0.54	
WSD-S-Stg2	–0.03	–0.42	–0.13	–0.20	–0.58	–0.30	–0.27	–0.38	0.04	–0.06	0.60

WSD observed under irrigated conditions at stage II was found to be negatively and significantly associated with EWL at stage II both under irrigated ($r = –0.76$, $P < 0.01$) and stress ($r = –0.69$, $P < 0.05$) conditions (Table 6).

Pearson's correlations worked out for morpho-physiological and phenological traits with yield traits showed that SLA obtained at stage I and II under both irrigated and stress conditions was negatively but weakly associated with pod yields obtained under irrigated as well as stress conditions (Table 7). SLA obtained under stress at stage I was negatively and significantly associated with HI under irrigated conditions ($r = –0.65$, $P < 0.05$), and SLA at stage II under irrigated conditions was also negatively associated with PY under irrigated conditions ($r = –0.64$, $P < 0.05$). EWL also showed a negative but weak association with all three yield traits in most cases; however, at stage I under stress conditions it showed a significant negative correlation ($r = –0.84$, $P < 0.01$) with HI obtained under stress conditions. Except at stage I under conditions of stress, WSD had positive but weak correlations with PY obtained under both irrigated and stress conditions. However, at stage I under irrigated conditions it was significantly and positively associated ($r = 0.74$, $P < 0.05$) with PY under stress conditions. DFI observed under stress was negatively associated with BY both under irrigated ($r = –0.65$, $P < 0.05$) and stress ($r = –0.89$, $P < 0.01$) conditions. DF_{25} under stress conditions was negatively and significantly associated ($r = –0.67$, $P < 0.05$) with BY under stress (Table 7). Correlations were also studied for two phenological traits of the study recorded under irrigated and stress conditions (data not provided). Positive and significant correlations were found for DFI ($r = 0.74$, $P < 0.05$) and DF_{25} ($r = 0.84$, $P < 0.01$) between the irrigation treatments. DFI and DF_{25} recorded under stress conditions were found to be positively and significantly associated ($r = 0.72$, $P < 0.05$) (Table 8).

Table 7. Correlation coefficients between morpho-physiological traits at stage I and II, and phenological traits with yield traits under irrigated and stress conditions

WSD, Water saturation deficit; EWL, epicuticular wax load; SLA, specific leaf area; PY, pod yield; BY, biological yield; HI, harvest index; DFI, days to flower initiation; DF_{25}, days to 25 flowers; I, irrigated; S, stress; Stg, stage. *$P < 0.05$; **$P < 0.01$

Trait	PY		BY		HI	
	Irr.	Str.	Irr.	Str.	Irr.	Str.
WSD-I-Stg1	0.26	0.74*	–0.39	–0.13	0.44	0.4
WSD-S-Stg1	0.36	0.56	–0.52	–0.50	0.36	0.38
WSD-I-Stg2	0.04	0.17	–0.04	0.16	0.48	0.46
WSD-S-Stg2	–0.57	–0.31	–0.26	–0.24	–0.30	0.26
EWL-I-Stg1	–0.18	–0.12	–0.39	–0.49	–0.32	–0.42
EWL-S-Stg1	0.17	–0.29	0.36	0.05	–0.21	–0.84**
EWL-I-Stg2	–0.24	–0.22	–0.14	–0.50	–0.51	–0.55
EWL-S-Stg2	0.14	–0.07	–0.30	–0.41	–0.06	–0.54
SLA-I-Stg1	–0.44	–0.42	0.11	0.18	–0.24	–0.28
SLA-S-Stg1	–0.61	–0.57	0.31	0.30	–0.65*	–0.27
SLA-I-Stg2	–0.64*	–0.46	–0.01	–0.28	–0.51	–0.19
SLA-S-Stg2	–0.61	–0.45	0.18	0.16	–0.47	–0.08
DFI-I	–0.30	–0.25	–0.53	–0.61	–0.31	–0.23
DFI-S	–0.55	–0.06	–0.65*	–0.89**	–0.46	0.01
DF_{25}-I	0.03	0.44	–0.13	–0.42	–0.09	0.36
DF_{25}-S	–0.08	0.40	–0.40	–0.67*	–0.22	0.19

Discussion

In general, genotypes yielding higher under irrigated conditions also gave higher yields under stress conditions as evident from the significant Pearson's correlation ($r = 0.67$, $P < 0.05$) as well as rank correlation ($r = 0.77$, $P < 0.01$) obtained between yields harvested under irrigated and stress conditions. However, percent reduction in PY was independent of the yields obtained under irrigated conditions ($r = –0.18$), indicating that tolerance to water stress is a genotype-dependent trait. A

Table 8. Correlation coefficients between phenological traits and reduction due to water stress in yield traits

DFI, Days to flower initiation; DF_{25}, days to 25 flowers; ΔHI, ΔBY, ΔPY, changes in harvest index, biological yield, and pod yield due to water stress; I, irrigated; S, stress. * $P < 0.05$; **$P < 0.01$

Trait	DFI-I	DFI-S	DF_{25}-I	DF_{25}-S	ΔHI	ΔBY
DFI-S	0.74*					
DF_{25}-I	–0.02	0.36				
DF_{25}-S	0.43	0.72*	0.84**			
ΔHI	–0.07	0.01	0.09	–0.04		
ΔBY	0.47	0.75*	0.47	0.65*	–0.01	
ΔPY	0.02	–0.49	–0.55	–0.60	–0.02	–0.38

drought-tolerant genotype is one that resists reduction in yield when grown under drought situations. Although Code 9 gave the highest pod yield under irrigated conditions, it was the second most susceptible to water stress, resulting in 60% reduction in yield. Although NCAc 17090 was the second most tolerant genotype to water stress, it was a poor yielder both under irrigated and stress conditions. GG 2, the third most tolerant genotype, gave the second highest yields both under irrigated and stress conditions. PBS 11049, the most tolerant genotype (recorded the least reduction in PY due to moisture stress), ranking fourth in yield under irrigated conditions, gave the highest yields under stress conditions. From the results it is very evident that yielding ability and tolerance to stress are independent of each other. Nevertheless, a genotype that yields satisfactorily under water stress or drought in comparison with other genotypes will be a preferred option for farmers in regions where occurrence of drought is a rule rather than exception. In central India, where mid-season drought is of common occurrence, genotypes such as PBS 11049 will be highly desirable. However, in regions where occurrence of drought is only intermittent, genotypes such as GG 2 will be highly desirable as they have the capability to perform better under drought situations as well as to use water, when available, for yield maximisation.

Change in HI under water stress, as observed in this study, has also been reported by Collino *et al*. (2001). HI recorded under irrigated and water stress conditions was poorly associated ($r = 0.25$). Change in HI due to water stress was also independent of HI recorded under irrigated condition ($r = 0.49$). However, a strong negative correlation ($r = -0.72$, $P < 0.05$) was observed between genotypes for HI under water stress conditions and change in HI due to water stress. It indicates that HI under water stress is a very important trait, and one should select for high HI under water stress conditions while selecting for drought tolerant genotypes.

Significant differences due to year of experiment observed only for morpho-physiological traits (WSD, SLA, and EWL) suggest that these traits are very sensitive to seasonal changes in weather parameters. Withholding irrigation water has resulted in water-deficit stress in plants as evident from the increased WSD, which also increased with increase in age of the crop. Reduction in leaf relative water content during the progressive water stress, which is the inverse of WSD, was also reported by Nautiyal *et al*. (2002). Clavel *et al*. (2004) also reported that relative water content decreased at about 3 weeks after the occurrence of moisture stress at the soil level. Increase in EWL observed with increase in age of the crop was much greater in the plants under water stress than in irrigated plants. These finding are in line with those reported previously by Samdur *et al*. (2003) in peanut. A general decrease in SLA due to imposition of water stress as observed in this study has also been reported both by Craufurd *et al*. (1999) and Nautiyal *et al*. (2002) in peanut.

In general, correlations of all three morpho-physiological traits with yield traits were fairly weak. Genotypes with low cuticular transpiration rates usually have a functional advantage in water-deficit environments due to more efficient water use (Walker and Miller 1986; Paje *et al*. 1988). The negative associations of EWL observed with yield traits in this study, being highly significant for HI under stress, suggest that increase in EWL as triggered by water-deficit stress has affected physiological mechanisms, which in turn have resulted in a reduced source and further reduction in translocation of assimilates of photosynthesis to the sink. Reduction in yield traits under water stress might have also been the outcome of reduced transpiration brought about by the increased EWL on the leaf surface. Although the correlations of SLA with yield traits were not significant under most combinations of observations (stages and growing conditions), perusal of data shows a definite negative trend of association, rather weak, of this trait with PY and HI, which is very commonly used in drought studies, particularly in peanut. From this it is evident that plant adaptations for tolerating reduced availability of moisture sometimes occur even at the cost of yield potential.

Considering the strong negative correlation of EWL with HI under stress conditions, it might be concluded from this study that peanut plants resort to increasing EWL when water availability becomes scarce, which in turn affects the physiological process leading to HI. Also, a significant and negative relationship observed for HI under water stress and its reduction due to decreased availability of water renders this trait an important selection criterion for plant breeders for identification of drought-tolerant peanut genotypes. Considering the trends of associations of SLA observed in this study with PY, it might be considered that this trait is also important for identifying drought-tolerant genotypes with high PY.

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