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DROUGHT STRESS

Assessment of Groundnut under Combined Heat and Drought Stress

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Abstract

In semi-arid regions, particularly in the Sahel, water and high-temperature stress are serious constraints for groundnut production. Understanding of combined effects of heat and drought on physiological traits, yield and its attributes is of special significance for improving groundnut productivity. Two hundred and sixty-eight groundnut genotypes were evaluated in four trials under both intermittent drought and fully irrigated conditions, two of the trial being exposed to moderate temperature, while the two other trials were exposed to high temperature. The objectives were to analyse the component of the genetic variance and their interactions with water treatment, year and environment (temperature) for agronomic characteristics, to select genotypes with high pod yield under hot- and moderate-temperature conditions, or both, and to identify traits conferring heat and/or drought tolerance. Strong effects of water treatment (Trt), genotype (G) and genotype-by-treatment (GxTrt) interaction were observed for pod yield (Py), haulm yield (Hy) and harvest index (HI). The pod yield decrease caused by drought stress was 72 % at high temperature and 55 % at moderate temperature. Pod yield under well-watered (WW) conditions did not decrease under high-temperature conditions. Haulm yield decrease caused by water stress (WS) was 34 % at high temperature and 42 % under moderate temperature. Haulm yield tended to increase under high temperature, especially in one season. A significant year effect and genotype-by-environment interaction (GxE) effect were also observed for the three traits under WW and WS treatments. The GGE biplots confirmed these large interactions and indicated that high yielding genotypes under moderate temperature were different to those at high temperature. However, several genotypes with relatively high yield across years and temperature environments could be identified under both WW and WS conditions. Correlation analysis between pod weight and traits measured during plant growth showed that the partition rate, that is, the proportion of dry matter partitioned into pods, was contributing in heat and drought tolerance and could be a reliable selection criterion for groundnut breeding programme. Groundnut sensitivity to high-temperature stress was in part related to the sensitivity of reproduction.

Introduction

About 90 % of the world's groundnut production occurs in the tropical and semi-arid tropical regions. Much of the world's groundnut production regions are characterized by high temperature and low or erratic rainfall. Groundnut is sensitive to temperature (Vara Prasad et al. 1999) with an optimum for most processes being between 27 and 30 °C (Ntare and Williams 1998), while drought is estimated to cause millions in revenue losses to crop production (Sharma and Lavanya 2002). Thus, heat stress and water stress (WS) occurring simultaneously are considered to be two major environmental factors limiting groundnut growth and yield.

Plant responses to high temperature vary with plant species and phenological stages (Wahid et al. 2007). Reproductive processes are markedly affected by high temperatures in most plants, which leads to reduced crop yield. For example, both grain weight and grain number appeared to be sensitive to high-temperature stress in wheat, as the number of grains per head at maturity declined with increasing temperature (Ferris et al. 1998). Vara Prasad et al. (2000) investigated the effects of day-time soil and air temperature of 28 and 38 °C, from start of flowering to maturity of groundnut, and reported 50 % reduction in pod yield at high temperatures. These authors observed that day temperature above 34 °C decreased fruit-set and resulted in fewer numbers of pods. However, Greenberg et al. (1992) and Ndunguru et al. (1995) reported that varieties grown by farmers in the Sahel yielded 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 above that in normal temperatures. Here, we test the range of genotypic variation in pod yield under hot conditions, using a large and representative set of genotypes.

Although under field conditions, drought stress is often associated with high-temperature stress in the Sahel, the impacts of drought and high-temperature stress on groundnut productivity have mostly been studied independently. Ntare and Williams (1998) reported that temperature tolerance is an important component of drought resistance and a necessary attribute for varieties destined for the Sahel. This is because large gaps in the rains that cause drought are also paralleled by period of temperature increase. Moreover, authors showed that heat tolerance results in improved photosynthesis, assimilate partitioning, water and nutrient use efficiency, and membrane stability (Camejo et al. 2005, Ahn and Zimmerman 2006, Momcilovic and Ristic 2007). There exists a strong relationship between the plant water status and temperature, thus making it very difficult to separate the contributions of heat and drought stress under field conditions (Vara Prasad and Staggenborg 2008). Understanding of combined effects of heat and drought on physiological traits, yield and its attributes is of special significance for groundnut breeding programme to improve productivity and to predict the consequences of climate change on groundnut production in the Sahel.

The working hypothesis of this work is that drought and heat tolerance involve in part independent processes, and the ultimate goal was to identify genotypes with specific or combined tolerance to drought and heat. This was achieved by assessing a large and diverse set of groundnut genotypes in two seasons characterized by large differences in temperature during the reproductive phase, and in which different water regimes (intermittent drought and full irrigation) were imposed. Specifically, the study aimed at (i) identifying the component of the genetic variance and their interactions with water treatment, year and season (temperature) for agronomic characteristics, (ii) selecting genotypes with high pod yield under hot and moderate conditions, or both and (iii) identifying traits conferring heat and/or drought tolerance.

Material and Methods

Experimental conditions

Four experiments were conducted: two during the rainy seasons 2008 and 2009 characterized by moderate temperatures (MT08 and MT09) (between August and December) and two during the summer seasons 2009 and 2010 characterized by high temperature (HT09 and HT10) (between February and June) in the field at the ICRISAT Sahelian Centre (ISC) in Sadore, Niger, 45 km south of Niamey, 13°N, 2°E. The soils at ISC are arenosols (World Reference Base) with low pH, a very low water-holding capacity, low inherent soil fertility and organic matter content. The moderate-temperature experiments have been reported in part by Hamidou et al. (as ISC08 and ISC09, 2012) and are used here to test the genotypic and genotype-by-environment interactions with the high-temperature trials.

In all experiments, fertilizer NPK (15-15-15) and farm yard manure (200 kg ha^{-1}) were incorporated; the field was ploughed and irrigated twice before sowing. The experiments were kept disease- and insect-free all throughout by regular checking and sprays if needed. Hand weeding was performed between 30 and 50 DAS. Two hundred and sixty-eight genotypes, including 259 entries of the groundnut reference collection, were evaluated. The experimental design was an incomplete randomized block design with water treatment as main factor and genotypes as sub-factor randomized within each factor and replicated five times. Each plot (2 m^2) contained two rows (2 m each), with a 50 cm distance between rows, and 10 cm spacing between plants per row. Plants were irrigated twice a week with 20 mm of water using a linear movement system (Valmont Irrigation Inc., Valley, Nebraska, USA) until drought stress imposition. Calcium–ammonium–nitrate (200 kg ha^{-1}) and gypsum (200 kg ha^{-1}) were applied during pod formation.

Management of irrigation

All plots were irrigated with 20 mm twice a week until flowering (30–35 days after sowing). From that time, half of the plots were exposed to intermittent stress until maturity. The drought stress was imposed by irrigating WS plots only once in two times that the well-watered (WW) plots were irrigated. Thus, 40 mm were provided for irrigating all plots (WW and WS) at the time of flowering. The next irrigation was supplied to the WW plots only, based on the estimated evapotranspiration. The next irrigation was supplied to all plots (both WW and WS), and the decision to irrigate was based on a leaf wilting assessment of the WS plots, irrigation being supplied when the wilting score of the WS plots reached a value of 3. The scoring of wilting symptoms was recorded early afternoon as follows: score 1 = no wilting symptoms, score 2 = few leaves wilted in a minority of plants from the plot, score 3 = a majority of plants in a plot have wilted leaves, but none has reached permanent wilting, score 4 = a minority of plants show at least partial symptoms of permanent wilting and score 5 = most plants show symptoms of permanent wilting. Dry-down assessment under controlled imposition of WS shows a score of 3 is reached when the transpiration of the WS plants is about 40–50 % of the transpiration of the WW plants, indicative of a substantial stress, yet not too severe (Bhatnagar-Mathur et al. 2007, Ratnakumar et al. 2009). All irrigation provided 40 mm, so that following this irrigation scheme, the irrigation of WS plots was half of that in the WW plots.

Measurements

During the crop growing period, soil temperature at 5 and 10 cm at the hottest period of the day, the maximum (Max) and minimum (Min) air temperatures and the relative humidity were recorded daily from a meteorological station located close to the experimental field. The soil in which soil temperatures were measured was covered by vegetation in the moderate-temperature season, but this vegetation had dried in the high-temperature season. The air temperature and relative humidity were used to determine the vapour pressure deficit (VPD) (Prenger and Ling 2001).

Time of emergence and time to flowering (50 % of the plants started flowering) were recorded before WS imposition. The SPAD chlorophyll meter reading (SCMR) was measured using a Minolta SPAD-502 meter (Tokyo, Japan) in the MT09 and HT10 experiments during WS period. Time to maturity and time to harvest were recorded. To record the maturity date, border plants were randomly picked, pods number was counted, and the internal pod wall was examined. Mature pods were characterized by the blackening of the internal pod wall. At harvest, the entire two rows per plot were sampled (2.0 m^2). The plants were air-dried for 1 week before pods were separated from the haulms along with some roots that came up with the pods on lifting. For each plot, haulm weight and pod weight were recorded. Crop growth rate (CGR, kg ha^{-1} per day), pod growth rate (PGR, kg ha^{-1} per day) and partitioning (P, proportion of dry matter partitioned into pods) were estimated following a modified procedure from Williams and Saxena (1991):

$$\begin{aligned} &\mathrm{CGR} = (\mathrm{Hwt} + (\mathrm{Pwt} \times 1.65))/\mathrm{T}_2), \\ &\mathrm{PGR} = (\mathrm{Pwt} \times 1.65)/(\mathrm{T}_2 - \mathrm{T}_1 - 15), \mathrm{P} = \mathrm{R/C} \end{aligned} \quad (1)$$

Where T_2 is the number of days from sowing to harvest, T_1 is the number of days from sowing to flowering, and 15 is the number of days between the beginning of flowering and the start of pod expansion (Ntare et al. 2001).

Haulm weight and pod weight were converted in haulm yield (Hy) and pod yield (Py), expressed in g m^{-2} and used to determine the total biomass (Bt = Hy + Py × 1.65), and the pod weight was multiplied with a correction factor of 1.65 (Duncan et al. 1978) to adjust for the differences in the energy requirement for producing pod dry matter compared with vegetative part. Harvest index (HI) was determined as a ratio of adjusted pod weight to total biomass (HI = 1.65*Py/Bt).

Statistical analysis

The results were obtained with GENSTAT software (VSN International Ltd, Hemel Hempstead, UK), version 13. The data were subjected to analysis of variance (ANOVA) procedure for a linear mixed model. The residual maximum likelihood (ReML) method of GENSTAT was used to obtain the unbiased estimate of the variance components and the best linear unbiased predictions (BLUPs) for the different parameters measured within each treatment, considering genotypes as random and replications as fixed effects. The significance of the genetic variability among accessions within treatment was assessed from the standard error of the estimate of genetic variance $\sigma^2{}_g$. Two-way ANOVAs were also performed to assess the effects of water treatment (Trt) and genotype-by-water treatment (GxTrt) interaction, year (Y) and genotype-by-year (GxY) interaction, and environment (E) and genotype-by-environment (GxE) interaction, for the different traits measured. In this case, variation components involving G were considered as random effects, whereas Trt, Y, E and replication effects were considered as fixed. The significance of genetic variability across treatments or of the interaction effect was assessed in a similar above-mentioned manner. The significance of the fixed effect was assessed using the Wald statistic that asymptotically follows a chi-square distribution.

Results

Weather

The determined VPD during the high-temperature season 2009 and 2010 (3.68 and 3.66 kPa, respectively) was higher than the VPD during the moderate-temperature season 2008 and 2009 (2.0 kPa and 1.8 kPa, respectively) (Fig. 1a). Higher maximum temperatures (41 °C in average) were observed during high-temperature experiments (Fig. 1b), than during the moderate-temperature season experiments. In addition, Figure 1c shows that the averaged soil temperature at 5cm during high temperature reached 49 °C, while it reached 42 °C during the moderate-temperature season experiments. At 10 cm, the soil temperature in the high-temperature season was 40 °C compared to 35 °C in the moderate-temperature season.

Genotype, water treatment, and genotype-by-water treatment interaction (GxTrt)

The combined analyses of variance for pod yield (Py), haulm yield (Hy) and harvest index (HI) of the 268 genotypes for the HT09 and HT10 experiments showed a strong water treatment effects in both years (Table 1). The genotype (G) and genotype-by-treatment (GxTrt) effects were also highly significant for the three traits in both years, and the magnitude of their effects was similar for each of the traits in both years.

Under fully irrigated conditions, the trial mean for pod yield was similar in the high-temperature and the moderate-temperature seasons. By contrast, the haulm weight was somewhat higher in the high-temperature than in the moderate-temperature seasons, especially in the HT09 trial (Table 2). As a consequence, the harvest index (HI) was slightly higher in the moderate-temperature seasons (0.38 and 0.37) than in the high-temperature season (0.25 and 0.34). The high-temperature seasons were about 10 days longer than the moderate-temperature seasons (130 vs. 120 days).

Drought stress decreased the pod and haulm yield and HI in both moderate-temperature and high-temperature

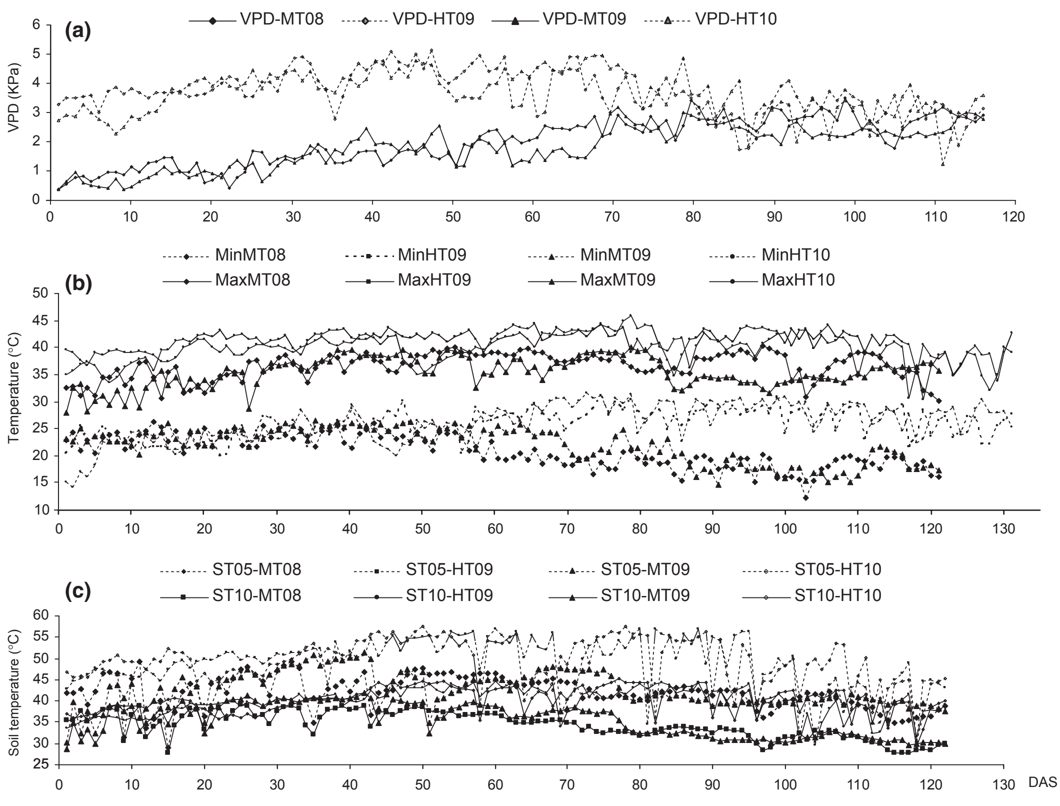

Fig. 1 Weather conditions during the experimental periods of the moderate temperature season 2008 and 2009 (MT08 and MT09) and the high temperature season 2009 and 2010 (HT09 and HT10) at Sadore. VPD = vapor pressure deficit (a), Max = maximum (b), Min = minimum (b), ST05 and ST10 = soil temperature at 5 and 10 cm (c).

Table 1 ANOVA (F value) for pod (Py), haulm (Hy) and harvest index (HI) at Sadore during the high temperature 2009 (HT09) and 2010 (HT10), in which genotype (G), water treatment (Trt) and GxTrt interaction effects were tested (d.f. = degree of freedom). ANOVA for the moderate-temperature trial is reported by Hamidou et al. 2012

		High Temperature 2009 (HT09)			High Temperature 2010 (HT10)		
	d.f.	Py	Hy	HI	Py	Hy	HI
G	267	3.67***	6.28***	8.18***	3.30***	2.58**	7***
Trt	1	3061***	1812***	1475***	1955***	86***	1386***
GxTrt		4.47***	7.34***	6.31***	3.48***	4.29***	3.79***

Significance at **0.01 and ***0.001 level.

Table 2 Trial means, range of expected means (Max and Min), variance component, standard error (S.E.), F-probability, standard error of differences (S.E.D.) within treatment of pod yield (Py), haulm yield (Hy) and harvest index (HI) during moderate temperature (MT) and high temperature (HT) under well-watered (WW) and water stress (WS) treatments

	Moderate temperature 2008 (MT08)						Moderate temperature 2009 (MT09)					
	WW			WS			WW			WS		
	Py	Hy	HI	Py	Hy	HI	Py	Hy	HI	Py	Hy	HI
Mean	272.3	433.6	0.4	121.2	252.7	0.3	238.3	403.4	0.4	84.5	710.4	0.1
Max	360.1	615.4	0.5	149.4	404.7	0.5	310.9	571.2	0.5	216.2	1922	0.2
Min	194.6	277.3	0.2	86.0	130.2	0.2	192.8	201.9	0.2	59.5	493.8	0.1
Component	1727	4944	0.0027	302	2160	0.0040	1000	8014	0.0033	545	35820	0.0018
SE	275	679	0.0003	51	261	0.0005	215	955	0.0004	120	6289	0.00014
Prob	6.28***	7.28***	8.96***	5.92***	8.28***	8.25***	4.65***	8.39***	8.51***	4.54***	5.70***	8.45***
SED	39.2	59.81	0.035	16.96	34.68	0.047	34.83	70.59	0.044	25.43	188.4	0.025
	High temperature 2009 (HT09)						High temperature 2010 (HT10)					
Mean	311.5	1086.6	0.2	84.5	710.4	0.1	232.3	447.8	0.3	95.9	397.6	0.2
Max	458.1	3008.9	0.4	216.2	1922.2	0.2	276.5	612.8	0.5	139.7	509.6	0.3
Min	195.7	503.6	0.1	59.5	493.8	0.1	167.5	267.2	0.2	61.8	236.2	0.1
Component	2566	176452	0.00538	545	35820	0.00117	880	7461	0.00470	422	4008	0.00235
SE	385	18128	0.000523	120	6289	0.00014	152	860	0.00048	70	516	0.00029
Prob	6.66***	9.73***	10.30***	4.54***	5.69***	8.44***	5.78***	8.67***	9.79***	6.028***	7.76***	7.99***
SED	46.08	234.2	0.03412	25.43	188.4	0.02478	30.46	67.79	0.04581	20.71	54.6	0.04087

Significance at ***0.001 level.

experiments (Table 2). However, the pod yield decrease caused by drought stress was lower in the MT08 and MT09 (55 % and 38 %, respectively) than in the HT09 and HT10 seasons (72 % and 59 %, respectively). These results indicated that the intermittent drought stress had a more severe effect on pod yield during the high-temperature than during the moderate-temperature seasons, which likely relates to the higher temperatures of the high-temperature seasons (Fig. 1). The HI decrease caused by drought stress was also higher during the high-temperature seasons (50 % and 33 % in HT09 and HT10, respectively) than in the moderate-temperature seasons (25 % for both MT08 and MT09. The contrary was observed for haulm yield, which decreased less in the high-temperature seasons (34 % and 11 %) than in the moderate-temperature seasons (42 % and 31 %).

Year effect and genotype-by-year interaction (GxY)

In the high-temperature trials, a significant year (Y) effect was found for pod yield, haulm yield and HI for both WW and WS conditions (Table 3). For each of the water treatments, the genotype (G) and genotype-by-year (GxY) effects were both significant for all three traits, and the magnitude of the GxY effect was similar or above the magnitude of the G effect for pod and haulm yield, while it was less than the G effect for the harvest index. The high significance of GxY interaction under WW and WS conditions suggests a close interaction between the environmental conditions and the genotypic response to drought in combination with a high-temperature stress effect, leading to GxY variation for pod and haulm.

Table 3 Two-way ReML analysis for pod yield (Py), haulm yield (Hy) and harvest index (HI) under well-watered (WW) and water stress (WS) conditions at Sadore during the high temperature season 2009 and 2010, in which genotype (G), year (Yr) and genotype-by-year interaction (GxYr) effects were tested (d.f. = degree of freedom)

		WW			WS		
	d.f.	Py	Hy	HI	Py	Hy	HI
G	267	4.43***	1.21	9.13***	2.78**	3.54***	6.82***
Yr	1	297***	257***	141***	67***	482***	55***
GxYr	267	3.74***	8.5***	5.23***	3.59***	4.18***	4.57***

Significance at **0.01 and ***0.001 level.

Environment effect and genotype-by-environment interaction (GxE)

A combined analysis of variance (ANOVA), carried out within treatment, showed that genotype, environment and genotype-by-environment (GxE) effects were all significant for pod yield, haulm yield and HI under both water treatments. The environment effect appeared to be particularly strong under WS for all three traits. For each water treatment, the magnitude of the GxE interaction effect was higher than the magnitude of the G effect for all three traits, in particular for pod yield (Table 4). The high significance of GxE under both water treatments compared to G effect indicates that while part of the variation was explained by genotypic effects, a larger part of the phenotypic variation was explained by GxE interaction effects across environment-treatments combination.

Genotype and Genotype-by-Environment (GGE) biplot analysis

One of the objectives was to test whether the selection of high yielding genotypes under WW and/or WS conditions in the moderate-temperature season would be different from those selected during the high-temperature season.

Table 4 Two-way ReML analysis for pod yield (Py), haulm yield (Hy) and harvest index (HI) under well-watered (WW) and water stress (WS) conditions at Sadore during the moderate-temperature season of 2008 and 2009, and high-temperature season 2009 and 2010, in which genotype (G), environment (E) and genotype-by-environment interaction (GxE) effects were tested (d.f. = degree of freedom)

		WW			WS		
	d.f.	Py	Hy	HI	Py	Hy	HI
G	267	2.55**	4.43***	8.77***	3.07**	6.68***	8.77***
E	3	102***	756***	204***	255***	353***	1191***
GxE		7.20***	11.33***	10.49***	7.75***	8.77***	8.98***

Significance at **0.01 and ***0.001 level.

The statistical analysis above indicate that large GxE and GxY interactions took place, and, therefore, several GGE biplot analyses were performed to identify superior high yielding genotypes under WW and WS conditions within and across moderate- and high-temperature seasons.

A first effort consisted in identifying high yielding genotypes across years within temperature seasons for each of the water treatments (WW and WS) (Fig. 2). For each of the combinations, the GGE biplot organized the genotypes against two axes. Genotypes being the farthest on the left in the axis carrying the arrow were those with the highest yield across 2 years, within each temperature and water treatment combinations. For instance, under WW treatment and moderate temperature, the ten highest yielding lines under high-temperature conditions were 133, 206, 131, 135, 254, 130, 132, 220, 139, 119, (Fig. 3a) and are given with a genotype name in Table 6 as high yielding under WW treatment and high temperature (HY-HT). For moderate-temperature seasons under WW treatment, genotypes 45, 245, 240, 253, 168, 51, 33, 267, 90, 221 were the highest yielding (Fig. 3b; Table 6; Table S1). A similar selection was performed for the WS treatment in each of the high and moderate-temperature environments (Table 6; Fig. 3c,d). The fact that the four combination of water and temperature regime did not yield the same list of highest yielding genotypes also reflects the high GxY interactions that are reported in Table 3.

To identify genotypes with broad adaptation within water regime and across temperature conditions, a comparison biplot was developed (Fig. 3), in which each genotype's position relative to the ideal genotype (center of the target) under WW (Fig. 3a) and WS conditions (Fig. 3b). Under WW conditions, genotypes 242, 240, 253, 168, 220, 140, 244, 245, 46 and 165 (Fig. 3a; Table 6; Table S1) were the most adapted across both moderate- and high-temperature environments (Fig. 3a). Under WS conditions, the most adapted genotypes across moderate- and high-temperature environments were 153, 21, 131, 116, 191, 111, 185, 102, 163 and 164 (Fig. 3b; Table 6; Table S1). The poorest adapted genotypes under WW across both MT and HT environments were ICG 188, ICG 1534, ICG 4906, ICG 6402 and ICG 6667, while ICG 188, ICG 8083, ICG 9362, ICG 11862 and ICGV 99001 were the poorest adapted under WS conditions. Figure 3 also reflects the large GxE interaction reported in the Table 4.

Correlations between pod yield and possible traits

Correlation analysis between pod weight and traits recorded during the growing season and after harvest is shown in Table 5. As observed previously (Hamidou et al.

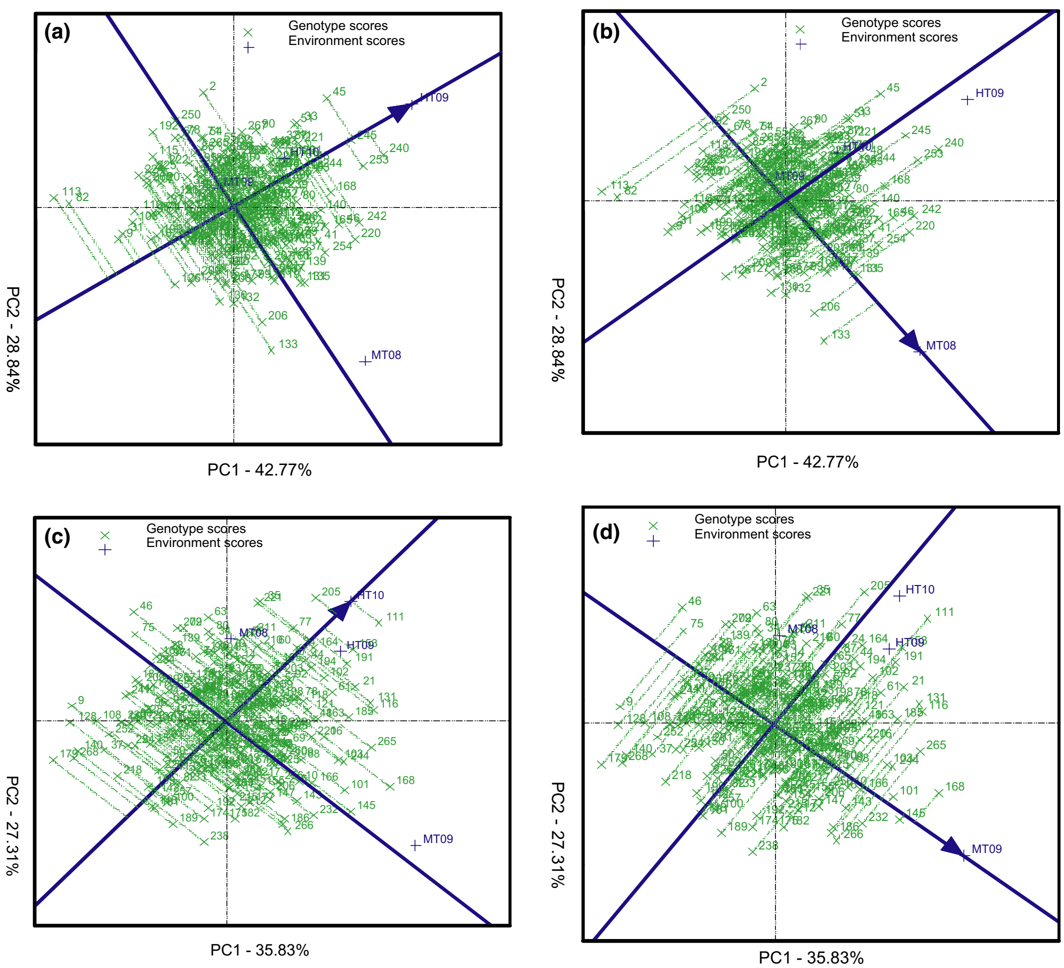

Fig. 2 ranking genotypes based on yield performance in the moderate temperature (a and c) and high temperature season (b and d) under WW (a, b) and WS (c, d) conditions. For full name of genotypes, see Table annex.

2011), the pod weight was significantly related to the CGR and PGR under both WW and WS conditions in both moderate-temperature seasons (Table 5). By contrast, no significant relationship was observed between pod weight and CGR or PGR in the high-temperature trials, except a weak relationship of pod yield with PGR in the HT10 trial. The partition rate (P) was significantly correlated to the pod yield in MT08, HT09 and HT10 experiments under the two water treatments. Under WW and WS conditions during the four experiments, pod weight was not significantly correlated to the time to flowering (Flo) and neither to the SPAD chlorophyll meter reading (SCMR).

Discussion

This study revealed a wide genotypic variation for pod yield, haulm yield and harvest index during high temperature in the 2 years. Drought stress decreased pod yield and the harvest index (HI) more during the high-temperature season than during the moderate-temperature season. A combined analysis across environments showed the predominance of GxE effects on the three traits under both WW and WS conditions, showing that genotype's performance in the moderate and high-temperature seasons differed. Under both WW and WS treatments, GGE biplot allowed the identification of genotypes having specific adaptation to moderate- and high-temperature conditions, or both. The partition rate was significantly correlated to pod weight in the moderate-temperature season but not in the high-temperature season, whereas SPAD and time to flowering were not significantly related to pod weight in any of the seasons.

Drought stress decreased pod yield in both moderate-temperature and high-temperature seasons, but the effect was higher during the high-temperature (72 %) than during the moderate-temperature season (55 %). Under drought conditions, the harvest index also decreased more

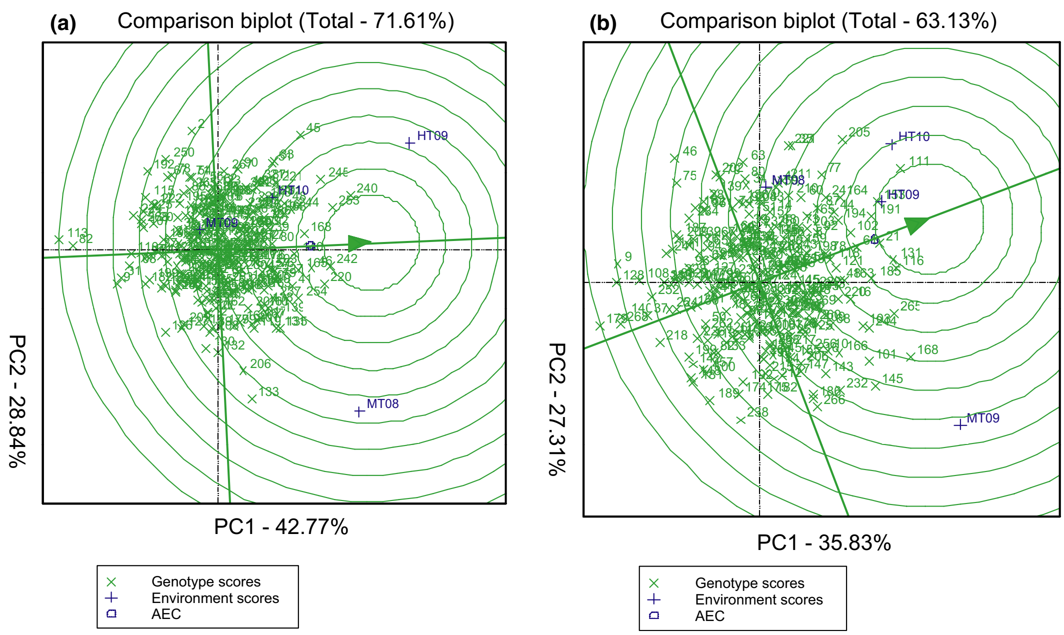

Fig. 3 ranking for selecting genotypes with broad adaptation (all environments) under WW (a) and WS conditions (b). For full name of genotypes, see Table 6.

Table 5 Correlation analysis between the pod yield and crop growth rate (CGR), pod growth rate (PGR), partition (P), time to flowering (Flo) and SPAD chlorophyll meter reading (SMCR) that were recorded in the field under well-watered (WW) and water stress (WS) conditions during the moderate-temperature (MT08 and MT09) and high-temperature (HT09 and HT10) seasons

		Pod yield			
	Trait	MT08	HT09	MT09	HT10
WW	CGR	0.69**	0.068	0.45**	0.0067
	PGR	0.76**	0.061	0.80**	0.12*
	P	0.17*	0.25*	0.18*	0.22*
	SCMR	–	–	0.063	0.009
	Flo	0.037	0.01	0.07	0.015
WS	CGR	0.38**	0.01	0.51**	0.00001
	PGR	0.85**	0.009	0.91**	0.07
	P	0.47**	0.19*	0.16*	0.21*
	SCMR	–	–	0.026	0.012
	Flo	0.13*	0.001	0.012	0.055

Significant at *P < 0.05 and **P < 0.01.

during the high-temperature season (50 %) than during the moderate-temperature season (25 %). On the contrary, drought decreased haulm yield relatively more in the moderate-temperature season (42 %) than in the high-temperature season (34 %) and under WW conditions, and haulm yield was somewhat increased in the high-temperature season. In addition, the HI was relatively lower in the high-temperature season (0.25 and 0.34) than in the moderate-temperature season (0.37 and 0.38). The daily VPD (3.67 PKa), the maximum air temperature (41 °C) and the soil temperature (49 °C) at high temperature were higher than those under moderate temperature (1.9 PKa, 35 °C, 42 °C, respectively). The decrease in HI under high-temperature conditions under WW condition suggests an effect of the high temperature on the reproductive processes, but not on plant growth. The small differences in pod yield between moderate-temperature and high-temperature seasons are then explained by a higher growth in the high temperature, in part explained by the longer season duration, than in the moderate-temperature season. Then, under high temperature combined with drought stress, the effect of heat on the reproductive processes is reinforced. Thus, the greater depressive effect of drought on pod yield and harvest index in the high-temperature season compare to the moderate-temperature season can be explained by the additional effect of high temperature on the reproductive processes under drought. Previous works reported that reproductive processes in groundnut are sensitive to temperature. Increasing air and soil temperatures reduced fruit-set, pods number and yield in groundnut (Craufurd et al. 2000, 2003, Vara Prasad et al. 2000). In addition, Ntare et al. (2001) showed that pod yield of groundnut genotypes declined by more than 50 % when flowering and pod formation occurred when maximum temperatures averaged 40 °C.

We observed that under WW conditions, the partition rate was 0.82 and 0.77 under moderate temperature 2008 and 2009 while it decreased to 0.59 and 0.60 under high temperature. Under WS conditions, the partition rate under moderate temperature 2008 and 2009 was 0.69 and 0.68, respectively, whereas it was 0.28 and 0.26 at high temperature 2009 and 2010. These findings indicate a difference of partition rate between high-temperature and moderate-temperature season. The effect of high-temperature stress on pod formation during high temperature can explain part of these differences. In addition, high-temperature stress could decrease the partition rate. Songsri et al. (2008) reported that the ability to partition dry matter into harvestable yields under limited water supply is an important trait for drought tolerant genotypes.

Table 6 Highest yielding (HY) and lowest yielding (LY) genotypes under either well-watered (WW, bold) or water stress (WS, bold) conditions during moderate (MT), high (HT) and/or across (MTHT) temperature seasons. For either selection case (WW or WS), pod yield (Py, g m^{-2}) is also given for the other water treatment (WS or WW, normal font). For MT and HT, the means are those of two seasons within each temperature regime and water treatment, whereas for MTHT, the means are those of the four seasons within water treatment. Genotypes labelled with MTHT are those with broad adaptation to different temperature conditions

WW				WS			
Genotypes	Py-WW	Py-WS	Characteristics in WW conditions	Genotypes	Py-WW	Py-WS	Characteristics in WS conditions
ICG 7181	**406**	116	HY-MT	ICG 5891	244	**215**	HY-MT
ICG 8253	**384**	150	HY-MT	ICG 6057	245	**192**	HY-MT
ICG 8285	**434**	68	HY-MT	ICG 9777	244	**225**	HY-MT
ICG 8490	**404**	152	HY-MT	ICG 9809	208	**130**	HY-MT
ICG 8517	**477**	139	HY-MT	ICG 11109	269	**197**	HY-MT
ICG 8751	**433**	158	HY-MT	ICG 11542	354	**218**	HY-MT
ICG 9315	**412**	147	HY-MT	ICG 12625	244	**211**	HY-MT
ICG 13982	**442**	119	HY-MT	ICG 15386	368	**218**	HY-MT
ICG 14985	**417**	52	HY-MT	J 11	224	**203**	HY-MT
ICGV 02271	**409**	125	HY-MT	ICGV 97183	375	**227**	HY-MT
ICG 1668	**464**	98	HY-HT	ICG 862	245	**181**	HY-HT
ICGV-SM99507	**506**	103	HY-HT	ICG 8285	280	**181**	HY-HT
ICG 2925	**442**	105	HY-HT	ICG 1703	265	**108**	HY-HT
ICG 5236	**384**	120	HY-HT	ICG 4729	249	**144**	HY-HT
ICG 11219	**441**	109	HY-HT	ICGV-SM99504	279	**154**	HY-HT
ICG 15042	**430**	134	HY-HT	ICG 10053	243	**173**	HY-HT
ICG 15403	**559**	104	HY-HT	ICG 12991	316	**171**	HY-HT
ICGV 02266	**493**	85	HY-HT	ICG 12879	193	**181**	HY-HT
ICGV 98294	**398**	134	HY-HT	ICG-13943	247	**130**	HY-HT
ICG 1668	**464**	98	HY-HT	ICG 15042	286	**104**	HY-HT
ICG 2738	**295**	117	HY-MTHT	ICG 862	265	**140**	HY-MTHT
ICG 9362	**313**	90	HY-MTHT	ICG 6022	300	**108**	HY-MTHT
ICG 11088	**283**	153	HY-MTHT	ICG 6646	277	**142**	HY-MTHT
ICG 11219	**323**	176	HY-MTHT	ICG 6813	273	**157**	HY-MTHT
ICG 14985	**315**	109	HY-MTHT	ICG 8285	311	**124**	HY-MTHT
ICG 15403	**327**	120	HY-MTHT	ICG 10053	302	**167**	HY-MTHT
ICG 15415	**342**	115	HY-MTHT	55-437	313	**161**	HY-MTHT
J 11	**312**	150	HY-MTHT	ICG 10950	319	**149**	HY-MTHT
ICGV 01232	**329**	136	HY-MTHT	ICG 12509	274	**155**	HY-MTHT
ICGV 02266	**344**	112	HY-MTHT	ICG 12879	267	**168**	HY-MTHT
ICG 76	**138**	92	LY-MT	ICG 188	162	**54**	LY-MT
ICG 6667	**118**	83	LY-MT	ICG 2738	136	**66**	LY-MT
ICG 6766	**154**	88	LY-MT	ICG 4670	193	**76**	LY-MT
ICG 12921	**129**	106	LY-MT	ICG 8083	182	**64**	LY-MT
ICGV 02148	**124**	128	LY-MT	ICG15390	164	**83**	LY-MT
ICG 188	**181**	53	LY-HT	ICG 9905	134	**130**	LY-HT
ICG 1534	**185**	89	LY-HT	ICG 11862	178	**65**	LY-HT
ICG 4906	**116**	67	LY-HT	ICG 12189	152	**145**	LY-HT
ICG 6667	**104**	83	LY-HT	ICG 12682	187	**169**	LY-HT
ICG 7963	**184**	125	LY-HT	ICG 1823	147	**94**	LY-HT

Genetic variation is an essential prerequisite for any crop improvement programme (Ober and Luterbacher 2002), and wide genotypic variation was shown for pod yield, haulm yield and harvest index under control (WW) and drought (WS) conditions across years, in agreement with previously reported results (Rebetzkea et al. 2004, Singh et al. 2008). Genotypic and genotype-by-water treatment interaction (GxTrt) were both significant and had similar magnitude for both moderate-temperature and high-temperature seasons 2009 and 2010, indicating the need to select genotypes under each respective water treatment. In this study, significant year (Y) and genotype-by-year interaction (GxY) effects were also observed on pod and haulm yield in each of two water treatments. The high significance of GxY interaction under WW and WS conditions suggests a close interaction between the environmental conditions and the genotypic response to drought within moderate-temperature and high-temperature conditions.

The magnitude of GxE therefore suggests that the selection for best genotypes is specific to the screening environment, which was confirmed by GGE biplots, used to analyse GxE interactions. Therefore, in each water regimes, the highest yielding genotype in the moderate-temperature season differed from those in the high-temperature season. Table 6 provides a list of genotypes that were high yielding across years within temperature seasons, for the WW and WS conditions, respectively. For instance genotypes, ICG 7181, ICG 8253, ICG 8285 are three of the ten highest yielding genotypes under WW conditions across moderate-temperature reported in Table 6. Similarly, genotypes ICG 5891, ICG 6057, ICG 9777 are three of the ten highest yielding genotypes under WS conditions across moderate-temperature season. This specific adaptation could be exploited in breeding programme to develop cultivars targeted to environments with differing temperatures. Interestingly, the selection for highest yields under WW conditions in either moderate or high-temperature seasons tended to select genotypes that would yield relatively poorly under WS conditions (third column). Reversely, the selection of the highest yielding genotypes under WS across moderate or high-temperature seasons clearly selected genotypes with moderate yield under WW conditions (sixth column). This, in fact, was a clear reflection of the large GxY and GxE interactions reported earlier. Similar results were found by Ntare and Williams (1998).

As it is also reported that highest yielding genotypes are those with high yield in different environments and producing consistently from year to year (Finlay and Wilkinson 1963, Reza et al. 2010), other GGE biplots were developed to identify genotypes with consistently high yield across year and temperature seasons, for each of the WW and WS treatments. A number of genotypes having broad adaptation to moderate and high-temperature conditions are also reported in Table 6. These could be considered as having the most 'stable' yields across seasons, although they may not have the highest yield within specific temperature season This study suggests that according to the target environment (moderate or high temperature), the water treatment (WW, WS) and the yield and stability, different genotypes could be recommended.

Conclusions

High temperature had major effects on the reproductive processes, both under WW and WS conditions, whereas growth processes were not affected in the high-temperature season. Large GxE interaction for pod yield in both water regimes indicated the need for selection of genotypes in each environment. Several broadly adapted genotypes were identified, with the capacity of securing reproduction at temperature above 40 °C.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Pod weight (Pwt), Haulm weight (Hwt) and harvest index (HI) of 268 genotypes under Well water (WW and water stress (WW) conditions under moderate temperature 2008 (MT08) and 2009 (MT09), and at high temperature 2009 (HT09) and 2010 (HT10).

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