



## Selection of intermittent drought tolerant lines across years and locations in the reference collection of groundnut (*Arachis hypogaea* L.)

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### ABSTRACT

Intermittent drought is the most important yield limiting factor affecting groundnut (*Arachis hypogaea* L.) production in rain-fed regions of Sub-Saharan Africa and Asia. Improvement of crop adaptation to drought is needed and this starts by having a thorough assessment of a large and representative set of germplasm. In this study, 247 lines belonging to the reference collection of groundnut were assessed under well-watered (WW) and intermittent water stress (WS) conditions in India and Niger for two years, following similar experimental protocols. The WS treatment reduced pod yield (31–46%), haulm yield (8–55%) and the harvest index (1–10%). Besides a strong treatment effect, yield differences within locations and years, were attributed to both genotypic and genotype-by-treatment interactions. Pod yield under WW and WS conditions were closely related in both years (Patancheru,  $r^2 = 0.42$  and  $r^2 = 0.50$ ; Sadore,  $r^2 = 0.22$  and  $r^2 = 0.23$ ). By contrast, within location and treatment, pod and haulm yields were affected predominantly by genotype-by-year (G × Y) effects, especially under WS. Within treatment across locations and years, pod and haulm yields were mostly ruled by genotypic effects, which allowed identifying a group of entries with contrasting pod yield across locations under WS. However, genotype and genotype by environment (GGE) biplot analyses distinguished India from Niger, suggesting that the selection remains environment-specific and also revealed dissimilarity between years in Niger. A close relationship was observed between yield and pod growth rate ( $r^2 = 0.51$ ), and partition ( $r^2 = 0.33$ ) under WS conditions, whereas no significant relationship was found between yield under WS and SCMR, or specific leaf area (SLA). These results showing a close interaction between the environmental conditions and the genotypic response to intermittent drought shows the necessity to carefully choose environments that truly represent target environments. This is an important result in the current breeding context of marker-assisted recurrent selection or genome-wide selection. This work opens also new ways for the breeding of drought tolerant groundnut, by bringing new highly contrasting lines currently used for crossing and deciphering drought adaptation traits to better understand G × E interactions, while it challenges the relevance of long-time used surrogates such as SCMR or SLA.

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### 1. Introduction

Drought is by far the most important factor contributing to crop yield loss in the semi-arid tropics (SAT) characterized by low and erratic rainfall. Therefore, identification of genotypes that have a better ability to use limited available water is important to enhance

crop productivity in the SAT. Groundnut (*Arachis hypogaea* L.) is an important food and cash crop grown mainly under rainfed conditions in the semi-arid regions. Unpredictable and intermittent periods of water deficit commonly occur during its growth period (Vorasoot et al., 2003). Drought stress has depressive effects on groundnut productivity (Nageswara Rao et al., 1989; Nautiyal et al., 2002; Nigam et al., 2005; Songsri et al., 2008a,b). The depressive effect of drought on growth and yield components depends on the time, the intensity and/or the duration of drought stress (Nautiyal et al., 2002; Nigam et al., 2005). Intermittent drought, which is

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an episodic water deficit during plant growth, is the most prevalent drought type affecting groundnut production in the rain-fed regions of SAT and remains a major limiting factor in groundnut productivity, evaluated to 500 million US\$ every year (Sharma and Lavanya, 2002). Therefore, breeding for drought adaptation is an important strategy in alleviating drought effects on groundnut productivity.

There are numerous reports on groundnut response to drought but most studies have been limited to small numbers of groundnut genotypes (e.g. Vorasoot et al., 2003). Other studies have used larger number of germplasm (e.g. 36, 60, and 120 in Ndunguru et al., 1995; Jongrunklang et al., 2008; Painawadee et al., 2009) and revealed a significant genotypic variation in drought tolerance. However, none of these studies used a structured set of germplasm representative of the genetic variation available in the germplasm collection. Therefore, our hypothesis is that testing a larger and representative range of groundnut genotypes could lead to the identification of new and/or better sources of intermittent drought tolerance for targeted groundnut breeding programs, following the example in other crops (Krishnamurthy et al., 2010). The germplasm collection of groundnut holds 15,445 accessions and would provide an adequate resource to identify tolerance sources. To provide a gateway to the germplasm collection, a mini core collection consisting of 184 accessions (Upadhyaya et al., 2002) has been developed. More recently, a reference collection of 300 genetically most diverse accessions from a composite collection using data on 21 SSR markers (Upadhyaya et al., 2008) has been assembled.

Assessing such a reference collection in different locations (environment) and years is also an important step in the selection of contrasting entries, especially to determine whether genotypes showing good performance under drought across locations and environments is possible, or whether the selection needs to be environment-specific. The genotype  $\times$  environment ( $G \times E$ ) interaction in groundnut under drought, as it occurs in many other crops, indeed complicates selection and slows down the breeding progress (Wright et al., 1996; Mothilal et al., 2010). However, this has not been done on large and representative sets of entries in groundnut. It is also critical to carry out an assessment of genotypes under both fully irrigated conditions and water stress conditions to examine whether the genotypes' response interacts with the water regime or whether the yield under stress is in fact mostly depended on the yield potential. For example, Bidinger et al. (1987) showed that about half of the pearl millet yield under terminal drought conditions depended on the yield under controlled conditions. Similar situation occurred in a salinity tolerance study of chickpea (Vadez et al., 2007). Reflecting the breeder's perspective, Blum (1996) and Panthuan et al. (2002) argue that potential yield has a large impact on yield only under moderate drought stress conditions, before stress is severe enough to induce a genotype and environment ( $G \times E$ ) interaction for yield. Recently, Boontang et al. (2010) reported that for pod yield of groundnut, high potential under well watered conditions alone gave significant contribution to maintaining high pod yield under drought. However, Talebi et al. (2009) found that the grain yield under irrigated conditions was adversely correlated with rain-fed condition and suggested that high potential yield of wheat under optimal conditions does not necessarily result in improved yield under stress conditions. So, the question of the significance of a genotype-by-treatment interaction remains open and needs to be tested in groundnut to guide the breeding objectives. This is particularly important for the current shifts in breeding, where new approaches such as marker-assisted recurrent selection or genome-wide selection (MARS, GWS) involve the phenotyping in a fairly limited number of environments.

The overall objective of the present research was to select genotypes with high tolerance to intermittent drought. This effort included the following steps: (1) assess the range of interaction

between genotype and water regime; (2) assess the range of interaction between the genotype and season within treatment and location, and between the genotype and the location within treatment; (3) identify a set of contrasting material; (4) identify field-measured traits related to better performance of genotypes under intermittent drought stress conditions.

## 2. Materials and methods

### 2.1. Experimental conditions

Two experiments were conducted in the field during the rainy season 2008 and 2009 (between August and December, at a late planting date to avoid the bulk of rains, and so that there was no rain during the treatment imposition period) at the ICRISAT Sahelian Centre in (Sadore, Niger, 45 km south of Niamey city, 13°N, 2°E). Other two experiments were conducted at ICRISAT headquarters (Patancheru, AP, India, 17°30'N; 78°16'E; altitude 549 m) between November 2008 and April 2009 and November 2009–April 2010. In Patancheru, a poststray planting was used because a late planting in the rainy season usually exposes the crop to severe groundnut bud necrosis and was then not reliable. The soils at the ICRISAT Sahelian Centre (ISC) are arenosols (World Reference Base) with low pH, a very low water holding capacity, low inherent soil fertility and organic matter content. At ICRISAT headquarters Patancheru (IHQ) the soils used for growing groundnut are sandy-clay loam Alfisol, with a pH of about 7.0. In both sites, crops was maintained pest and disease free by regular observations of possible attack and preventing sprays for the most common pests and diseases.

In Sadore experiments, fertilizer NPK (15–15–15) at a rate of 200 kg ha<sup>-1</sup>, and farm yard manure (2000 kg ha<sup>-1</sup>) were incorporated; the field was plowed and irrigated twice with a one day interval before sowing. Two hundred and sixty-eight (268) genotypes, including 247 entries of the groundnut reference collection were evaluated in two consecutive years, referred to as ISC08 and ISC09 trials. Seeds were sown by hand; the 268 entries were planted in 6 replicated plots arranged in an incomplete randomised block design. Each plot (2 m<sup>2</sup>) contained 2 rows (2 m long, 50 cm distance between rows) and 20 plants per row. Plants were irrigated two times per week with 20 mm of water using a linear movement system (Valley Irrigation Inc.) until drought stress imposition. Plots were regularly observed for good agronomic control, calcium-ammonium-nitrate (200 kg ha<sup>-1</sup>) and gypsum (200 kg ha<sup>-1</sup>) were applied during pod formation at 60 days after sowing.

At Patancheru experiments, basal fertilizer single super phosphate (SSP) (375 kg ha<sup>-1</sup>) was applied before sowing. The field was previously cultivated with pearl millet and maintained under fully irrigated conditions so that the soil moisture profile was full at the time of planting. Seeds were also hand planted in 2-row plots of four meters long with 33 cm between rows and 10 cm between plants. In the first and second year, referred to as IHQ08 and IHQ09 trials, 288 and 320 entries were tested, which included in both cases 258 entries from the reference collection itself including the 247 entries that were tested in Niger. The experimental design was an Alpha-lattice design with water treatment as the main factor and genotypes as sub-factors in three replications, with 16 blocks and 19 plots per block in IHQ08 and 16 blocks and 20 plots per block in IHQ09.

### 2.2. Management of irrigation for treatment application

Crop was maintained fully irrigated until flowering time by providing about 40 mm weekly. The plants were exposed to intermittent stress from the time to flowering (30–45 days after sowing in Sadore and 40–45 days after sowing in Patancheru until

maturity in both locations. The drought stress was imposed by irrigating drought stress (WS) plots only once every two times that the well-watered (WW) plots were irrigated. This consisted in providing a first 40 mm irrigation for all plots (WW and WS) at the time of flowering. The second irrigation was supplied to the WW plots only based on the estimated evapotranspiration, about 7 days later. The third 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 a majority of WS plots reached a value of 3. The fourth irrigation was supplied to the WW only, while the fifth irrigation supplied again to both WW and WS. Therefore, odd number irrigations were applied to both WW and WS treatments, whereas even number irrigations were given to WW only and this scheme was followed until maturity. The scoring of wilting symptoms was recorded early on a visual score of 1–5 where, 1 = no wilting symptoms, score 2 = few leaves wilted in a few 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 water stress show a score of 3 is reached when the transpiration of the water stress plants is about 30–40% of the transpiration of the well-watered (WW) plants, indicative of a substantial stress (Ratnakumar et al., 2009; Bhatnagar-Mathur et al., 2007). All irrigation provided 40 mm, so that following this irrigation scheme, the irrigation of WS plots was half of that in the WW plots.

### 2.3. Measurements

Parameters were measured before and/or during drought stress imposition. These included time to emergency, time to flowering (50% of the plants started flowering) and maturity. The SPAD chlorophyll meter reading (SCMR) was recorded using SPAD-502 (Minolta Corp., Ramsey, NJ, USA) in IHQ08 and ISC09 experiments in three plants per plot and two fully developed leaves per plant. At the same time, the specific leaf area (SLA) was measured by sampling two most fully developed leaves per plant in three plants per plot. The leaflet were taken out, leaf area measured, and leaf dry weight measured after drying for two days in a forced-air oven at 70 °C. To record the maturity date, 1–2 border plants were randomly picked, pods number was counted and the internal pod wall was examined. Mature pods are indicated by the blackening of the internal pod wall (Williams and Drexler, 1981) and when at least, 80% of pods were mature. At Sadore, the entire two rows per plot were harvested (2.0 m<sup>2</sup>). At Patancheru, 2 linear meters within each row were harvested (1.33 m<sup>2</sup>). The plants were air-dried during one week before pods were separated from the haulms along with some roots that came up with the pods on lifting. Haulm weights (Hwt) and pod weight (Pwt) were recorded. At Sadore, crop growth rate (C, kg ha<sup>-1</sup> per day), pod growth rate (R, kg ha<sup>-1</sup> per day) and partitioning (P, proportion of dry matter partitioned into pods) were estimated following a modified procedure from Williams and Saxena (1991) and using five representative plants per plot:

$$C = \frac{\text{Hwt} + (\text{Pwt} \times 1.65)}{T_2}, \quad R = \frac{\text{Pwt} \times 1.65}{T_2 - T_1 - 15}, \quad P = \frac{R}{C}$$

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 flowering and the start of pod expansion (Ntare et al., 2001).

Hwt and Pwt were used to determine the total biomass (Bt = Hwt + Pwt × 1.65) and the pods yield (Yp, t ha<sup>-1</sup>). Pods 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 × Pwt/Bt).

### 2.4. Statistical analysis

The results analyzed using GENSTAT program version 10 (Genstat, Release 10.1). The analysis of variance procedure for a linear mixed model was used. 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  $\sigma_g^2$ . Two-way analyses of variance were also performed to assess the effects of water treatment (T) and genotype-by-water treatment (G × T) interaction, year (Y) and genotype-by-year (G × Y) interaction, and environment (E) and genotype-by-environment (G × E) interaction, for the different traits measured. In this case, variation components involving G were considered as random effects whereas T, 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 manner similar to the above. The significance of the fixed effects was assessed using the Wald statistic. The purpose of these different two-way analyses was to assess different possibilities of interactions between genotypes and either the year (reflecting on possible weather condition differences), or the environment (reflecting possible soil/field differences).

## 3. Results

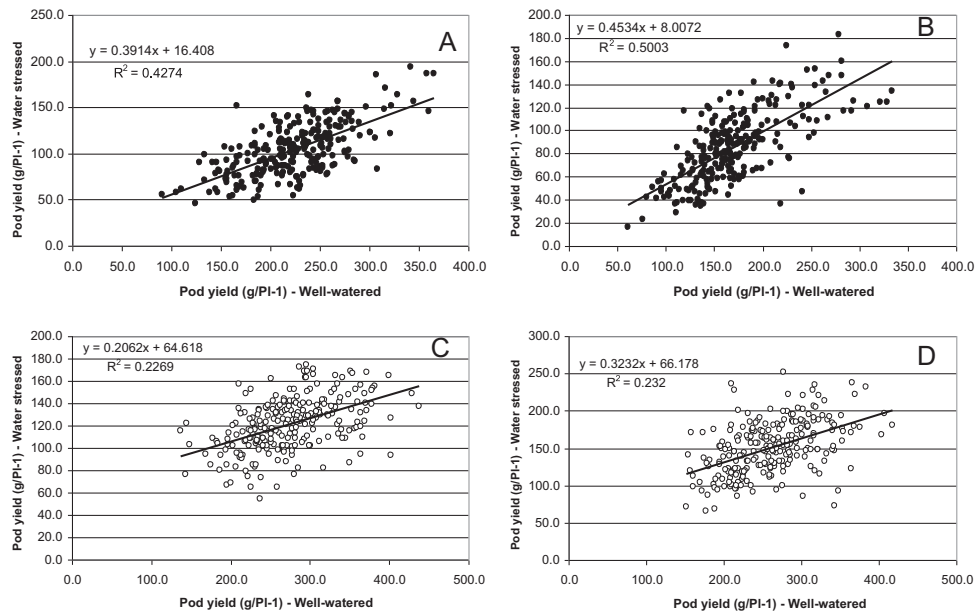
### 3.1. Water treatment effect, genotype × water treatment interaction (G × T) and range of mean of yield and its components

The analysis of variance for pod yield, haulm yield and harvest index (HI) of the 268 genotypes grown in Sadore (ISC08 and ISC09) and 288 (IHQ08) and 306 (IHQ09) genotypes grown in Patancheru under WW and WS treatments are presented in Table 1. Yields and components of the entire set across both environments is provided in Supplementary Table 1. Genotype and water treatment effects were significant ( $P < 0.05$ ) for pod yield, haulm yield and HI in the two locations during the 2 years except for a non-significant G effect on pod yield in IHQ08. In Patancheru, the G × T interaction was significant for all three parameters in IHQ08 and for pod yield and HI in IHQ09 whereas in Sadore it was significant for pod yield and HI in ISC08 and for haulm yield and HI in ISC09. It appeared also that in both locations and years, the magnitude of the G effect was always superior to the effect of the G × T interaction for all three traits, except for pod and haulm yield in IHQ08, indicating that mostly genotypic effect drove the differences in pod and haulm yield and HI within location-year combinations. The pod yield decrease due to drought stress was 46% and 36% in IHQ08 and IHQ09, and 41% and 31% in ISC08 and ISC09. Haulm weight decreased 23 and 8% in IHQ08 and IHQ09, but as much as 55% and 38% in ISC08 and ISC09. The trial's grand mean pod yields at Sadore under both water treatments were higher than those in Patancheru in both years (Table 1). The grand means of HI were similar in the two locations across years and treatments.

The predominant genotype effect on the pod yield within year and location were also shown by the significant relationships between pod yield under WW conditions and that under WS conditions (Fig. 1). However, these relationships were higher in

**Table 1**  
Two-way ReML analysis (Wald statistic/degree of freedom) within location and year, to test for genotype (G), treatment (T) and genotype-by-treatment (G × T) interaction effect on pod (Py), haulm (Hy) and Harvest index (HI). One-way ANOVA within location and year for pod (Py), haulm (Hy) and harvest index (HI), standard error of differences (SED), trial mean (average), SED, maximum (Max) and minimum (Min) values, and percentage decrease under water stressed (WS) compared to well-watered (WW) conditions.

		Patancheru						Sadore					
		Pod yield		Haulm yield		HI		Pod yield		Haulm yield		HI	
2008	G	-0.65		-2.93		10.06		4.59		5.62		8.44	
	T	182.9		1673.17		473.71		2236.6		1485.16		557.59	
	G × T	9.15		10.15		4.37		2.94		1		2.18	
2009	G	8.76		9.09		10.23		6.81		8.88		9.2	
	T	430.81		267.2		71.45		1099.6		718.13		348.22	
	G × T	6.17		0.78		4.51		-0.27		2.03		1.15	
2008		2008											
		Py		Hy		HI		Py		Hy		HI	
		WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
Component		1684	736	6798	4563	0.006161	0.005684	1727	302	4944	2160	0.00277	0.004027
SE		195	78.9	646	450	0.0006	0.000567	275	51	679	261	0.000309	0.000488
Significance		8.63	9.32	10.52	10.14	10.26	10.02	6.28	5.92	7.28	8.272	8.96	8.25
SED		29.9	17.67	40.03	36.8	0.04131	0.04239	39.2	16.96	59.81	34.68	0.03491	0.04751
Average		168.8	89.7	319.7	244.2	0.35	0.25	272.3	121.2	433.6	252.7	0.38	0.33
Max		274.4	162.7	517.5	389.5	0.59	0.45	360.1	149.4	615.4	404.7	0.57	0.56
Min		69.2	27.9	116.5	66.0	0.12	0.06	194.6	86.0	277.3	130.2	0.24	0.15
Decrease (%)		46		43		-		41		55		-	
2009		2009											
		Py		Hy		HI		Py		Hy		HI	
		WW	WS	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
Component		2502	941.6	8108	4739	0.007236	0.00945	8014	6332	1000	659	0.003322	0.005559
SE		233	89.1	759	652	0.000708	0.000846	955	644	215	97	0.00039	0.000541
Significance		10.74	10.6	10.68	7.3	10.22	11.2	8.39	9.83	4.65	6.79	8.51	10.27
SED		24.96	16.07	46	59.41	0.04861	0.04199	70.59	50.09	34.83	24.07	0.0445	0.04271
Average		118.15	75.2	259.45	200.2	0.31	0.25	403.4	277.4	238.3	146.7	0.38	0.33
Max		333.89	174.4	517.86	667.9	0.55	0.42	571.2	477.9	310.9	199.8	0.59	0.52
Min		21.49	15.4	51.52	86.0	0.13	0.04	201.9	124.5	192.8	96.3	0.18	0.15
Decrease (%)		36		8		-		31		38		-	



**Fig. 1.** Relationship between pod yield ( $\text{g m}^{-2}$ ) under well watered (WW) and water stressed conditions across year and location: IHQ08 (A), IHQ09 (B), ISC08 (C), and ISC09 (D).



**Table 2**

Two-way ReML analysis (Wald statistic/degree of freedom) within location and treatment to test for genotype (G), year (Y) and genotype-by-year ( $G \times Y$ ) interaction effect on pod (Py), haulm (Hy) and harvest index (HI). All terms were highly significant, except when mentioned (ns, non-significant).

	df	Patancheru								
		WW				WS				
		Py	Hy	HI	Py	Hy	HI	Py	Hy	HI
G	287	6.7	8.4	9.42	–2.09 ns	–1.92 ns	9.85			
Y	1	276.19	159.71	75.43	1454.5	369.3	1.79 ns			
$G \times Y$		7.06	7.1	5.62	9.55	6.96	6.39			

	df	Sadore								
		WW				WS				
		Py	Hy	HI	Py	Hy	HI	Py	Hy	HI
G	267	–1.49 ns	1.07 ns	1.38	–1.59 ns	5.77	6.85			
Y	1	60.06	1085.3	14.83	160.57	29.40	92.91			
$G \times Y$		5.16	8.18	4.34	6.25	6.69	6.07			

Patancheru ( $r^2 = 0.43$  and  $0.50$  in IHQ08 and IHQ09, respectively) than in Sadore ( $r^2 = 0.22$  and  $0.23$  in ISC08 and ISC09).

### 3.2. Year effect and genotype by year interaction ( $G \times Y$ )

Within each location, there was a significant year (Y) effect for pod yield, haulm yield and harvest index (HI) for each of the water treatments, except HI under WS in Patancheru (Table 2). Under WW conditions, the G effect was significant for the three parameters at Patancheru while it was non-significant at Sadore. Under WS conditions, the G effect was non-significant for pod yield but significant for HI at both locations. The G effect was significant for haulm under WS only at Sadore (Table 2). Significant genotype-by-year ( $G \times Y$ ) interaction was observed for pod, haulm and harvest index for each of the water treatments at the two locations (Table 2). In contrast to most  $G \times T$  interactions, the magnitude of the  $G \times Y$  effect under WS condition was higher than the magnitude of the G effect for both pod and haulm yield in both locations. By contrast, under WW conditions in Patancheru, the magnitude of G and  $G \times Y$  effects were similar for pod and haulm yield, although in Sadore, these effects were not similar.

The high significance of  $G \times Y$  interaction under WS conditions suggests a close interaction between the environmental conditions and the genotypic response to drought, leading to  $G \times Y$  variation for pod, haulm and HI. At Patancheru, the daily mean VPD especially during reproductive period (approximately between 40 and 80 DAS) was 1.4 and 1.18 MPKa in 2008 and 2009, respectively (Fig. 2). The minimum temperature at Patancheru during the reproductive period was 15 °C in both 2008 and 2009 but there was some notable maximum temperature differences between the years (32.7 and 30.6 °C, respectively in 2008 and 2009). In Sadore, the daily VPD during reproductive period (40–80 DAS) was higher in ISC08 (2.22 MPKa) than in ISC09 (1.9 MPKa) (Fig. 2). The minimum temperature in Sadore during the reproductive period was 21.0 and 23.9 °C in 2008 and 2009, respectively while the maximum temperature in 2008 and 2009 was, respectively 38.1 and 37.1 °C. Therefore, there were clear differences in the weather conditions across years within locations.

### 3.3. Environment effect and genotype by environment interaction ( $G \times E$ )

An important question of this work was whether the same or different genotypes would be selected for high yield under WS or WW across locations. This question was not relevant to this work only but to the overall shift in breeding approach towards MARS or GWS, approaches that involves phenotyping in a fairly limited

number of environments. This information was also highly relevant to decide on the most suitable breeding strategy for groundnut. Within treatment, genotype and environment effects were significant for HI under both water treatments. For pod yield, genotype effect was significant only under WS but not under WW conditions. The genotype effect was significant for haulm yield under both WW and WS conditions but the environment effect was significant only under WW conditions. A significant  $G \times E$  interaction was observed for haulm and harvest index under both water regimes but for pod yield this interaction was significant only under WW conditions. The magnitude of the G effect was higher than the magnitude of the  $G \times E$  interaction for haulm yield and HI under WS conditions whereas the contrary was observed under WW conditions. The high significance of G effect under WS compared to  $G \times E$  indicates that despite the fact that genotypes showed different performances across years within locations and water treatment for the three traits (Table 3), the differences in pod, haulm yield, and HI across year-treatments combination were mostly due to genotypic effects under WS and by  $G \times E$  interaction effects under WW conditions.

### 3.4. Genotype and genotype by environment (GGE) biplot analysis

To identify genotypes with either broad or specific adaptation under different water regimes at the two locations, we used GGE biplot which represents graphically the genotype (G) main effects plus genotype-by-environment interaction ( $G \times E$ ) effects. Fig. 3A shows each genotype's position relative to the ideal genotype (center of the target), based on the mean performance and stability under WS conditions at Patancheru and Sadore in 2008 and 2009. For example, genotypes ICGV 97183 (no. 244), ICGV 97182 (no.

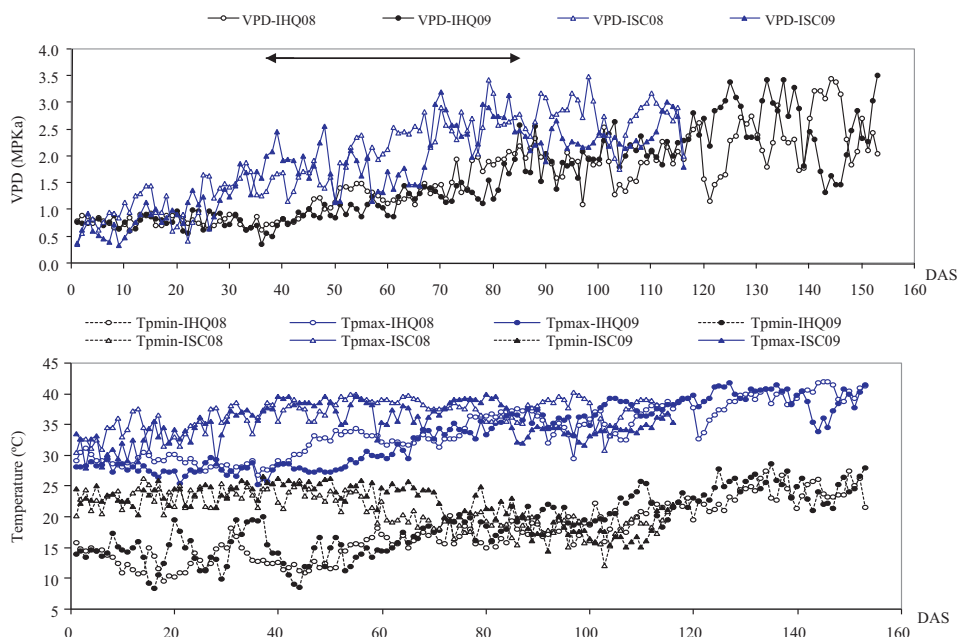
**Table 3**

Two-way ReML analysis (Wald statistic/degree of freedom) within treatment to test for genotype (G), environment (E) and genotype-by-environment ( $G \times E$ ) interaction effects on pod (Py), haulm (Hy) and harvest index (HI). All terms were highly significant, except when mentioned (ns, non-significant).

	df	WW		
		Py	Hy	HI
G	247	0.56 ns	4.3	4.76
E	3	416.03	128.24	89.04
$G \times E$	991	1.88 ns	5.18	6.42

	df	WS		
		Py	Hy	HI
G	247	3.69	5.84	7.67
E	3	488.75	0.81	308.6
$G \times E$	991	–1.09 ns	1.32 ns	5.1



**Fig. 2.** Vapor pressure deficit (VPD) (A), minimum temperatures ( $T_{p\ min}$ , dashed lines) and maximum temperatures ( $T_{p\ max}$ , solid lines) (B) during the groundnut cropping season (in days after sowing) of 2008 (open symbols) and 2009 (closed symbols) in Sadore (ISC08 and ISC09) (triangle) and Patancheru (IHQ08 and IHQ09) (circle). Arrow headed horizontal line indicate approximate reproductive period (40–90 DAS).

243), ICGV 01232 (no. 211) and ICGV 02189 (no. 217) were top yielding genotypes for their highest coordinates on the average environment coordinate (AEC) abscissa. These genotypes were also the most stable across locations under WS conditions as they positioned near the average environment coordinate (AEC) abscissa. For example also, genotypes ICG 11862 (no. 30), ICG 12235 (no. 33), ICG 4598 (no. 134), ICGV 99001 (no. 246) had among the lowest coordinates on the AEC abscissa and were the lowest yielding genotypes under WS conditions across environments. The GGE biplot also revealed the close location of both Patancheru trials (IHQ08 and IHQ09) whereas Sadore trials (ISC08 and ISC09) were very distant.

The four location trials (IHQ08, IHQ09, ISC08, and ISC09) were positioned in two sectors (Fig. 3B). IHQ08, IHQ09, and ISC08 were located in a same mega environment (ME1). By contrast, ISC09 was located in a second mega environment (ME2). ICGV 97183 (no. 244) and ICGV 02266 (no. 219) which are on the vertices of ME1 sector were the highest yielding in ME1 while ICG 5475 (no. 152) was the highest yielding in ME2. IHQ08 and IHQ09 are far from the biplot origin indicating they had high discriminating ability.

Based on that, the performance of genotypes was compared in environments IHQ09 and ISC09, representative of each mega-environment in order to identify specifically adapted genotypes for each location (Fig. 4). Genotypes performing above average were at the right of the vertical axis for Patancheru, and above the horizontal axis for Sadore. The list of the 25 best genotypes for Patancheru and Sadore is provided in Supplementary Table 2.

On the basis of GGE biplots (Fig. 4), genotypes consistently contrasting across both locations were listed in Table 4. The most tolerant genotypes were those in the top and far right corner of the biplot. Similarly, the most sensitive genotypes were those in the bottom and far left corner of the biplot. To pinpoint those lines showing consistent performance (highest/lowest performance) across both locations, the yields under WS of lines identified from Fig. 4 were normalized in each year and environment against the respective mean trial yield. Then these normalized values were averaged across locations and years and ranked from top to bottom. Since, one purpose of the work was to select contrasting entries for breeders, who usually prefer using genotypes with good

agronomic performance, the mean pod yield under WW conditions of lines identified from Fig. 4 were averaged across the four year–location combinations and varied between about 180 and 350  $\text{g m}^{-2}$ . Genotypes having a mean below 230  $\text{g m}^{-2}$ , i.e. about one standard deviation below the grand mean, were excluded from the list. Therefore, Table 4 provides a list of the 50 most contrasting lines across environments under WS conditions, based on the average of their normalized yield under WS conditions, however excluding entries having a relatively low agronomic performance under WW conditions.

### 3.5. Correlations between pod yield and related traits

Since pod yield under WS conditions was significantly related to pod yield under WW conditions in both years at Patancheru and Sadore (Fig. 1), the pod yield under WS conditions could not be attributed to the drought tolerance of genotypes alone, but to a yield potential component, accounting for 42, 50, 22, and 23% of the pod yield variation under WS in IHQ08, IHQ09, ISC08, and ISC09, plus a residual (Res) yield variation explained by the WS effect and attributable to drought tolerance *per se*. The residual yields unexplained by the yield potential were computed as the difference between yield under WS ( $Y_{ws}$ ) and the predicted yield under WS ( $\hat{Y}_{ws}$ ),  $\text{Res} = Y_{ws} - \hat{Y}_{ws}$ .  $\hat{Y}_{ws}$  was calculated based on the regression equation coefficients of the relationships between yield under WW and WS conditions, such as:

$$\hat{Y}_{ws} = 0.39Y_{ww} + 16.4 \quad \text{and} \quad \hat{Y}_{ws} = 0.45Y_{ww} + 8 \quad (\text{IHQ08 and IHQ09, respectively}).$$

$$\hat{Y}_{ws} = 0.20Y_{ww} + 64.6 \quad \text{and} \quad \hat{Y}_{ws} = 0.32Y_{ww} + 66.2 \quad (\text{ISC08 and ISC09, respectively}).$$

Residuals for pod yield, averaged over 2 years in each environments, ranged from  $-40$  to  $41 \text{ g m}^{-2}$  in Sadore and from  $-82$  to  $46 \text{ g m}^{-2}$  in Patancheru. The absolute values of this range ( $81$  and  $128 \text{ g m}^{-2}$  in Patancheru and Sadore, respectively) were similar to the WS pod yield average in Patancheru and to 50% of those in Sadore, indicating a large range of genotypic variation for drought

**Table 4**

Pod weight (Py, in g m<sup>-2</sup>) and harvest index (HI) of consistently contrasting genotypes (30 tolerant and 20 sensitive) in Patancheru and Sadore under intermittent water stress. Genotype values under well watered conditions are also reported.

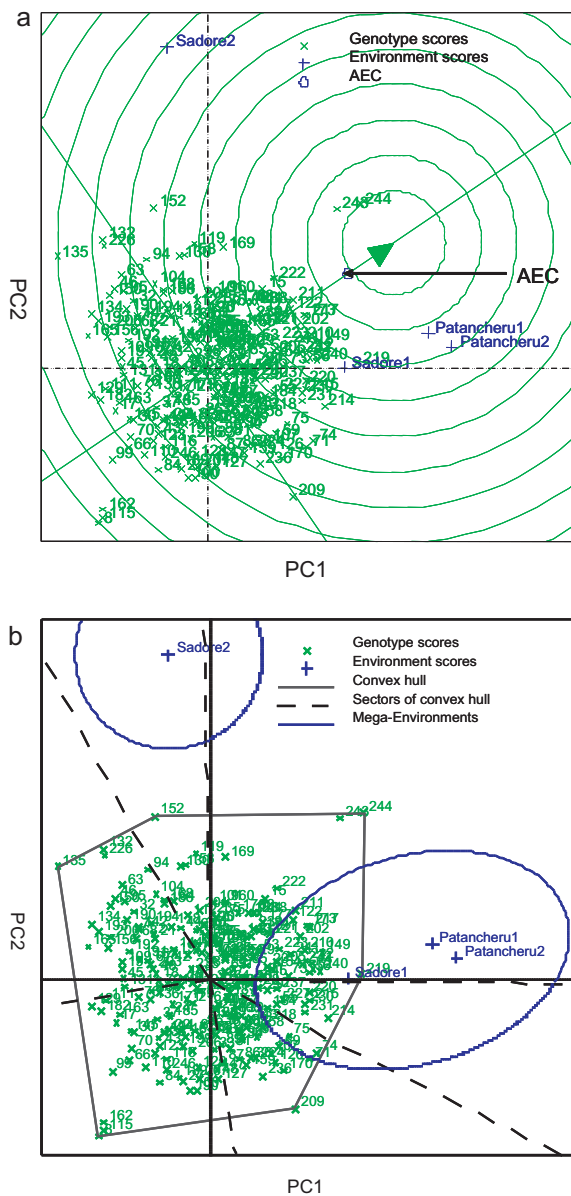
	Entry name	WS				WW			
		Patancheru		Sadore		Patancheru		Sadore	
		Py	HI	Py	HI	Py	HI	Py	HI
Tolerant	ICGV 97183	173.46	0.37	189.66	0.39	303.87	0.49	316.50	0.41
	ICGV 97182	164.54	0.33	184.87	0.40	313.76	0.47	264.25	0.39
	ICGV 02266	165.45	0.32	140.39	0.32	299.09	0.45	299.30	0.43
	ICGV 02189	137.31	0.33	164.24	0.43	273.61	0.46	269.59	0.37
	ICG 11088	140.92	0.36	162.24	0.38	274.41	0.45	285.51	0.42
	ICG 12697	140.61	0.34	156.82	0.36	265.16	0.42	217.50	0.39
	ICG 8751	126.60	0.24	172.90	0.34	211.01	0.31	371.56	0.36
	ICGV 01232	136.32	0.40	162.14	0.42	314.65	0.50	290.88	0.43
	ICG 3140	135.84	0.33	153.23	0.41	257.06	0.43	234.31	0.35
	ICGS 44	135.05	0.35	157.00	0.39	261.85	0.44	292.87	0.44
	ICG 3584	130.56	0.36	158.92	0.45	199.04	0.36	294.87	0.47
	ICGV 95377	148.06	0.35	137.30	0.30	242.82	0.45	275.41	0.43
	ICG 2106	143.39	0.35	141.34	0.43	271.88	0.44	292.22	0.41
	ICGV 02290	131.48	0.25	163.53	0.37	326.25	0.38	288.22	0.46
	ICGV 01276	142.54	0.29	139.29	0.42	250.27	0.35	288.92	0.44
	ICGV 88145	137.99	0.31	142.73	0.37	271.18	0.38	257.11	0.44
	ICGV 02271	133.18	0.36	145.82	0.49	238.02	0.48	269.55	0.55
	ICGV 02022	144.98	0.40	133.12	0.41	244.17	0.50	222.71	0.41
	ICGV 96466	132.35	0.39	148.40	0.41	222.12	0.46	272.97	0.42
	ICG 434	128.36	0.33	153.86	0.39	247.02	0.49	284.35	0.39
	ICG 4729	119.89	0.38	159.45	0.52	235.44	0.39	280.59	0.45
	ICG 12991	111.42	0.33	174.98	0.42	209.24	0.38	302.32	0.45
	ICGV 02038	141.47	0.40	128.89	0.38	241.73	0.48	212.81	0.41
	ICG 4750	130.02	0.35	134.70	0.40	223.06	0.37	280.59	0.42
	ICGV 87378	138.02	0.34	129.77	0.37	308.02	0.45	253.56	0.42
	ICG 15287	123.31	0.30	148.20	0.35	178.11	0.28	306.44	0.40
	ICGV 94169	122.78	0.30	154.01	0.34	194.50	0.36	288.44	0.46
	ICG 12879	112.00	0.33	169.01	0.46	221.64	0.41	275.86	0.49
	ICG 8567	126.87	0.36	144.91	0.38	176.42	0.31	288.04	0.37
	ICG 12625	105.46	0.25	178.22	0.34	217.01	0.33	277.69	0.37
Mean	135.34	0.34	154.33	0.39	249.75	0.41	277.83	0.42	
Sensitive	ICG 5663	84.27	0.14	100.46	0.24	179.60	0.21	274.16	0.37
	ICG 13723	71.08	0.16	124.92	0.25	157.71	0.25	291.79	0.46
	ICG 14482	62.87	0.15	135.41	0.29	213.58	0.27	287.91	0.39
	ICG 10010	59.54	0.14	132.68	0.28	185.43	0.26	341.24	0.41
	ICG 9961	69.38	0.11	122.58	0.32	197.11	0.26	306.95	0.43
	ICG 1834	71.26	0.22	117.18	0.42	191.07	0.34	213.73	0.39
	ICG 3053	72.73	0.15	116.13	0.27	176.12	0.26	232.13	0.32
	ICG 8106	65.45	0.28	119.92	0.29	182.89	0.33	223.60	0.30
	ICG 2777	49.77	0.10	143.90	0.26	182.01	0.25	327.06	0.42
	ICG 2772	70.88	0.11	110.74	0.31	191.89	0.23	222.56	0.36
	ICG 721	59.05	0.11	130.39	0.26	185.84	0.22	214.51	0.31
	ICG 8760	67.22	0.12	110.30	0.22	184.66	0.29	291.73	0.31
	ICG 14523	55.36	0.25	129.95	0.25	165.06	0.20	270.53	0.38
	ICGV 99001	80.00	0.24	89.59	0.21	196.47	0.36	201.62	0.29
	ICG 5286	65.76	0.12	104.06	0.32	215.12	0.28	233.71	0.35
	ICG 12000	50.51	0.07	126.21	0.29	140.48	0.17	281.68	0.40
	ICG 4598	57.10	0.09	111.32	0.26	146.65	0.16	279.26	0.38
	ICG 12235	52.08	0.12	121.48	0.24	118.20	0.17	297.15	0.34
	ICG 13787	48.54	0.08	114.09	0.26	164.09	0.21	277.92	0.37
	ICG 11862	54.18	0.10	63.39	0.18	152.29	0.20	290.16	0.41
Mean	107.11	0.26	139.39	0.35	220.95	0.35	273.96	0.40	

tolerance *per se* in the two locations. We also tested possible relationships between pod yield and flowering and maturity but found no significant relationship (data not shown).

The residuals were strongly related to the harvest index under WS conditions ( $r^2 = 0.36$  and  $0.40$  for IHQ08 and IHQ09,  $r^2 = 0.34$  and  $0.10$  for ISCQ08 and ISCQ09) while no relation was observed under WW treatment at the two locations in both years (Table 5). In contrast, the residuals were poorly correlated to the haulm yield. The residuals were also highly correlated to the ratio of pod yield, i.e. pod yield under (pod yield WS/pod yield WW) (Table 5), showing that the ratio of pod yield could be used as a simple proxy for the residuals and then to discriminate genotypic differences in water stress tolerance. A significant relationship was observed between the residuals and plant growth rate (C) ( $r^2 = 0.15$ ), pod growth rate

(R) ( $r^2 = 0.51$ ) and partition index (P) ( $r^2 = 0.33$ ) under WS conditions in 2008 whereas no significant relationship was found under WW conditions in 2008 and under both water regimes in 2009 (Table 6). The heritability ( $h^2$ ) of C, R and P was high under the two water regimes in both years at Sadore (Table 6).

Correlations were also tested between residuals or haulm weight and SPAD (Soil and Plant Analyzer Development, Japan) chlorophyll meter reading (SCMR), leaf area (LA), leaf dry weight (LDW) and specific leaf area (SLA) measured during the water stress period at Patancheru and/or Sadore in 2008 and/or 2009 (Table 7). In all cases, residuals were unrelated to SPAD reading, SLA or wilt (leaf scoring) across water regimes and locations, regardless of the date when the SPAD/SLA/wilt measurement were made. At Patancheru, a significant relationship was observed only between

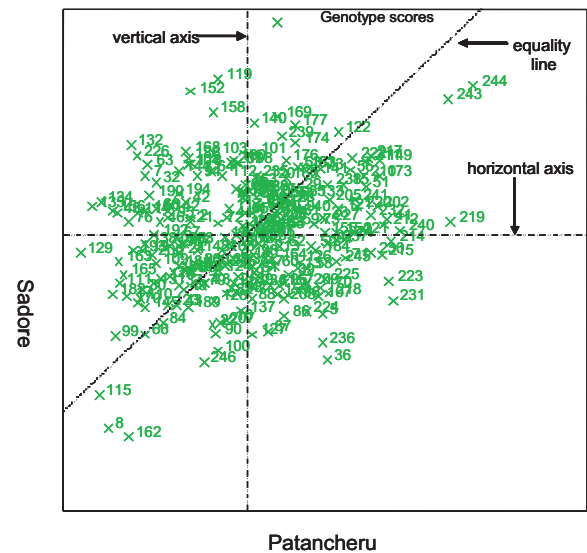


**Fig. 3.** Ranking of genotypes based on the mean performance and stability of pod yield under WS conditions in Patancheru and Sadore during the experimental period of 2008 and 2009 (A). Comparison of GGE biplots indicating the existence of mega environment for the experimental sites of Patancheru and Sadore during the experimental period of 2008 and 2009 (B). The principal component 1 (PC1) and 2 (PC2) are represented as the X- and Y-axis and explained, respectively 43.2% and 35.5% of the phenotypic variation. The AEC represents the average environment coordinate.

Hwt and SPAD under WS conditions in 2008. At Sadore in 2008, residual was correlated to LA and SLA only under WW while Hwt was related to LA and LDW under both water regimes. These relationships were not observed in 2009.

#### 4. Discussion

The present research showed a large genotypic variation for pod yield, haulm yield and harvest index under the two water regimes in the two locations and reports new source of highly contrasting germplasm for pod yield under intermittent drought. A combined analysis across environments showed the predominance of genotypic effects on the pod yield under WS. However, predominant genotype-by-year interaction affected pod yield under WS within both environments. Therefore, under drought stress,



**Fig. 4.** Comparison biplot of the pod yield performances of 247 genotypes using the pod yield in Patancheru in 2009 and that in Sadore in 2009 as a representation of the two major mega environments.

some genotypes showed specific adaptation while some genotypes revealed a broad adaptation to environment, and two mega environments were identified by GGE biplots, one including both Patancheru datasets plus one season in Niger, the second one including the other season in Niger. This study also showed a relationship between the pod yields under WS and WW conditions. The residual yields not explained by the yield potential, which accounted for drought tolerance *per se*, were significantly correlated to the harvest index in the two locations and to the pod partition rate, but they were not correlated to either SPAD readings or to SLA. The large variation for pod yield under drought, the new lines identified, and the preliminary ideas on the cause for the tolerance open a great scope for improving groundnut's drought adaptation and for better understanding the mechanisms of tolerance.

Large genotypic variation for pod yield, haulm yield and harvest index under control (WW) and drought (WS) conditions within locations and across year was observed in this study. Combined analyses of variance for these traits under WS conditions across years and environments indicated that the magnitude of  $G \times E$  interaction was lesser than the magnitude of genotype effect, suggesting that the selection for best genotypes was similar in both environments (Patancheru and Sadore). The predominance of G effect indicates that genotypic effect drove the differences in pod and haulm yield and HI and that genotypes with broad adaptation could be identified (Table 4). Genotypes ICGV 97183, ICGV 97182, ICGV 01232 and ICGV 02189 were indeed high yielding under WS and stable in the two environments, indicating limited interaction of these genotypes with the environment. These lines are currently being used in the crossing program at ICRISAT and they are also used, along with a set of highly sensitive lines to understand the underlying mechanisms of drought tolerance, using both field and controlled environment (Ratnakumar et al., 2009; Ratnakumar and Vadez, in press).

However, GGE biplot also revealed some dissimilarity between Patancheru and Sadore under drought conditions and showed the existence of two mega environments. The GGE biplot pins the slight differences between the environments suggesting that it is effective for analyzing  $G \times E$  interactions through the identification of mega environments. We observed that during the experimental period, the VPD in Sadore was higher than in Patancheru. In addition, the



**Table 5**

Analysis of correlation between the residual yield variations that were not explained by the yield potential and the haulm yield (Hy), the harvest index (HI) under well-watered (WW) and water stressed (WS) conditions in Patancheru (IHQ08 and IHQ09) and Sadore (ISC08 and ISC09). Residual were also correlated with the ratio of pod yield (ratio = pod yield WS/pod yield WW).

		Trait	Residual			
			IHQ 2008	ISC 2008	IHQ 2009	ISC 2009
WW	Hy		0.16	0.09	0.13	0.005
	HI		0.058	0.0624	0.069	0.0079
WS	Hy		0.019	0.016	0.035	0.07
	HI		0.36	0.34	0.40	0.10
Ratio			0.91	0.66	0.93	0.80

**Table 6**

Heritability of the plant growth rate (C), the pod growth rate (R), and the partition index (P). Correlation coefficients between the residual, the pod yield ratio (ratio = pod yield WS/pod yield WW), or the harvest index (HI) and the plant growth rate, the pod growth rate, and the partition index under well-watered (WW) and water stressed (WS) conditions in Sadore in 2008 and 2009 (ISC08 and ISC09).

		Trait	ISC08			HI
			Heritability (%)	Residual	Ratio	
WW	C		83	0.008	0.22	0.009
	R		83.5	0.0003	0.17	0.23
	P		48	0.022	0.016	0.61
WS	C		76.8	0.15	0.018	0.018
	R		76.8	0.51	0.12	0.37
	P		69	0.33	0.10	0.80
		Trait	ISC09			HI
			Heritability (%)	Residual	Ratio	
WW	C		40.6	0.028	0.06	0.002
	R		59	0.009	0.05	0.16
	P		39.3	0.004	0.0007	0.56
WS	C		44.8	0.025	0.008	0.045
	R		48	0.074	0.043	0.35
	P		59	0.087	0.083	0.81

soil in Sadore are arenosols while there is a sandy-clay loam Alfisol in Patancheru. Since the protocol for imposing the water stress was rigorously the same at Patancheru and Sadore, the existence of two mega environments suggests that the selection for best genotypes

is not similar but specific to the environment, which is contrary to previous findings on a more limited set of breeding lines (Ntare, pers. comm.). The mega environment delimitation showed highest yielding genotypes in Patancheru, ICG 1132, ICG 12697 and ICG

**Table 7**

Correlation analysis between the residual yield variations that were not explained by the yield potential or the haulm yield (Hy) under well watered (WW) and water stress (WS) conditions in Patancheru (IHQ08) and Sadore (ISC08 and ISC09), and the SPAD reading values, the specific leaf area, and the wilting scores (wilt) that were recorded in the field. During the 40 days following the treatment imposition, SPAD was measured twice at Patancheru (IHQ08) and 8 times at Sadore (ISC09).

		IHQ08										
		WW				WS						
		SPAD1	LA1	LDW1	SLA1	SPADWS	LA1	LDW1	SLA1			
Residual		0.002	0.006	0.0034	0.001	0.0014	0.002	0.004	0.0006			
Hy		0.05	0.007	0.0119	0.0043	0.22*	0.0086	0.00004	0.0118			
		SPAD2	LA2	LDW2	SLA2	SPADWW	LA2	LDW2	SLA2			
Residual		0.0018	0.00068	0.0085	0.0003	0.0034	0.0006	0.004	0.002			
Hy		0.019	0.0006	0.0001	0.057	0.14*	0.0151	0.0108	0.0181			
		ISC08										
		LA1	LDW1	SLA1	Wilt1	LA2	LDW2	SLA2	Wilt2			
Residual		0.009	0.004	0.003	0.009	0.013	0.004	0.0022	0.013			
Hy		0.159	0.329	0.135	–	0.16	0.23	0.021	–			
		ISC09										
		SPAD1	SPAD2	SPAD3	SPAD4	SPAD5	SPAD6	SPAD7	SPAD8	Wilt1	Wilt2	Wilt3
Residual		0.0005	0.004	0.0013	0.003	0.012	0.011	0.012	0.006	$7 \times 10^{-5}$	$2 \times 10^{-5}$	$3 \times 10^{-4}$
Hy		0.0004	0.003	0.00	0.005	0.0002	0.0002	0.0004	0.0003	–	–	–

\*  $P < 0.05$ .

2106 indeed differed from the top genotypes at Sadore, ICG 12625, ICG 434 and ICGV 02290. These data clearly indicate that a specific adaptation of groundnut genotype needs to be understood. Nevertheless these lines are currently exploited for future groundnut breeding for drought adaptation.

Under WS conditions, our results indeed showed a significant genotype and genotype-by-year ( $G \times Y$ ) interaction effects for pod, haulm and harvest index at each of the two locations. The magnitude of the  $G \times Y$  effect was higher than the magnitude of the  $G$  effect for pod and haulm yield. The high significance of  $G \times Y$  interaction under drought conditions suggests a close interaction between the environmental conditions in which the experiments were carried out and the genotypic response to drought, leading to some differences in how genotypes performed across years. The difference of genotypes performance under water stress compared to well water conditions suggests that intermittent drought tolerance is adaptive. These results agree with previous findings on groundnut (Girdthai et al., 2010; Mothilal et al., 2010; Hariprasanna et al., 2008; Mekontchou1 et al., 2006; Ntare and Williams, 1998). Our interpretation is that the differences in VPD between the seasons within an environment, or across environment could have played a major role. Differences in the sensitivity of transpiration to the vapor pressure deficit have indeed been found in groundnut (Devi et al., 2010). This trait, which gets triggered at VPD around 2 kPa, close to the mean values in the trials, could lead to major water savings in VPD-sensitive genotypes, with likely major effect on their water relations and response to drought. Although we have not measured any transpiration response, it is a possibility that this trait could have played a role in those days when the VPD was above 2 kPa, as was the case in Sadore in 2008. Therefore, the significant  $G \times Y$  interaction observed in this study suggests that genotypic response is driven by how specific plant productive processes interact with the environment, and calls for a better understanding of the mechanisms that lead to increasing yield in different mega-environment, something critical for making targeted progress in the breeding of drought tolerant varieties. This information is also critical in the context of using marker-assisted recurrent selection (MARS) for breeding (Bernardo and Charcosset, 2006) and where the quantitative trait loci (QTL) are first identified being used in recombination between most promising progenies. Large  $G \times Y$  interaction, and the existence of different mega-environments clearly indicates that caution should be used while using MARS, to ensure that QTL detection is made in locations that are representative of most stress environments.

The pod yield under stress conditions was significantly related to pod yield under non-stress conditions at both locations and years. Similar results were previously observed on groundnut (Songsri et al., 2008a,b; Vorasoot et al., 2003; Ntare et al., 2001) and other crops (Vadez et al., 2007; Ober and Luterbacher, 2002). These results showed that the genotypic variation for pod yield under WS conditions could be divided into a component of yield potential and a component of tolerance to intermittent drought *per se*. Therefore drought tolerance *per se*, was closely related to the pod growth rate and the partition rate ( $r^2 = 0.51$ ,  $r^2 = 0.33$ , respectively) under WS conditions. These findings suggest that fast pod filling contributed significantly to the higher pod yield under intermittent drought. Similar results were observed in previous studies (Songsri et al., 2008a,b; Painawadee et al., 2009; Ntare and Williams, 1998; Vorasoot et al., 2003). Ntare et al. (2001) reported a positive correlation between the partition and yield under water deficit and high temperature conditions and suggest partitioning as a screening tool for development of heat-tolerant genotypes, especially in the Sahelian environment. Moreover, partition is less affected by environment and indirect selection for yield via partitioning would result in a 22% increase over direct selection for yield (Ntare and Williams, 1998).

In this study, a close relationship was also observed between the residuals and the harvest index, which points to the likely importance of having reproduction tolerance to drought conditions in groundnut. This was also related to the lack of a significant relationship between the residuals and the haulm weights. For the improvement of drought tolerance based on yield, many studies suggested that an alternative breeding strategy is to use surrogates traits specially when  $G \times E$  interaction is highly significant (Nageswara Rao et al., 2001; Nigam et al., 2005; Painawadee et al., 2009). However, if any trait is to be used as an indirect selection criterion for yield improvement, heritability of such trait should be greater than the heritability of yield (Ntare and Williams, 1998). Our results showed that the heritability of pod yield was 78% in 2008 and 87% in 2009 at Sadore while the heritability of pod growth rate and partition were, respectively 76.8% and 69% in 2008, 48% and 59% in 2009. Investigations are needed to confirm the use of these traits as selection criteria for improving intermittent drought tolerance in groundnut. In addition, our results showed very clearly the lack of any relationship with SPAD reading and SLA. These surrogate traits for transpiration efficiency have been widely used and recommended for drought tolerance screening (Nageswara Rao et al., 2001; Nautiyal et al., 2002; Bindu Madhava et al., 2003; Nigam et al., 2005; Sheshshayee et al., 2006; Upadhyaya, 2005). However, more recent report shows that care should be taken in their use (Krishnamurthy et al., 2007; Devi et al., 2011). Here we clearly show here that they have a likely limited use for groundnut selection for drought tolerance.

## 5. Conclusion

This work reports a large variation for pod yield under intermittent stress conditions and therefore provide new sources of tolerance that are currently used in breeding and to better understand the mechanisms of adaptation, and their interactions with the environment. Importantly, we showed clear evidence that these interactions with the environment condition their response to drought, which indicates that care should be taken when choosing groundnut testing environments. This has important consequences for the choice of the breeding strategy to breed for improve drought adaptation in groundnut, and it also requires research on the mechanistic causes of these large  $G \times Y$  interactions.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.fcr.2011.10.009](https://doi.org/10.1016/j.fcr.2011.10.009).

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