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Original article

Potential agronomic and physiological traits of Spanish groundnut varieties (*Arachis hypogaea* L.) as selection criteria under end-of-cycle drought conditions

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Abstract – Groundnut grown in the Sahel is often exposed to end-of-season drought. The aim of this study was to identify traits associated with yield variation during end-of-cycle water deficit, which could be used as selection criteria. Five new selected Spanish varieties (80–90 days) were compared with the check cultivar, 55-437. Earliness and general adaptation of the varieties did not impair the expression of significant genetic variation for some traits relative to flowering, productivity and physiology. The partitioning coefficient (p) and yield under water stress conditions of the five varieties were higher than those of cultivar 55-437. The water deficit affected leaf area index, relative water content and transpiration at about 2 weeks after the occurrence of water deficit at the soil level. Since genotypic differences seemed to be greatest at this time, measuring physiological traits during this period may provide useful information for breeding early groundnut varieties under end-of-season water deficit conditions.

Spanish groundnut / drought adaptation / end-of-season water deficit / selection criteria / traits variation

1. INTRODUCTION

Groundnut (*Arachis hypogaea* L.) is a major oilseed and cash crop in the Sahel. It is cultivated mainly during the rainy season, characterised by low rainfall ranging between 300 and 600 mm, poor rainfall distribution and high variation. The growing season is short, starting more or less early in July and ending regularly in early October [22]. This short growing season is a consequence of the significant reduction in the length of the rainy season, which since 1970 has been linked to the deteriorating rainfall conditions in the Sahel [13]. In this context, groundnut is mainly cultivated under water-limited environments [23].

Water deficit stress occurring during the seed-filling phase has been observed to cause the greatest reduction in groundnut pod yield [14]. Stress occurring at the pod-development phase is found to be detrimental to several physiological and biochemical processes [17]. Groundnut grown in the Sahel is very often affected by water deficit occurring during the pod-filling phase, which usually coincides with the end of the rainy season [19]. If selection is based only on drought-escape mechanisms, which are mainly provided by the genotype's earliness, yield would be limited particularly under abundant rainfall conditions. The development of groundnut cultivars that withstand water deficit stress better during the pod-formation and pod-filling stages is therefore an important research objective for this region.

A wide range of putative selection criteria that could be used to increase drought tolerance in plants is available. There are, however, very few examples of success obtained using physiological traits in breeding programmes [25]. The main reason for this is that few of these traits have been studied in terms of their functional significance to seed yield [2, 25]. In addition, screening techniques using these traits have usually proved to be laborious and costly [20, 25]. Physiological traits that contribute to drought resistance in groundnut have, however, been identified [18, 28, 15], but they have had very little relevance to breeders. The approach developed here therefore focuses on testing a range of agronomic and physiological traits in order to identify those that could be useful for selecting drought-tolerant genotypes under the targeted environment.

Research work conducted in Senegal has led to the creation of early groundnut cultivars through precocity transfer and association of favourable physiological and agronomic traits using recurrent selection [5]. The aim of the present study is to refine the comparative assessment of yield, phenological, physiological and seed quality traits under both end-of-cycle drought and well-watered conditions. The extent of the variation of these traits between genotypes, and their relationship to grain

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Table I. General description of the six Spanish groundnut varieties from Senegal studied in the experiment conducted in 1994, 1995 and 1996.

Variety designation	0rigine	Botanical classification	Cycle duration[2]	Pedigree	Comments
55-437	Isra-Cirad[1]	Spanish	90	Unknown: ancient selection (1955)	Commonly cultivated cultivar from Africa
Fleur 11	Isra-Cirad	Spanish	90	Spanish × Virginia (China origin)	Recently released in Central Senegal
GC8-35	Isra-Cirad	Spanish	80	55-437 × Chico (genealogical selection)	Recently released in Northern Senegal
55-114	Isra-Cirad	Spanish	80	55-437 × Chico (back-cross selection)	Experimental line
55-138	Isra-Cirad	Spanish	80	55-437 × Chico (back-cross selection)	Experimental line
SR1-4	Isra-Cirad	Spanish	90	Recurrent selection from a population selected for drought adaptation	Experimental line

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[2] In days, from sowing to maturity under rainfed conditions in Senegal.

yield, will be analysed in order to identify useful selection criteria for breeding cultivars with increased yield under drought.

2. MATERIALS AND METHODS

The experiment was conducted during the 1994, 1995 and 1996 rainy seasons in the field, located at the experimental station of the National Centre for Agronomic Research in Bambey, Senegal (14.42°N, and 16.28°W). This is one of the centres of the Senegalese Institute of Agricultural Research (ISRA). The station is situated in the semi-arid zone (isohyets 400–500) of the "Groundnut Basin" of Senegal.

2.1. Plant material

The study was carried out on six early Spanish varieties, all of which were developed in Senegal, within the framework of a European project aimed at improving groundnut adaptation to drought (Tab. I). Three of these varieties have an 80-day (d) cycle and the other three a 90-d cycle. One of the 90-d cycle varieties, cultivar 55-437, commonly grown in the Sahel [11, 19], was used as a check. The others were chosen for physiological studies (1996 experiment) because they generally produced higher yields than 55-437 under natural end-of-cycle drought conditions.

2.2. Experimental conditions

The plants were sown on a sandy (91–94%), ferruginous tropical soil with low clay content (3–6%) which is very frequent in the sub-Saharan region. Two seeds, pre-treated with Granox (Captafol 10%-Benomyl 10%-Carbofuran 20%) to protect them against soil-borne pests and diseases, were hand-planted per hole, at a depth of about 4 cm. Inter- and intra-row spacings were 50 cm and 15 cm, respectively. The seedlings were thinned to one per hole one week after sowing. This corresponds to a sowing density of 133 300 plants/ha. In order not to deviate from the farmers' usual cultural practices for groundnut in the Sahel, no fertiliser was applied. The crop was protected against pests and kept weed-free throughout the study. The 1994 and 1995 comparative variety trials were sown in mid-July after the first significant rainfall. The varieties were harvested 90 or 80 days after sowing (DAS) according to their precocity group. These dates corresponded to about ten to twenty days after the end of the rains. In the 1996 trial, the sowing date was slightly delayed in order to simulate an end-of-cycle water deficit [19]. Two hand-harvests were carried out on the 11th and 20th November according to the maturity group of the genotypes, corresponding, respectively, to 83 and 92 DAS. The harvested plants were exposed to ambient temperatures of 30 to 35 °C so as to allow complete drying of haulms and pods to less than 5% pod moisture.

2.3. Rainfall pattern and watering regime

The total amount of rainfall recorded during the 1994 and 1995 growing seasons was 494 and 495 mm, respectively. Though these amounts were the same for the two years, differences were observed in their distribution. In 1994, 68 mm of the total amount of rainfall was recorded between 60 and 90 DAS, whereas in 1995, during the same period, 130 mm of the total amount of rainfall was recorded. Thus a higher water deficit was produced at the end of the cycle in 1994. During the 1996 trial, rainfall was supplemented by irrigation using an oscillating ramp system. Before planting, 30 mm of water was supplied to all the plots. The first complementary irrigation was applied 23 DAS. However, plants subjected to water deficit conditions did not receive any complementary irrigation until 84 DAS, when 60 mm of water was supplied only to the 90-day cultivars (Fig. 1b). The total amount of water, including the rainfall three weeks prior to sowing, supplied to the 80-d cycle genotypes was 319 mm for plants subjected to water deficit conditions compared with 494 mm for non-stressed plants (+35%). The total amount supplied to the 90-d cycle genotypes was 379 mm for plants subjected to water deficit conditions against 554 mm for non-stressed plants (+32%) (Fig. 1).

2.4. Experimental design

The 1994 and 1995 trials were arranged in a completely randomised block design with four replicates. The plots consisted of 6.6-m-long rows, with each row containing 41 plants. Data

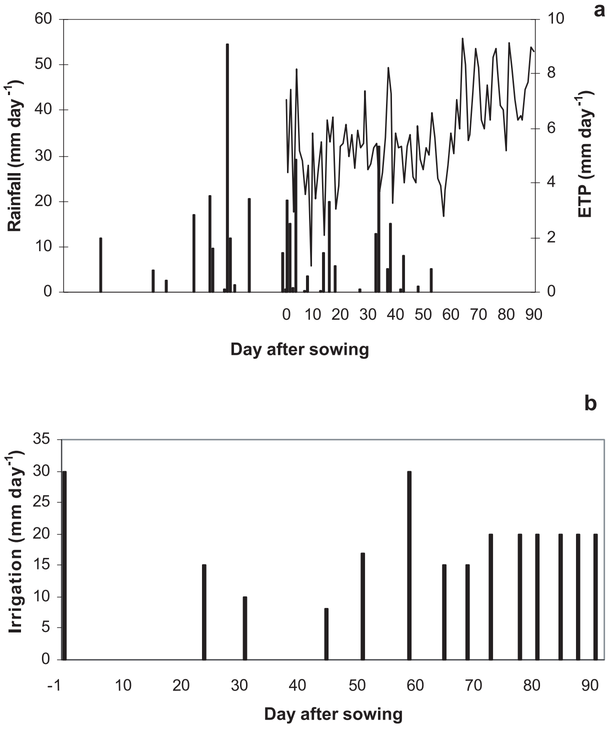


Figure 1. Daily rainfall and evapotranspiration (a), irrigation timing and amounts (b) throughout the 1996 trial.

were collected from the 4 central rows of each plot, corresponding to an area of 12.30 m^2.

The experimental design of the 1996 trial was a split-plot with three replications. Water treatment at two levels, irrigated and end-of-cycle water deficit, was arranged in main plots. The six varieties were arranged in sub-plots. There was a total of 36 sub-plots consisting of 8.4-m-long rows, with each row containing 27 plants. Data were collected from the 4 central rows of each plot, corresponding to an area of 8.30 m^2.

2.5. Measurements and observations

Soil moisture measurements were made during the 1996 trial using a neutron probe (Troxler 4300, Laboratories, Research Triangle Park, North Carolina). The probe calibration, based on gravimetric measurements made in the same field, was calculated according to the following formula:

$$\text{HV (cm}^3\text{ cm}^{-3}) = 0.037X - 0.503, (R^2 = 0.94; n = 44),$$

where HV is the soil water content and X the measured neutron count.

Readings were taken weekly through access tubes installed in the central row of each plot, at distances of 10 cm, at a soil depth of between 0.1 and 2.7 m. The degree of soil drying was expressed as the fraction of transpirable soil water (FTSW) according to the definition of Sinclair and Lecoeur [24] FTSW can be expressed in terms of water availability as follows:

$$\text{FTSW (\%)} = (\text{stock ERD} - \text{stock Pf 4.2}) / (\text{stock Pf 3} - \text{stock Pf 4.2}),$$

where:

- Stock ERD is the soil water content at the "effective rooting depth";
- Stock Pf 4.2 is the soil water content at the permanent wilting point at the effective rooting depth;
- (Stock Pf 3–stock Pf 4.2) is the difference between total soil moisture stored in the root zone at field capacity and permanent wilting point;
- ERD was indirectly estimated during soil water deficit from the intersection point of two successive water profiles when irrigation was withheld.

The flowering traits measured were date of appearance of the 1st flower (1st F), date of appearance of at least one flower on 50% (F50%) and 75% of the plants (F75%) and number of flowers appearing daily from 20 to 40 DAS (FL-dx). The latter measurement was made only during the 1996 trial.

Pod and haulm yields were determined as the dry mass of pods and haulms after air-drying to constant weight. These measurements were made on the whole area of the given plots, except for FL-dx, which was only made on five plants from the given plots.

Seed quality traits were evaluated on a 200 g sample of dried pods randomly taken from each plot and then hand-shelled. The maturity, shelling and sound mature kernel (SMK) percentages were determined. Only sound mature kernels were considered when estimating the 100-kernel weight in grams. The maturity % was estimated based on a visual classification of the colour of the internal pericarp of the hull of opened pods [26].

Leaf area index (LAI) and physiological measurements were recorded in the 1996 experiment. LAI was computed as the ratio of sample leaf area to ground area using a leaf area meter (LAI-2000, LI-COR Inc., Lincoln, Nebraska, USA). The measurements were made weekly, at 36, 44, 51, 58, 64, 79 and 86 DAS.

Leaf transpiration (E), stomatal conductance (G_s) and relative water content (RWC) measurements were made on the second pair of leaflets of the third leaf, counting from the top of the main shoot, of three randomly-selected plants in the given plot. A steady state Porometer (LI-1600, LI-COR Inc., Lincoln, Nebraska, USA) was used for measuring E and Gs, at 36, 43, 50, 64, 71 and 78 DAS. RWC was determined by the gravimetric method, 36, 43, 64, 71, 78 and 90 DAS using the following formula:

$$\text{RWC} = (\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight}).$$

The measurements were made using 10 0.5-cm-diameter leaf disk samples obtained using a cork borer. The fresh weight of the disks was obtained by weighing immediately after they were punched out. They were then rehydrated for 4 h in the dark at room temperature, 28 ± 1.5 °C, and then reweighed to obtain the turgid weight. The dry weight was determined after oven drying for 24 h at 85 °C.

2.6. Derived measurements

Two drought-response indices, a stress-susceptibility index (SSI) and a stress-tolerance index (STI) were calculated:

$$\mathrm{SSI} = 1 - (\mathrm{Ys}/\mathrm{Yi}) \,/\, 1 - (\bar{Y}\mathrm{s} \,/\, \bar{Y}\mathrm{i})\ [9]$$
$$\mathrm{STI} = (\mathrm{Yi} \times \mathrm{Ys}) \,/\, (\bar{Y}\mathrm{i})^2\ [8],$$

where Yi is the pod yield of plots subjected to maximum evapotranspiration, Ys, the pod yield of plots subjected to water deficit, and $\bar{Y}$s and $\bar{Y}$i, the mean yield of all genotypes under stress and non-stress environments, respectively.

A functional relation derived from the harvest index was used for analysing yield (Y) variation as follows [7, 25]:

$$\mathrm{Y} = \mathrm{CGR} \times \mathrm{Dr} \times p,$$

where CGR is the crop growth rate, Dr, the duration of reproductive growth, and p the partitioning coefficient of assimilates to pods. The CGRs, PGRs and p were estimated using the method of Williams [27]:

$$\mathrm{CGR} = \text{Haulm yield} + (\text{Pod yield} \times 1.65) \,/\, \mathrm{Dt}$$
$$\mathrm{PGR} = (\text{Pod yield} \times 1.65) \,/\, (\mathrm{Dv} - \mathrm{Dr} - 15)$$
$$p = \mathrm{PGR} \,/\, \mathrm{CGR},$$

where 1.65 is the fixed adjusting value for the higher energy of pods [7], PGR is the pod growth rate, Dt is the number of days from sowing to harvest and Dv is the duration of the vegetative phase (from sowing to 50% flowering). For the PGR calculation, the beginning of the pod-filling phase was taken as 15 days after the date of 50% flowering according to [19].

2.7. Statistical methods

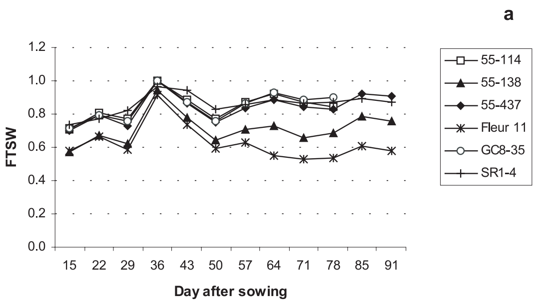
The data were processed for analysis of variance, means comparisons and regression analysis using the SAS/STAT software (version 6.22). Means were compared using the Student-Newman-Keuls (SNK) test for single effects or Duncan's multiple range tests in the case of significant interaction genotype × water regime, at the 0.05 probability level. While yield is clearly the breeding objective, the relationships between each measured trait and pod yield or indices were determined using simple linear regression analysis at the $P < 0.005$ level, with the measured trait as the explicative variable.

3. RESULTS AND DISCUSSION

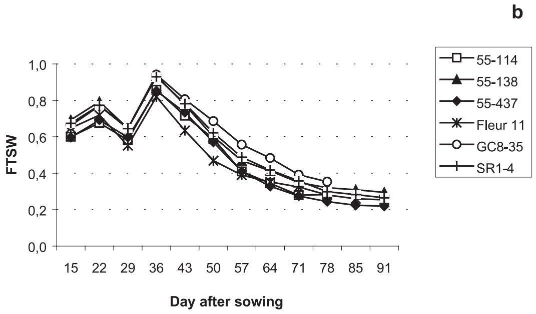
3.1. Soil moisture status

Rainfall and complementary irrigation in the 1996 trial maintained FTSW values of non-stressed plots between 0.6 and 1.0 for all varieties except Fleur 11, which showed values lower than 0.6 between 64 and 78 DAS (Fig. 2a). FTSW values between 0.6 and 0.8 are generally considered as optimum for maintaining the water status and leaf transpiration of plants [21]. Under irrigated conditions, therefore, only Fleur 11 could have been exposed to moderate water deficit conditions between 64 and 78 DAS (Fig. 2a).

In the case of the stressed plots, FTSW values progressively decreased below 0.6 to between 0.2 and 0.3, depending on the variety (Fig. 2b). These values correspond to the threshold value below which crop productivity is severely affected. All the varieties studied started experiencing water deficit conditions at about 50 DAS with the exception of Fleur 11, which started a few days before. This was due to the very poor rainfall of 34.5 mm recorded from 40 DAS to harvest (Fig. 1b).



SEs: 0.05-0.15 for 55-114; 0.02-0.22 for 55-138; 0.02-0.16 for 55-437; 0.08-0.30 for Fleur 11; 0.01-0.13 for GC8-35, and 0.02-0.25 for SR1-4



SEs: 0.05-0.11 for 55-114; 0.04-0.10 for 55-138; 0.00-0.06 for 55-437; 0.05-0.01 for Fleur 11; 0.03-0.11 for GC8-35, and 0.05-0.12 for SR1-4

Figure 2. Evolution of the "fraction of transpirable soil water" (FTSW) with time under well-irrigated (a) and stressed (b) conditions in the 1996 trial.

3.2. Yield component attributes

The data obtained from the 1994 and 1995 rainy season trials generally showed the highest pod yields for Fleur 11 and the lowest for 55-437 (Tabs. II and III). In 1996, variety differences for pod and haulm yields were highly significant ($P < 0.01$) under irrigated and water deficit conditions (Tab. IV). Fleur 11 produced the highest pod and haulm yields of 2116 and 4246 kg ha^{-1}, respectively, under irrigated conditions. Under water deficit conditions, its pod yield of 1049 kg ha^{-1} was among the highest, while its haulm yield of 2426 kg ha^{-1} was among the lowest. Conversely, 55-437 showed the lowest pod yield of 1475 and 791 kg ha^{-1} under both irrigated and stressed conditions, respectively. Its haulm yield of 4019 kg ha^{-1} was, however, not significantly affected under water deficit. In effect, the high drought tolerance of the aerial parts of 55-437, which is an important by-product in the Sahel, is one of the reasons why this cultivar is still largely cultivated in this region. The behaviour of the other varieties was intermediate between that of Fleur 11 and 55-437.

Table II. Agronomic traits of the six Spanish groundnut varieties measured under rainfed conditions during the 1994 trial (data come from three varieties trial including other genotypes).

Variety	1st F (DAS)	F50% (DAS)	F75% (DAS)	Pod (kg ha^{-1})	Haulms (kg ha^{-1})	Maturity (%)	Shelling (%)	SMK (%)	100-k.w. (g)
55-437 (Check)	23.0a	26.0a	27.7b	598.5b	2704.2a	26.2f	64.7bc	35.0b	26.7cde
55-114	22.7a	25.3a	26.2b	841.3a	3018.5a	53.1abc	66.2bc	44.3ab	31.0abc
GC8-35	22.0ab	24.7a	27.0b	612.5b	2466.1a	58.5ab	64.3bc	44.3ab	30.0abcd
55-437 (Check)	23.5a	27.0b	29.0ab	620.6ab	3114.6a	19.7d	62.3ab	37.2ab	25.0cd
55-138	23.0ab	26.0bc	27.0ab	725.7ab	3066.3a	46.0abc	64.3ab	38.8ab	27.3bc
GC8-35	23.0ab	25.0c	25.5ab	681.3ab	3320.1a	59.7a	66.0a	49.6ab	28.7bc
55-437 (Check)	23.5b	26.5abc	30.0	584.6c	2737.5	58.8cd	68.4abc	56.7	28.7c
SR1-4	25.5b	27.0ab	31.0	533.9c	2218.2	75.6a	74.6a	60.3	36.0abc
Fleur 11	23.0bc	24.5d	25.5	1410.9a	2956.9	61.5cd	66.1abc	50.3	43.8a

Means followed by the same letter are not significantly different ($P < 0.05$) according SNK test.
1st F, F50%, F75% = days after sowing (DAS) for the 1st flower appearance, 50%, and 75% of plants flowered, respectively.
Maturity, Shelling, SMK, and 100-k weight = percentages of maturity, of shelling, of sound mature kernels and 100-kernel weight, respectively.

Table III. Agronomic traits of the six Spanish groundnut varieties measured under rainfed conditions during the 1995 trial (data come from three varieties trial including other genotypes).

Variety	1st F (DAS)	F50% (DAS)	F75% (DAS)	Pod (kg ha^{-1})	Haulms (kg ha^{-1})	Maturity (%)	Shelling (%)	SMK (%)	100-k.w. (g)
55-437 (Check)	21.7ab	24.0bc	25.3b	952.2a	4074.2a	50.4ab	69.1bc	49.7a	28.2d
55-114	21.7ab	23.3bcd	24.7b	984.0a	3407.5b	49.7ab	67.9bcd	44.4ab	37.4ab
GC8-35	21.0ab	23.3bcd	24.0b	888.5ab	3212.1b	68.2a	67.7bcd	43.9ab	33.7bc
55-437 (Check)	21.8a	24.4ab	25.5bc	748.4abc	2842.9ab	47.8b	68.5bcd	39.5	27.1c
55-138	21.8a	24.1ab	24.8bc	981.0ab	3158.1ab	63.6ab	70.3bc	48.3	35.7b
GC8-35	20.7ab	23.6 b	23.9cde	754.1abc	3466.7a	62.5ab	69.4bcd	47.2	34.0b
55-437 (Check)	22.5b	24.3d	25.3d	1054.1f	2939.3a	83.3a	73.1bc	61.2a	32.9c
SR1-4	22.6b	26.0c	27.0b	1176.9cde	3182.5a	81.5a	77.4a	67.1a	41.3bc
Fleur 11	21.0c	23.0e	23.7e	1598.2a	3663.2a	68.6b	70.9d	52.9a	50.7a

Means followed by the same letter are not significantly different ($P < 0.05$) according SNK test.
1st F, F50%, F75% = days after sowing (DAS) for the 1st flower appearance, 50%, and 75% of plants flowered, respectively.
Maturity, Shelling, SMK, and 100-k.w. = percentages of maturity, of shelling, of sound mature kernels and 100-kernel weight, respectively.

Fleur 11 was ranked as being the most susceptible, with a SSI value of 1.22, and the most tolerant, with a STI value of 0.79 (Tab. IV). The ranking of the varieties based on these two indices were quite different and even completely opposed in the case of Fleur 11. The SSI is the most currently used index by authors and its calculation leads to the identification of stress-tolerant varieties with low yield potential. On the other hand, the STI allows the identification of varieties with high yield potential and stress tolerance [8]. This was confirmed by the regression curves of the values of these indices against yield under both conditions, which show no significant fit between yield and SSI under irrigated conditions (Figs. 3a and b).

Water treatments have no effect on the partitioning coefficient (p); therefore, all the varieties studied maintained partitioning under drought conditions (Tab. IV). Considering that under drought, p is a more reliable selection criterion for identifying genotypes tolerant to end-of-season drought than yield [19], it could be concluded that the varieties tested generally showed adaptation to drought. In addition, all the varieties showed a more suitable p performance than the 90-d check cultivar 55-437 (Tab. IV). From previous results obtained on groundnut, it was suggested that early genotypes have an advantage in p expression and the harvest index under end-of-season stress, and that differences in p may well be genetic rather than a response to drought [28]. Also, the fact that the p of the 90-d varieties, Fleur 11 and SR1-4, were comparable with the p of the 80-d cultivars confers upon them a particular interest for breeding purposes.

Table IV. Yield components, partitioning coefficient (*p*) and drought-response indices of the six Spanish groundnut varieties under well irrigated (irrigated) and water stressed (stressed) conditions in the 1996 trial.

Variety	Environment	Pod yield (kg ha^{-1})	Haulms yield (kg ha^{-1})	p[1]	*SSI*[2] (rank)	*STI*[2] (rank)
55-437	irrigated	1475	4019 a			
55-437	stressed	791	3293 ab			
55-437 mean		*1133 b*	*3656*			
				0.56 b	1.14 (5)	0.41 (6)
Fleur 11	irrigated	2116	4246 a			
Fleur 11	stressed	1049	2426 cd			
Fleur 11 mean		*1582 a*	*3335*			
				0.72a	1.22 (6)	0.79 (1)
GC8-35	irrigated	1657	3507 ab			
GC8-35	stressed	1003	2002 d			
GC8-35 mean		*1330 ab*	*2755*			
				0.81a	0.95 (4)	0.58 (4)
55-114	irrigated	1495	3364 ab			
55-114	stressed	987	1971 d			
55-114 mean		*1241 b*	*2667*			
				0.81a	0.83 (2)	0.52 (5)
55-138	irrigated	1792	3795 ab			
55-138	stressed	1076	2985 bc			
55-138 mean		*1434 ab*	*3390*			
				0.75a	0.94 (3)	0.67 (2)
SR1-4	irrigated	1666	3669 ab			
SR1-4	stressed	1097	2555 cd			
SR1-4 mean		*1331.1 ab*	*3112*			
				0.71a	0.77 (1)	0.62 (3)
Mean irrigated		1683.2 a	3766.7 a	0.75		
Mean stressed		1000.4 b	2538.6 b	0.71		
Variety (V)		**	***	***		
Environment (E)		*	***	n.s	n.s	n.s
V × E interaction		n.s	*	n.s		

Means followed by the same letter are not significantly different ($P < 0.05$) according SNK test, n.s. is non significant and *, **, *** are significant at the 0.05, 0.01, 0.001 probability levels, respectively.

[1] p = PGR/CGR [27].

[2] Drought-response indices: SSI (stress susceptibility index [9]) and STI (stress tolerance index [8]), following by the ranking according to drought tolerance between brackets.

3.3. Flowering pattern

In groundnut, the flowering pattern is the dominant attribute that determines fruit number [6]. Consequently, early flowering is an important phenological feature, because it contributes to drought escape, which is an essential drought adaptation mechanism of plants under terminal stress [16]. Only the first initiated flowers will effectively result in pods that contribute to yield when the rainy season is short [15]. Hence, traits regarding the flowering pattern were considered from 20 to 30 DAS.

The measurements made during the flowering period (1st F, F50% and F75%) in the rainfed variety trials conducted in 1994 and 1995 showed a significant difference between Fleur 11 and SR1-4 (Tabs. II and III). The results of the 1996 trial generally show a highly significant cultivar effect ($P < 0.001$) and no environment effect (Tab. V). The measurements of 1st F, F50% and F75% confirm previous results; that is, Fleur 11, despite its 90-d cycle duration, flowers the earliest and SR1-4 the latest. Similar results were obtained concerning the number of flowers appearing daily (FL-dx). Since the flowering dates and rank of varieties did not vary according to the year, the flowering pattern seems to be basically controlled by the genotype. Data concerning the rhythm of appearance of flowers (FL-dx) did not provide any additional information on variety differences. Selection for early flowering is therefore possible based on the first three traits, 1st F, F50% and F75%. Though Fleur 11 and SR1-4 showed different flowering durations, their *p* values are similar. This corroborates the hypothesis that *p* is genetically and specifically controlled [28] because it does not seem related to the length of the reproductive phase.

3.4. Seed quality traits

The results of the rainfed trials conducted in 1994 and 1995 showed low values for seed quality traits compared with the irrigated treatment of 1996. This was particularly pronounced in 1994 when the water deficit was very marked at the end of the cycle (Tabs. II and III). The data of the 1996 trial showed that all traits were strongly affected by water deficit stress (Tab. VI). Significant variety effects were observed in the 1996 trial for maturity level, seed weight, shelling and SMK % traits. Variety × environment interaction was significant ($P < 0.01$) for all traits except SMK %, which, in effect, was the most severely affected by water deficit stress ($P < 0.01$).

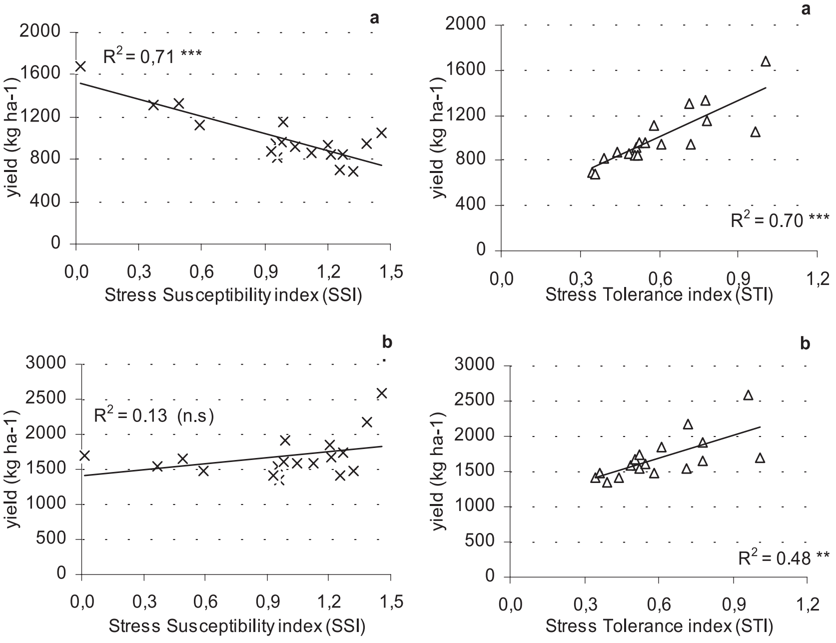


Figure 3. Relationships between yield under stressed conditions (graphs a) and yield under well-irrigated conditions (graphs b) and stress-response indices (SSI and STI) in the 1996 trial.

n.s. is non significant and *, **, *** are significant at 0.05, 0.01, and 0.001 probability levels, respectively

Maturity level, shelling percentage and 100-kernel weight of all the varieties, with the exception of SR1-4, were reduced under water deficit stress. These three traits were, however, significantly reduced only for Fleur 11. The opposite responses to water deficit of Fleur 11 and SR1-4 for these traits explain that the interactions G × E were significant ($P < 0.01$). The determination of the maturity percentage of pod set is essential to evaluate drought escape mechanisms in groundnut during late-season drought. Variety SR1-4 regularly showed the best maturity % in the trials conducted in 1994 and 1995 (Tabs. II and III). In 1996, this variety showed the highest maturity level in both environments, whereas it flowered later than the others (see Sect. 2.3). Conversely, water deficit stress caused the greatest decrease in Fleur 11 pod quality. This can be attributed to its large pod size, which requires more water for filling and ripening. Fleur 11 could therefore not be recommended for the northern areas of the Groundnut Basin of Senegal, which are characterised by very short rainy seasons [4].

Further information brought to light is that the measured traits appear to be genetically variable and very susceptible to drought. They should, therefore, be given particular

Table V. Flowering pattern of the six Spanish groundnut varieties at the beginning of the flowering period in the 1996 trial.

Variety	1st F (DAS)	F50% (DAS)	F75% (DAS)	FL-d23 (nb)	FL-d24 (nb)	FL-d25 (nb)	FL-d26 (nb)
55-437	20.5 a	22.3 b	23.3 b	1.4 c	2.3 b	4.2 c	4.8 bc
Fleur 11	19.0 b	21.2 c	22.0 c	4.3 a	5.0 a	6.0 b	6.2 a
GC8-35	19.7 ab	21.3 bc	22.0 c	4.5 a	6.0 a	8.0 ab	7.0 a
55-114	19.7 ab	22.0 bc	22.0 c	2.8 b	5.2 a	6.5 b	5.7 ab
55-138	19.7 ab	22.0 bc	22.8 bc	2.3 bc	5.5 a	8.8 a	6.7 a
SR1-4	20.4 a	23.3 a	25.2 a	1.1 c	1.9 b	2.8 c	3.8 c
Mean irrigated	20.0	22.0	22.9	2.4	4.0	5.9	4.7
Mean stressed	19.7	22.1	22.9	2.6	4.2	6.0	6.4
Variety (V)	***	***	***	***	***	***	***
Environment (E)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
V × E interaction	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*

Means followed by the same letter are not significantly different ($P < 0.05$) according SNK test, n.s. is non significant and *, **, *** are significant at the 0.05, 0.01, 0.001 probability levels, respectively.

1st F, F50%, F75% = days after sowing for the 1st flower appearance, 50%, and 75% of plants flowered, respectively.

FL-d23, FL-d24, FL-d25, FL-d26 = number of flowers appeared daily at 23, 24, 25, and 26 DAS, respectively.

Table VI. Percentage maturity, shelling, SMK (sound mature kernel) and 100-k.w. (kernel weight) of the six Spanish groundnut varieties under well irrigated (irrigated) and water stressed (stressed) environments in the 1996 trial.

Variety	Environment	Maturity (%)	Shelling (%)	SMK (%)	100- k w. (g)
55-437	irrigated	70.1 a	73.6 abc	69.1	34.7 d
55-437	stressed	51.9 ab	70.6 bcd	64.1	32.4 d
55-437 mean				67.0 ab	
Fleur 11	irrigated	77.6 a	74.5 ab	67.9	54.1 a
Fleur 11	stressed	41.9 b	68.7 d	57.1	45.5 b
Fleur 11 mean				62.5 bc	
GC8-35	irrigated	68.2 a	69.6 cd	62.0	36.1cd
GC8-35	stressed	64.1 a	68.8 d	56.5	34.4 d
GC8-35 mean				59.2 c	
55-114	irrigated	67.1 a	70.6 bcd	61.7	39.4 bcd
55-114	stressed	61.5 a	69.1 d	61.2	37.1 cd
55-114 mean				61.5 bc	
55-138	irrigated	73.7 a	73.6 abc	67.1	39.1 bcd
55-138	stressed	69.7 a	67.9 d	56.5	33.2 d
55-138 mean				61.8 bc	
SR1-4	irrigated	73.5 a	76.4 a	72.2	42.8 bc
SR1-4	stressed	81.0 a	75.5 a	71.4	42.5 bc
SR1-4 mean				71.8 a	
Mean irrigated		71.7	73.1 a	66.7 a	41.1
Mean stressed		61.7	70.1 b	61.3 b	37.5
Variety (V)		*	***	*	***
Environment (E)		n.s.	*	**	n.s.
V × E interaction		**	**	n.s.	**

Means followed by the same letter are not significantly different ($P < 0.05$) according to SNK test, n.s. is non significant and *, **, *** are significant at the 0.05, 0.01, 0.001 probability levels, respectively.

consideration during the process of selection in order to select cultivars with both high production and adequate seed quality under water deficit.

3.5. Development and physiological components

Significant variety differences were observed for LAI from the beginning of the measurements, at 36 DAS, 2 weeks before the occurrence of water deficit estimated based on the FTSW pattern, until 64 DAS (Tab. VII). The water treatment effect was significant from 64 DAS and thereafter. Fleur 11 showed the highest significant LAI of between 2.52 and 4.77 from 36 DAS to 58 DAS. At 58 DAS, corresponding to about 8 days after the onset of water deficit, no significant effect on the LAI was observed. A significant ($P < 0.05$) cultivar × environment interaction was observed at 64 DAS. This corresponded to a significant decrease in LAI under drought, revealed only for Fleur 11 (Tab. VII). As water deficit stress increased towards the end of the cycle, the LAI of Fleur 11 became comparable with those of the other genotypes. This same phenomenon was also observed for the FTSW (Fig. 2b). This suggests a probable link between leaf development of the genotypes and water consumption kinetics expressed by FTSW. It can be deduced, based on the early manifestation of cultivar differences, that the phenotypic expression of LAI is linked to the genotype and that the differential effect caused by water deficit stress on genotypes (interaction) appears to be temporarily accentuated after about 2 weeks of stress. This could probably be the best period to carry out selection based on this trait.

Significant water treatment by variety interaction effects ($P < 0.05$) were observed at 64 DAS for RWC measurements (Tab. VIII). The first group of varieties, 55-437, SR1-4 and GC8-35, showed weak changes of about 5% according to the water regime conditions, whereas 55-114, 55-138 and Fleur 11 showed a greater decrease in RWC of about 12–15% under drought. Measurements made before this date did not show any differences between environments or genotypes. As in the case of LAI measurements, the most interesting feature was observed at 64 DAS, when the varieties seemed to be arranged into groups. These observations, considered together with yield-related measurements (yield under stress, p and STI), show that a rapid decrease in RWC does not impart drought susceptibility, particularly in the case of Fleur 11 and 55-138.

The water treatment effect was also observed at 64 DAS for transpiration rates (E) as well as the closely related measurement of stomatal conductance Gs (results not shown). However, contrary to the other traits, regardless of the measurement date no variety effect was observed (Fig. 4). It could be concluded that genetic variability is difficult to observe for these transpiration-related traits, despite a strong water treatment effect observed between 50 and 64 DAS (Fig. 4).

3.6. Relationship between yield and measured traits

For a trait to be considered as a selection criterion for plant breeding, it must, above all, be variable, but also associated with yield. It is therefore essential to determine whether or not pod yield was correlated with a particular agronomic or physiological component [3, 25]. However, because the relationship of yield to physiological attributes is not clearly understood [2, 12], an essential step would consist of searching for simple correlations between variable traits and yield under stress or drought-response indices. In the 1996 trial, the traits that significantly correlated with pod yield or drought-response indices are E and Gs at 64 DAS, RWC at 64 DAS, maturity % and 100-kernel weight (Tab. IX). No significant regression was observed between flowering traits and yield in this study. This suggests that variety differences in flowering are not associated with yield. This could be attributed to the relative similarity in the phenology of the varieties. A significant correlation ($P < 0.05$) between E and Gs at 64 DAS and pod yield (Ys) was observed under the stressed environment. No significant correlation was found between E at 64 DAS and pod yield under irrigation (Yi). Though this trait showed significant negative correlation with SSI ($r = -0.592$, $P < 0.01$), no significant ($r = 0.391$) positive association with STI was observed. This confirms that a high transpiration rate and stomatal conductance under water deficit stress are favourable attributes for drought tolerance in groundnut, as already indicated by other authors [10, 18].

Table VII. Leaf area index (LAI) of the six Spanish groundnut varieties measured at 36, 44, 51, 64, 79 and 86 days after sowing (DAS) in the 1996 trial.

Variety	LAI 36	LAI 44	LAI 51	LAI 58	LAI 64	LAI 79	LAI 86
55-437 irrigated					3.59 b	2.81 a	
55-437 stressed					2.84 b	2.02 a	
55-437 mean	1.71 b	2.47 b	2.90 b	4.46 a	3.21 b	2.41 a	2.58 a
Fleur 11 irrigated					4.60 a	3.01 a	
Fleur 11 stressed					2.90 b	2.06 a	
Fleur 11 mean	2.52 a	3.10 a	3.98 a	4.77 a	3.75 a	2.53 a	2.40 a
GC8-35 irrigated					2.88 b	2.62 a	
GC8-35 stressed					2.65 b	1.63 a	
GC8-35 mean	1.71 b	2.46 b	2.64 b	3.81 b	2.76 a	2.12 a	
55-114 irrigated					3.14 b	2.63 a	
55-114 stressed					2.34 b	1.51 a	
55-114 mean	1.83 b	2.57 b	2.81 b	4.02 b	2.74 b	2.07 a	
55-138 irrigated					3.61 b	2.73 a	
55-138 stressed					2.70 b	1.42 a	
55-138 mean	1.85 b	2.80 ab	3.31 b	4.50 a	3.15 b	2.07 a	
SR1-4 irrigated					2.92 b	2.78 a	
SR1-4 stressed					2.36 b	1.62 a	
SR1-4 mean	1.71 b	2.43 b	2.67 b	3.86 b	2.64 b	2.20 a	2.47 a
Mean irrigated	1.93	2.69	3.06	4.40	3.45 a	2.76 a	2.93 a
Mean stressed	1.85	2.59	3.04	4.07	2.63 b	1.71 b	2.04 b
Variety (V)	***	*	**	***	***	n.s	n.s.
Environment (E)	n.s.	n.s.	n.s.	n.s.	*	*	*
V × E interaction	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.

Means followed by the same letter are not significantly different ($P < 0.05$) according SNK test, n.s. is non significant and *, **, *** are significant at the 0.05, 0.01, 0.001 probability levels, respectively.

Table VIII. Relative water content (RWC) at 64 days after sowing (DAS) of the six Spanish groundnut varieties cultivated under well irrigated and water stressed conditions in the 1996 trial.

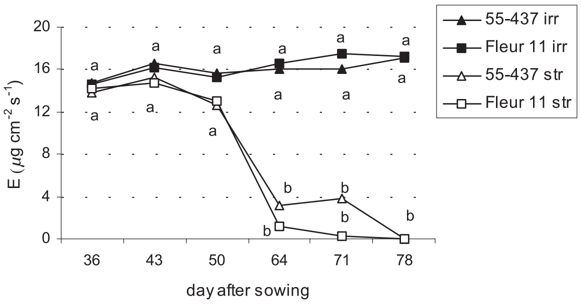
Variety	Well irrigated	Water stressed
55-114	93.56a	79.93b
55-138	92.52a	81.00b
55-437	94.92a	90.89a
Fleur 11	93.18a	79.28b
GC8-35	94.08a	85.78ab
SR1-4	94.92a	90.14a
Mean	93.86a	84.50b
Variety effect (V)		**
Environment effect (E)		**
V × E interaction		*

Means followed by the same letter are not significantly different ($P < 0.05$) according SNK test, n.s. is non significant and *, **, *** are significant at the 0.05, 0.01, 0.001 probability levels, respectively.

RWC at 64 DAS showed a close negative correlation (r = –0.601, $P < 0.001$) with Yi. The negative association (r = –0.446) with STI was significant at $P < 0.05$, but no relationship was found with SSI. These negative correlations confirm the unfavourable effect of a high RWC on pod yield under both environments as suggested above. This result could be explained by the lack of osmotic regulation mechanism in groundnut [1], which ensures a direct link between stomatal aperture (high carbon assimilation) and decreasing RWC.

The high value of seed quality traits such as maturity % and 100-kernel weight appears to be closely associated with high Yi ($P < 0.001$). However, no association was observed with Ys. Correlations were indeed observed between maturity % and SSI (r = –0.483, $P < 0.05$) and between seed size and STI (r = 0.557, $P < 0.05$) (Tab. IX). However, the weakness of these associations and the lack of correlation with Ys does not make these traits, when considered alone, relevant for an indirect assessment of drought adaptation.

The relationship between the studied traits and yield differed considerably under the two water treatments. This highlights the need for selection to be carried out as early as possible under both environments in order to select genotypes that perform



Same letter designates to the same statistical group according to the SNK test at $P < 0.05$

Figure 4. Evolution of the transpiration rates (E) from 36 to 78 days after sowing (DAS) on the most contrasting varieties, 55-437 and Fleur 11, under well-irrigated (irr) and stressed (str) conditions in the 1996 trial.

Table IX. Correlation coefficients (r) between transpiration rate (E) and relative water content (RWC) at 64 DAS, maturity % and 100-kernel weight traits, and pod-yield under both conditions as well two drought-response indices for the six Spanish varieties in the 1996 trial.

Attribute[1]	Correlation coefficient (r)			
	pod-yield[2]		drought-response index[3]	
	Yi	Ys	SSI	STI
E 64 DAS	0.116	0.574*	–0.592**	0.391
RWC 64 DAS	–0.601***	–0.267	0.002	–0.446*
Maturity %	0.655***	0.278	–0.483*	–0.023
100-kernel weight	0.672***	0.412	–0.145	0.557*

*, **, *** indicate significance at 0.05, 0.01, 0.001 probability levels, respectively.

[1] E 64 DAS = transpiration rate at 64 days after sowing (DAS); RWC 64 DAS = relative water content at 64 DAS; Maturity % = percentage of maturity at harvest; 100-kernel weight = weight of 100 SMK (sound mature kernels).

[2] Yi = pod-yield under irrigated conditions; Ys = pod-yield under stressed conditions.

[3] SSI = stress susceptibility index [9]; STI = stress tolerance index [8].

well even under favourable conditions. In the case of all four traits, when significant correlations were observed for SSI, they were non-significant for STI and vice versa.

3.7. Conclusion: selection criteria for groundnut drought adaptation

In this study, the relative similarity in the phenology of the varieties did not impair the expression of significant differences for some traits relative to flowering, productivity and physiological responses, during end-of-season water deficit stress. As such, some guidelines to improving the selection of groundnut cultivars could be given.

At the agronomic level, no direct link was found between flowering and productivity. The *p* coefficient was the same for Fleur 11 and SR1-4, the two varieties that showed the most pronounced difference in flowering. This confirms that flowering time and yield-related traits have to be selected independently to improve drought adaptation in groundnut.

Seed quality traits were very sensitive to drought. Their measurement has to be considered over and above yield by breeders, because they are not associated with yield under stress conditions, neither are they clearly related to drought-response indices.

The results of this work show that the genotypes did not respond in the same way to both of the stress-response indices calculated on the basis of yield, under stress and non-stress environments. This is particularly true for Fleur 11 and 55-437, with nearly the same indices, which were high in the case of SSI, and at both extremes in the case of STI. This confirms that the two indices do not give equal assessment of varieties.

The timing for the application of stress in order to have maximum genetic variability and/or interaction, was determined from soil moisture and physiological traits measured in the 1996 trial. Observations made on LAI, RWC and E can be summarised for practical use in a breeding programme. For these three traits, the water treatment effect appeared at the same date close to 64 DAS, corresponding to about two weeks after the onset of the water deficit stress. Before this period, no environment effect was observed for any of these traits. Since differences between varieties for these traits were not obvious beyond 64 DAS, measurements around this date will probably provide useful information for breeding early groundnut genotypes under end-of-season water deficit conditions.

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