Sources of Variation in Shelling Percentage in Peanut Germplasm and Crop Improvement for Calcium Deficiency-Prone Soils[1]

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ABSTRACT

Calcium (Ca) deficiency causes peanut pegs and pods to abort, resulting in decreased shelling percentages and yields. Environmental factors influencing calcium availability include soil Ca content and soil moisture. Genetic attributes that influence the sensitivity of cultivars to soil Ca supply include pod size, soil volume per pod (varied by plant growth habit), and pod wall attributes. Where Ca fertilization is not possible, genetic solutions to Ca deficiency are important, and breeders need information on the relative importance of these attributes. The objective of this research was to quantify the relative importance of these three sources of variation. Data from three trials were used to evaluate the relative importance of these attributes. The trials, sited on Ca-deficient alfisols, used between four and 12 germplasm lines with varied Ca sensitivity- determining attributes. Lines differed in growth habit (spreading or bunch), pod volume, pod yield, shelling percentage, and seed yield. The trial treatments and environments (sites and seasons) also varied Ca supply through soil type, fertilization, and water supply. Assuming that Ca supply has little impact on crop growth rates (CGR), a physiological model was used to set aside the contributions of CGR to yield differences between treatments. The three trials were analyzed separately and then combined for further regression analysis by defining each site and treatment combination as an environment. Within trials, variations in shelling percentage accounted for up to half the variations in seed yield between lines. In the combined analysis, easily selected attributes—pod volume (58% of germplasm sums of squares) and plant habit (8%) and their interaction (14%)—accounted for much of the variation in shelling percentage. The interaction was due to shelling percentage being less influenced by pod volume in spreading than in the bunch types. Thus, in Ca-limiting situations, the spreading growth habit allowed larger seeded peanuts to be grown than the bunch growth habit because of the greater pod dispersal of this type. Assuming that the lines tested typified peanuts for their relation between attributes and Ca deficiency-based shelling percentage variations, breeders should place the greatest emphasis on small pod size to decrease peanut sensitivity to Ca deficiency. Increased soil available to each pod by pod dispersal decreases the need for small pods to decrease sensitivity to Ca-deficient soils.

Key Words: *Arachis hypogaea*, groundnut, growth habit, pod volume, shelling percentage, germplasm, bunch type, spreading type, pod density.

In the semi-arid tropics (SAT), where soils are often low in mineral contents and mobility of nutrients may be limited by soil moisture deficits, peanuts often experience calcium (Ca) deficiency. Insufficient Ca in the pod zone is a well-established reason for the failure of pod formation and filling (Colwell and Brady, 1945; Cox *et al.*, 1976). When inputs are not limited, gypsum application is a standard agronomic practice by farmers growing peanuts on the sandy soils preferred for this crop. Calcium deficiency reduces pod yields and the quality of seeds. This situation may be aggravated by soil moisture stress (Conkerton *et al.*, 1989). Calcium deficiency may act both by decreasing the initiation of pods and the growth of embryos in expanded pods. In soils with adequate Ca levels, Rajendrudu and Williams (1987) found that application of gypsum could interact with drought stress by increasing the rate of pod initiation, effectively providing an escape mechanism from drought.

The cultivated peanut has a wide range of morphological attributes (Gibbons *et al.*, 1972) which are exploited in various agronomic situations. Various genetic attributes do, or may potentially, influence the development of Ca nutrient deficiencies. The most widely recognized attribute influencing Ca nutrition is pod size, which determines the Ca uptake-surface:volume ratio of the fruit (Keisling *et al.*, 1982). The plant growth habit also may influence Ca absorption. Hartmond *et al.* (1994) found that the greater dispersal of pods in the soil due to the spreading habit resulted in better pod-fill in situations where the shelling percentage was less than optimum. Walker *et al.* (1976) reported higher yields of a spreading cultivar when compared to bunch cultivars at low soil Ca levels. Finally, there is a range of other attributes, such as resistance to transport of Ca through the pod wall to the seed (Kvien *et al.*, 1988), which may affect Ca deficiencies.

Despite their widespread use in the intensive peanut cultivation in the USA, the spreading growth habit is apparently not considered advantageous for the SAT. Most lines developed for this region have the bunch growth habit. Reasons for the lack of interest in improving the spreading types are not well documented. Possible reasons include their generally long growth cycle, which exceeds the available rainy season length in many tropical environments and the greater difficulties in hand-harvesting spreading types. There is also contradictory information about yields of spreading types in less favorable environments. In Mexico, 10 spreading lines yielded significantly less than bunch types (Sedano Delgado *et al.*, 1988). Although the physiological basis for these effects was not determined, the result may reflect the difference in crop breeding effort invested into the two types. There are apparently no reports to show that the primary productivity of spreading types is less than that of bunch types.

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The yield of a crop (Y) can be described in terms of crop growth rate (CGR), duration of the reproductive phase (D_r), and partitioning (p) by Equation 1 (Duncan *et al.*, 1978):

$$Y = CGR \times D_r \times p \qquad [Eq.1]$$

Crop growth rate and the total biomass are closely related to resource use (light interception or transpiration) because of the conservative nature of radiation-use efficiency (Monteith, 1990). In peanut where the oil in the seed has a higher energy content than other plant parts, this must be adjusted when comparing total biomass across treatments with different fractions of seed (Duncan *et al.*, 1978). Ca deficiency can be expected to modify p but not greatly affect the CGR term of the model.

The objectives of this study were to improve the understanding of the role of morphological attributes in influencing peanut Ca nutrition in Ca deficiency-prone situations and to set priorities on selection criteria for improving yields in Ca-deficient areas by breeding.

Materials and Methods

During the rainy and post rainy seasons of 1989 and 1990, field experiments were conducted at Sadore, the Sahelian Center of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), 45 km south of Niamey, Niger, and at Tara, a research station of the Institute National des Researches Agronomique de Niger (INRAN), 300 km further to the south in the Sudano-Sahelian zone. At Sadore, the annual average rainfall between June and September is 560 mm. Soils are highly variable Psammentic Paleustalfs, with a very low exchange capacity (less than 0.03 meq g^{-1} soil), and with a $pH_{(KCl)}$ of 5 to 5.2. The top soil is 94% sand and only 3% clay (West *et al.*, 1984). At Tara (annual average rainfall 850 mm) the soil is classified as Haplic Acrisol with 90% sand in the top soil. It has a $pH_{(KCl)}$ of 4.9, and the cation exchange capacity is 0.06 meq g^{-1} (INRAN, 1990; Fechter *et al.*, 1991).

The fields used were all fallow preceding the experiments and grasses and bushes were removed manually. To preserve the soil structure, the peanut seed was sown directly by hand into the soil without further cultivation. Plant spacing was at 10 cm intervals in rows 50 cm apart. Twelve kg ha^{-1} nitrogen and 30 kg ha^{-1} phosphorus were applied as diamonium-phosphate before sowing. Calcium was applied at pegging as gypsum. All fertilizers were banded in a strip within 12 cm from the mainstem. Plots were 4 x 5 m, and treatments were arranged in a randomized block design with three (in Expt. 1) and then subsequently with five replications.

Experiment 1 was conducted at Tara in 1989 using 12 lines (Table 1) with different pod sizes and growth habits and with natural rainfall. Three levels (0, 120, or 240 kg ha^{-1}) of Ca were applied as gypsum at pegging.

Experiment 2 was conducted at Sadore in 1989 toward the middle of the rainy season. The bunch lines 28-206 and ICG MS 42, and the spreading lines 47-16 and M13, were grown at two levels of Ca (0 and 240 kg ha^{-1}) with five replications. Lines within plant-habit groups have different pod sizes. Late season water stress occurred from 65 d after sowing following the cessation of rain.

Table 1. Seed yields, shelling percentage, and pod volume of 12 peanut lines grown at three levels of Ca application at Tara, 1989 (Expt. 1).

Growth habit[a]	Germplasm line	Ca applied (kg ha^{-1}) Seed yield 0	120	240	Shelled seed 0	120	240	Pod volume[b]
		--- kg ha^{-1} ---			--- % ---			mL pod^{-1}
B	Chico	636	693	719	69.1	62.9	67.4	0.87
B	55-437	554	556	611	58.0	63.6	58.9	1.20
B	28-206	356	486	480	52.3	65.7	65.0	1.60
B	ICGS 11	677	785	843	56.7	66.3	74.4	1.75
B	ICG MS 63	397	588	559	43.2	60.9	67.8	2.21
B	ICG MS 42	450	475	523	39.5	55.9	59.5	2.42
B	ICG MS 189	383	398	297	57.6	56.3	51.6	2.49
B	ICGV MS 83030	183	443	381	22.9	37.1	36.9	2.93
B	ICG MS 525	198	187	399	7.5	32.9	45.1	3.00
S	47-16	565	624	666	66.0	71.5	73.5	1.20
S	Kadiri 71-1	426	406	511	63.5	65.6	67.1	1.69
S	M13406	406	551	359	46.4	58.8	61.4	2.81
	LSD (0.05)		205			14.2		
	CV (%)		24.5			15.4		

[a]S = spreading, B = bunch.
[b]Bulk sample data; no statistical analysis.

Experiment 3 was conducted in the dry season of 1990 from the beginning of February and with the same four lines as used in Experiment 2. Treatments were increased to include two Ca and two irrigation levels. The crop was irrigated weekly with 25 mm of water until pod formation commenced. Differential water stress was then achieved by applying either weekly irrigations of 36 mm (reflecting increased evaporative demand) for the unstressed treatment, or 12 mm for the stress treatment until harvest.

In all experiments, pod and haulm yields were recorded; yield components and shelling percentage were assessed on a 500-g subsample. Pod volume was determined by displacement of water on a treatment bulk sample in Experiments 1 and 2, but on a plot sample in Experiment 3.

Statistical analysis was initially conducted using analysis of variance for individual experiments as indicated by their design. To normalize yields for differences associated with variation in resource capture, the energy adjusted biomass (Duncan *et al.*, 1978) was calculated and used as a covariate in the analysis of pod yield.

A combined analysis using all experiments was conducted after assigning dummy variables to individual genotypes for growth habit, and redefining each combination of Ca and irrigation treatment in each experiment as a separate environment. This provided a highly unbalanced set of data that was analyzed using regression methods in the REML procedure of GENSTAT (Numerical Algorithms Group Ltd.). These techniques were used to examine the variation in yield and shelling percentage, as influenced by environment (based on experiment, site, year, irrigation and Ca fertilization components), habit, pod size, and other (residual) genetic attributes. Because the order in which attributes were included in this regression analysis could influence the results, variables were examined for their contributions to variance in several different sequences.

Results and Discussion

At Tara in the 1989 rainy season, 530 mm of rain were received. Although this was well below the long-term average, neutron probe measurements (data not reported) showed adequate soil water throughout most of the experiment. Calcium applications (120 and 240 kg ha^{-1}) enhanced the exchangeable Ca content of the pod zone (0-15 cm) soil from 54 g kg^{-1} to 100 and 149 g kg^{-1} (measured, after extraction with 1N ammonium acetate, by atomic absorption spectrophotometry) 4 wk after application. However, by the time of harvest these soils only contained 64, 70, and 78 g kg^{-1} of Ca, respectively, presumably because of leaching.

The use of biomass as a covariate partitions the variance for yield into that associated with resource capture (the covariate), and the remainder; here assumed to be largely due to either genetic differences in potential partitioning, or Ca nutrition effects on the realization of this potential. This approach was used because it is well established that variation in yield associated with crop growth rates is due to differences in energy interception or transpiration (Monteith, 1990), and this source of variation has little significance to the interaction of peanut lines with Ca nutrition.

In Experiment 1, seed yields and shelling percentage (Table 1) only improved with Ca application in some lines, with most of the response due to the application of 120 kg ha^{-1} Ca. Further analysis using shelling percentage as a second covariate resulted in the Ca treatments and their interaction with genotypes no longer being statistically significant, supporting the hypothesis that the Ca deficiencies were manifest in the shelling percentage and that these varied with germplasm line.

Differences in seed yields of the 12 lines were very distinct (Table 1). Seed yield was dependent on shelling percentage (the linear regression accounted for 49% of yield variations across genotype within the control Ca treatment). Shelling percentage of lines was strongly influenced by germplasm line and Ca application. The large pod lines gave the lowest shelling percentage among the lines tested; without the addition of Ca, pods of ICG MS 525 contained almost no seeds. The mean pod and hundred seed weights were increased over all lines by Ca application (Table 2) without a significant interaction of lines with Ca treatment.

Table 2. Mean hundred seed weight, and weight from 12 peanut lines at three levels of Ca application (Expt. 1).

Ca applied	Seed mass	Pod mass
kg ha^{-1}	g 100^{-1}	g pod^{-1}
0	42.5	0.76
120	45.7	0.96
240	47.1	0.97
LSD (0.05)	0.03	0.08
CV (%)	16.7	22.4

In Experiment 2 at Sadore with end-of-season water stress, pod yields did not differ after the biomass covariate adjustment, indicating that the treatment effects were the result of variations in resource capture. The spreading cultivar M13 had the largest pods and the lowest shelling percentages (due to a high percentage of aborted ovules) of all lines (Table 3). The Ca application increased yields only for line 28-206.

In Experiment 3, the cultivars responded differently to Ca application and irrigation (Table 4). The small-

Table 3. Pod yield, shelling percentage, and pod volume of four peanut lines grown at two levels of Ca application, Sadore, 1989 (Expt. 2).

		Applied Ca (kg ha^{-1})				
		0	240	0	240	
Growth habit[a]	Germplasm line	Adjusted seed yield		Shelled seed		Pod volume[b]
		-- kg ha^{-1} --		-- % --		mL pod^{-1}
B	28-206	447	482	62.9	70.9	1.1
B	ICG MS 42	381	358	67.0	66.6	1.7
S	47-16	398	392	71.1	67.5	0.9
S	M13	352	362	51.4	56.2	1.9
LSD (0.05)		72		8.51		

[a]S = spreading, B = bunch.
[b]Bulk sample data; no statistical analysis.

Table 4. Pod yield, shelling percentage, and pod volume of four peanut lines grown at two levels of irrigation and Ca application at Sadore in the dry season, 1990 (Expt. 3).

	Irrigation[a] (%)					
	33	100	33	100	33	100
Germplasm line	Seed yield		Shelling		Pod volume	
	-- kg ha^{-1} --		--- % ---		- mL pod^{-1} -	
Ca (0 kg ha^{-1})						
28-206	697	1290	50.4	65.8	2.01	2.51
ICG MS 550	297	601	6.6	7.0	3.56	3.77
47-16	1026	1584	63.8	70.6	1.86	1.94
M13	605	990	45.4	54.2	2.96	3.51
Mean	657	1022	41.5	49.4	2.60	2.93
Ca (240 kg ha^{-1})						
28-206	590	985	42.8	58.4	2.04	2.37
ICG MS 550	224	689	28.8	40.4	3.90	5.00
47-16	1025	1632	59.2	72.4	1.91	2.14
M13	646	1267	47.0	62.6	3.20	4.37
Mean	716	1143	44.4	58.4	2.76	3.47
LSD (0.05)[b]	687		5.0		0.38	
LSD (0.05)[c]	447		10.0		0.77	
CV (%)	22.2		16.3		20.7	

[a]As a percentage of potential evapotranspiration.
[b]For comparing irrigation by Ca means.
[c]For the body of the table.

podded spreading cultivar 47-16 yielded more than the other lines and showed the highest shelling percentage in all treatments. The large-podded spreading type M13 yielded very little when the water supply was insufficient. This low yield was largely due to the effects of water supply on total growth since the biomass adjusted yields were comparable to other lines. ICG MS 550 exhibited a very poor shelling percentage without the addition of Ca.

Calcium application in the drought-stressed treatment did not enhance pod yields and shelling percentage, except for ICG MS 550. The higher irrigation amounts augmented the effect of the Ca treatment on the shelling percentage. However, irrigation operated mainly through its effects on total biomass because the effect of irrigation was not significant in the covariate analysis (Table 5).

Table 5. Analysis of variance table for seed yields in Experiment 3 using biomass as a covariate.[a]

Source of variation	d.f.	Sums of squares	Mean squares	F-value
REP Stratum				
Covariate	1	45581	45581	1.05
Residual	3	129942	43314	0.17
REP*IRR Stratum				
IRR	1	318658	318658	1.23
Covariate	1	405500	405500	1.57
Residual	3	777073	259024	6.71
REP IRR*Units*Stratum				
GL	3	6838077	2279359	59.08***
CA	1	161375	161375	4.18
IRR x GL	3	983512	327837	8.50**
IRR x CA	1	18682	18682	0.48
GL x CA	3	893215	2977384	7.72**
IRR x GL x CA	3	132368	4123	1.14
Covariate	1	2152840	2152840	55.80***
Residual	55	2122122	38584	
Total	79	14978945		

[a]GL = germplasm line, IRRI = irrigation, CA = calcium level.
*,**,***Significant at the P = 0.05, 0.01, and 0.001 levels, respectively.

Pod size varied markedly between lines. ICG MS 550 and M13 had the largest pods with an average of 4.1 and 3.5 cm^3 pod^{-1}, respectively, while 28-206 and 47-16 only had pods of 2.2 and 2.0 cm^3 pod^{-1}. Calcium application only enhanced the pod size of the large podded lines whereas the higher irrigation intensity increased pod volume in all genotypes.

The pod yields observed in this study were fairly low but fall within the range of yields that were reported for these environments by Boote (1983). The irrigation applied to match evaporation improved yields and the shelling percentage in Experiment 3. Cox *et al.* (1976) obtained similar large yield responses to irrigation. Cox *et al.* (1976) and Rajendrudu and Williams (1987) found a stronger response to Ca application under drought than under higher levels of irrigation. However, 240 kg ha^{-1} Ca only slightly enhanced the shelling percentage. The shelling percentage increased only when the soil water was sufficient. However, since these irrigation effects were not significant once the effects of irrigation on total growth were considered, it seems that pod growth is more rapidly modified by carbon fixation than Ca transport in the soil solution. This agrees with Balasubramanian and Yayock (1981) who concluded that a Ca application without correcting a severe moisture stress could not always alleviate unfilled pod problems in Ca-deficient soils.

To compare results from all experiments, each combination of experimental site, the level of Ca, and irrigation treatment was considered as a separate environment, thus defining nine environments (Finley and Wilkinson, 1963). The data for spreading and bunch types were pooled and subjected to stability analysis. The regression demonstrates that spreading lines yielded comparatively well in all environments (Fig. 1), in contrast to the findings of Sedano Delgado (1988). While the effects of genetic differences in yield potential cannot be separated completely from Ca-deficiency effects, 40 to 50% of the variation in seed yield was associated with variations in shelling percentage and therefore may be attributed to Ca deficiency.

A germplasm line by Ca application interaction also

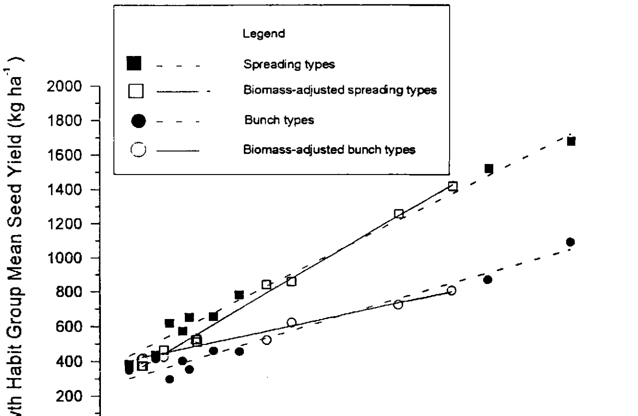

Fig. 1. Relative seed yield of spreading and bunch habit peanuts (actual and biomass-covariate adjusted) in environments in Niger. Environments differ in Ca supply as influenced by site, sowing time, Ca fertilization, and irrigation/rainfall pattern.

was observed in Experiment 1. The shelling percentage of several genotypes was increased with the addition of 120 kg of Ca, while a further 120-kg increase had a small effect on the pod filling (Table 1). The application of 240 kg ha^{-1} Ca enhanced the soil Ca level by 80 ppm so, in these experiments, the soil Ca levels were always below the threshold level of 150 ppm suggested by Wolt and Adams (1979). For the experiments at Tara and Sadore, soil Ca levels of 60 to 140 ppm were measured, but most responses were observed with the addition of only 120 kg ha^{-1}. Clearly, the Ca levels necessary for pod filling are influenced by other factors, including variety and growth habit.

A highly significant negative correlation between pod volume and shelling percentage was detected in all the experiments, as previously observed by Keisling *et al.* (1982). However, the regressions of the shelling percentage on pod size for the spreading and bunch germplasm lines show pod filling of spreading types to be less sensitive to pod size (Fig. 2). This interaction between growth habit and pod volume was highly significant (Table 6) and was probably due to reduced competition for Ca in the soil associated with more uniform pod distribution (Hartmond *et al.*, 1994). Although these results are based on a small selection of lines, the results suggest a priority for breeders to use spreading peanut types for solving the problem of Ca deficiency where fertilizer inputs are not possible.

The combined regression analysis examining the contribution of environment, pod volume, habit, and "other" unmeasured attributes of lines to the total sums of squares (Table 6) indicated that all these factors contribute to shelling percentage. Of these traits, the pod volume was most significant, but there was a strong interaction between growth habit and pod volume. The growth habit and its interaction with pod volume were more important than other (residual) varietal factors—such as transport resistance (Kvien *et al.*, 1988)—but this ranking could depend on the particular lines evaluated. This order of significance was not influenced by the sequence in which the terms were included in the analysis, although the relative fraction of variance was (as expected) influenced.

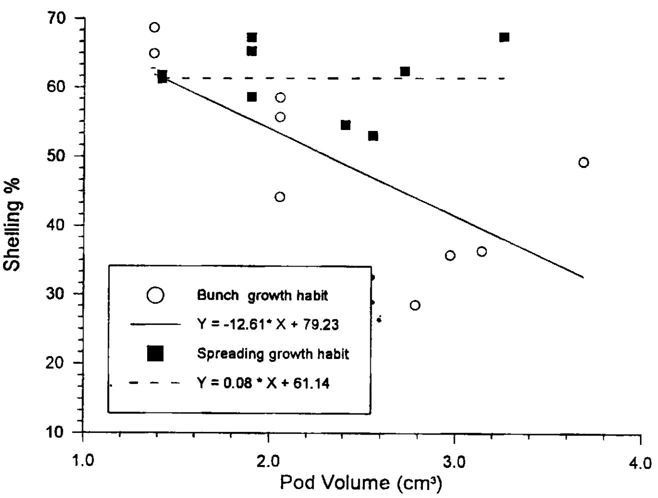

Fig. 2. Relationship between pod volumes and shelling percentage of spreading and bunch growth habits across a range of Ca supply-determining environments.

Table 6. Analysis of variance for factors contributing to variations in shelling percentage combining experiments, Ca and irrigation environments.

Factor	d.f.	Sum of squares	Mean squares	F-value
Pod volume	1	5799.39	5799.39	93.28***
Plant growth habit	1	837.91	837.91	13.48**
Volume x growth habit	1	1425.84	1425.84	22.93***
Other factors[a]	8	1915.09	239.39	3.85**
Environments	8	2115.73	264.47	4.25**
Residual	34	2113.76	62.17	
Total	53	14207.71	268.07	

[a]Residual genetic effects.

*,**,***Significant at the P = 0.05, 0.01, and 0.001 levels, respectively.

These results have significance for selecting lines within breeding programs targeting improvement in Ca deficiency-prone soils. For areas where pod filling is an important problem, the easiest crop improvement solution is provided by selection for smaller pods. However, peanut quality and market value are determined also by size, so pod dispersal through plant habit should be considered as a selection criterion. Where Ca fertilization is not used by farmers, it is important that breeders either do not use Ca fertilization in their selection plots, or they select pod sizes which match the Ca supply potential of the target soils. Better pod dispersal need not be associated with the prostrate plant forms since peanut does have semi-spreading types. Achieving sufficient dispersal of pods through the intermediate spreading bunch types may be possible if there is strong reason not to use the spreading types. A simulation model to allow breeders, agronomists, and farmers to examine the interaction of plant attributes and soils for Ca nutrition of pods could help define the extent of pod dispersal needed to maximize pod size. The limited number of lines tested in the present study demands further evaluation of the scope for genetic solutions to Ca deficiency.

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