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Heritability of components of a simple physiological model for yield in groundnut under semiarid rainfed conditions

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Abstract

Use of physiological models has been suggested as a means to improve efficiency of breeding for higher yield. Our objectives were to estimate heritabilities of yield components of groundnut (*Arachis hypogaea* L.) identified in a yield model [crop growth rate (C), reproductive duration (D_R) and partitioning (p)] and determine their predictive value in early generations. Forty bulk populations and nine parental lines were evaluated in replicated trials in 1992 (F_2), 1993 (F_3) and 1994 (F_4) at three contrasting locations in Niger. Physiological components of yield were estimated from final yield and biomass as well as data on flowering and maturity. Differences were observed among populations for pod yield and model components. The effects of locations were significant ($P < 0.01$) for C , p and D_R in F_2 and F_3 but nonsignificant for yield and C in F_4 . Heritabilities were estimated by parent–offspring regression of F_3 on F_2 and F_4 on F_3 . Heritability estimates for C , p , D_R and yield based on the $F_2:F_3$ regression were 0.10, 0.45, 0.10 and 0.16, respectively. Heritabilities based on $F_3:F_4$ regression were 0.20 for C , 0.46 for p , 0.14 for D_R and 0.57 for yield. These results reveal that none of the yield-model traits had larger heritability than yield and that selection for these traits in segregating bulk populations is difficult. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Peanut; Heritability; *Arachis hypogaea*; Selection; Groundnut; Breeding

1. Introduction

Selection for yield has been the basis for improving groundnut productivity in semiarid environments (Nigam et al., 1991), but gain from such selection has been slow. This is due in part to year-to-year variability in amounts and temporal distribution of rainfall. Additional or improved selection criteria and procedures are needed.

Use of physiological models offer a means for identifying traits linked with yield and may contribute to improvements in efficiency of breeding (Williams, 1992). This approach has been hindered by low heritabilities and complex relationships among those traits and with yield. There are also difficulties of measuring physiological traits on individual plants without either destroying the plant or incurring great cost.

Selection based on physiological traits in early generations has been reported by Bandyopadhyay et al. (1985). They evaluated the genetic potential of F_2

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progeny from single and three-way crosses of groundnut using traits such as leaf area, specific leaf weight and leaf dry weight and components of yield. They concluded that the use of a selection index based on both physiological and yield components can be made as early as the F_2 generation. They also found that a selection index based on physiological and yield components was more efficient than an index based on yield components alone. Prabhu et al. (1990) also advocated the use of physiological traits such as leaf area in selecting for relative yield performance in groundnut. Wallace et al. (1993) suggested that indirect selection for yield will be most effective when applied to processes that already integrate most of the genetic and environmental effects that lead to yield.

A simple yield model such as that proposed by Duncan et al. (1978) provides a framework for understanding yield variation among different genotypes in variable environments. In this model, yield (Y) is definable as the product of crop growth rate (C , in g dry matter $m^{-2} day^{-1}$), length of the reproductive period (D_R , days) and partitioning (p) of new material to reproductive sinks. Thus,

$$Y = pCD_R \quad (1)$$

These model components integrate many physiological processes. While a full understanding of these processes is desirable, much can be achieved by working with integrated parameters rather than yield only. While the model is simple, and caution needs to be exercised in its use, it allows interpretation of differences in yield in a more mechanistic manner than is possible from original data. Crop growth rate is determined by resource capture and the efficiency with which the resources are used in biosyntheses. On the other hand, variations in partitioning are determined by another set of physiological factors. In variable semiarid environments such as those of west Africa, it should be possible to identify those lines that perform well under different conditions for one or the other of the factors contributing to yield (Greenberg et al., 1992; Ndunguru et al., 1995). The application of this methodology in early generation of breeding is as yet unproven.

The growth analysis measurements summarized in Eq. (1) must be economically feasible for the large number of lines, progenies and environments required

for effective selection. Fortunately methods have been developed that allow largely nondestructive growth analysis on the necessary scale and accuracy (Williams and Saxena, 1991).

Our objectives were to estimate heritabilities of crop growth rate, partitioning and reproductive duration and to determine their predictive value for efficient selection in early generations.

2. Material and methods

2.1. Site characteristics

Field experiments were conducted at three locations in Niger from 1992 to 1994: the ICRISAT Sahelian Center, Sadore ($13^{\circ}15' N$, $2^{\circ}17' E$, alt 240 m) near Niamey; where the mean annual rainfall is 580 mm from June to September. Surface horizons at Sadore are sandy loams classified as sandy, silicious, Isohy-pothermic Psammentic Paleustalf (USDA taxonomy). The top soil is 94% sand and 3% clay. The second location was Gaya ($11^{\circ}59' N$, $3^{\circ}30' E$, alt 160 m) where the annual average rainfall is 850 mm. The soil is an alfisol (clayey-skeletal, mixed isohypotheric family of Udic Rhodastalf) with 12% clay, 70% sand in the top soil. The third location was Tara ($11^{\circ}59' N$, $3^{\circ}30' E$, alt 200 m and annual average rainfall of 700 mm). The soil is classified as Haplic Acrisol with 86% sand in the top soil and 8% clay (Fechter et al., 1991). Gaya and Tara are 30 km apart. Monthly rainfall, dates of sowing, flowering and maturity are presented in Table 1.

2.2. Populations and parents

Forty F_2 populations were chosen from crosses made in 1991 for an ongoing breeding program for yield and adaptation in west Africa. Their selection was based on availability of sufficient F_2 seed needed for a replicated trial (a minimum of 300 seeds). The populations involved parents predominantly of the Spanish botanic group. Lines 55–437, 796, TS 32–1, J 11, JL 24 and Chico served as male parents. They are all of short-duration (≤ 90 days sowing to maturity) Spanish bunch types. The first three lines are widely grown in the Sahel region of west Africa and have high partitioning coefficients (Greenberg et al., 1992). J11

Table 1

Mean monthly rainfall (mm), dates of sowing, flowering and maturity, mean pod yield and mean crop growth rate at three locations in 1992–1994

Variable	Sadore			Gaya			Tara		
	1992	1993	1994	1992	1993	1994	1992	1993	1994
<i>Rainfall</i>									
June	85	86	145	0	81	138	102	69	165
July	164	197	153	189	148	232	162	206	94
August	227	229	306	265	241	319	228	186	319
Sept.	53	21	126	93	121	0	66	133	18
Total	529	533	730	547	591	689	558	594	759
<i>Phenology</i>									
Sowing date	2 June	17 June	16 June	6 July	7 June	6 June	—	2 July	8 June
Flowering	30 June	15 July	15 July	2 Aug	5 July	2 July	—	30 July	10 July
Maturity date	30 Sept	10 Oct	10 Oct	15 Oct	5 Oct	30 Sept	—	20 Oct	30 Sept
Pod yield (ton ha ⁻¹) ^a	0.32	0.25	0.94	2.02	2.18	1.82	—	1.52	1.81
C (kg ha ⁻¹ day ⁻¹)	17.1	12.6	29.6	68.6	73.2	61.8	—	47.0	53.6

^a Mean of 49 entries (40 populations plus 9 parental lines).

and JL 24 are introductions from India. Female parents included both Spanish and Virginia botanic groups. The Spanish group included ICGV 86015, ICGV-SM 83005 and ICGV 87123, which are of medium duration (110 days sowing to maturity). The Virginia group included ICGV 87121, M13 and ICG-MS 42, which mature in 120 days. Lines with the prefix 'ICGV' and 'ICGV-SM' are elite lines developed by ICRISAT in India and Malawi. The list of populations is presented in Table 3.

2.3. Yield tests

In 1992, 49 entries (40 F₂ populations plus 9 parental lines) were grown at Sadore and Gaya. Individual plots were three rows, 3 m long and 0.5 m apart. A basal dose of 18 kg P ha⁻¹ as single superphosphate was incorporated into the soil by broadcasting during land preparation. Seeds were hand sown at each location. Neither gypsum nor fungicides were applied. These inputs are not used by farmers in west Africa. The plots were kept weed free by regular manual weeding. No supplementary irrigation was given.

At maturity, all plants in a plot were hand-lifted. Maturity was indicated by the blackening of internal shell wall (Williams and Drexler, 1981). First, a sample of three two-seeded mature pods was harvested from each plant per plot at each location. The remaining pods (including immature ones) were

separated from the haulms (aboveground parts) and bulked together with pods recovered from the soil. Pods and haulms (including recoverable fallen leaves) were sun-dried separately. After air drying, the pods from individual plants were threshed and seed were bulked across locations and replications. This constituted the F₃ bulk. The F₃ trial was conducted at Sadore, Gaya and Tara in 1993. The plot size was four rows, 4 m long and 0.5 m apart. Using the same sampling and harvesting procedures as for the F₃, F₄ seeds were prepared for sowing at the same locations as for F₃ in 1994. In all trials the experimental design was a 7×7 triple lattice.

2.4. Measurements

In all generations, plots were regularly observed to decide the date at which 50% of the plants had started flowering. The beginning of the pod development was taken as 15 days after the date of 50% flowering as earlier observed for most groundnut lines at these locations. Total dry matter at harvest (aboveground parts plus pods) and economic yields (yield of pods) were determined for each plot. These data along with the timing of flowering and maturity (Williams and Saxena, 1991) were used to calculate crop growth rate (C), pod growth rate (R) and partitioning (p). Pod dry matter was multiplied by a correction factor of 1.65 (Bell et al., 1992) to adjust for the differences in

energy requirement for producing vegetative vs. pod dry matter. C and R were computed as:

$$C = W/t_m \quad (2)$$

$$R = W_R/(t_m - t_r + 15) \quad (3)$$

$$p = R/C \quad (4)$$

where W is the adjusted total dry matter at harvest (haulm yield+(pod weight \times 1.67), t_m is the time in days from sowing to maturity, W_R is the adjusted pod weight (pod weight \times 1.67), t_r is the time in days from sowing to 50% flowering and 15 represents the days between flowering and start of podding. Reproductive duration was the difference between maturity and flowering dates.

2.5. Data analysis

Separate analyses of variance were done for each generation and location using GENSTAT procedures (Genstat 5 Committee, 1993). For each generation a weighted analysis of variance across locations was done. Populations and parents were treated as fixed

effects and locations and replications as random effects.

Heritability was calculated by parent–offspring regression of means of F_3 bulks on F_2 bulks and F_4 bulks on F_3 bulks (Frey and Horner, 1957). Adjusted means from lattice analysis were used in the regressions. Heritability was not adjusted for inbreeding based on the coefficient of additive variance in the covariance regression (Nyquist, 1991).

3. Results

Mean pod yields at Gaya and Tara were over five times greater than at Sadore in 1992 and 1993 (Table 1) indicating the contrasting nature of the locations. C was also much smaller at Sadore than the other two locations. Results of analyses of variance of pod yield, C , p and D_R , are presented in Table 2. Populations and parents differed for all traits measured in all generations. Averaged over generations, mean values for pod yield and C were relatively low in F_2 but high in F_4 (Table 3). D_R means were higher in F_2 than

Table 2

Mean squares from analyses of variance for yield, crop growth rate (C), partitioning (p) and reproductive duration (D_R) of 40 groundnut populations and 9 parental lines in F_2 , F_3 and F_4

Source	df	Yield	C	p	D_R
<i>F₂ Generation</i>					
Location (L)	1	209.47**	194657.25**	14.14**	33557.42**
Replication (R)/L	4	0.10	383.03	0.06	70.48
Population/Parents (P)	48	0.14**	359.28**	0.03**	147.97**
L \times P	48	0.09*	206.85**	0.01**	78.65**
Error	192	0.06	89.76	0.01	30.25
CV (%)		21	22	17	6
<i>F₃ Generation</i>					
Location (L)	2	141.60**	135832.84**	2.12**	8843.82**
Replication (R)/L	6	0.18	143.89	0.05	7.79
Population/Parents (P)	48	0.18**	85.75**	0.05**	10.43**
L \times P	96	0.13**	80.25*	0.02**	5.24*
Error	288	0.08	59.60	0.01	4.07
CV (%)		22	17	21	3
<i>F₄ Generation</i>					
Location (L)	2	37.42**	4116.26**	0.475**	937.04**
Replication (R)/L	6	0.62	463.60	0.033	23.86
Population/Parents (P)	48	0.34**	176.50**	0.038**	56.67**
L \times P	96	0.14	124.50	0.005*	18.64**
Error	288	0.13	109.8	0.003	5.24
CV (%)		24	22	8	3

*,** Significant at 0.05 and 0.01 probability levels, respectively.

Table 3

Mean pod yield (ton ha⁻¹), crop growth rate (*C*, kg ha⁻¹ day⁻¹) partitioning (*p*) and reproductive duration (*D_R*, days) in F₂, F₃ and F₄ populations of groundnut averaged area locations in Niger, 1992–1994

Population/ parents	Identification	Yield			<i>C</i>			<i>p</i>			<i>D_R</i>		
		F ₂	F ₃	F ₄	F ₂	F ₃	F ₄	F ₂	F ₃	F ₄	F ₂	F ₃	F ₄
	<i>Population</i>												
1	ICGV 87121 × 796	1.25	1.52	1.59	45.5	48.2	48.4	0.57	0.59	0.75	87	79	77
2	ICGV 87121 × TS 32-1	1.06	1.25	1.60	36.3	44.0	50.3	0.52	0.58	0.74	89	79	76
3	ICGV 78121 × ICGV 87003	1.30	1.33	1.49	48.5	45.9	45.7	0.57	0.58	0.74	85	79	78
4	ICGV 87121 × 55-437	1.03	1.23	1.79	40.7	41.3	53.2	0.52	0.58	0.77	88	78	76
5	ICGV 87121 × Chico	1.18	1.11	1.29	42.7	42.7	41.7	0.58	0.55	0.72	86	78	77
6	ICGV 87121 × J11	1.24	1.36	1.53	94.5	48.0	47.7	0.57	0.59	0.76	88	78	76
7	ICGV 87121 × ICGV 86015	0.95	1.40	1.72	27.5	45.6	53.4	0.62	0.71	0.75	91	80	76
8	ICGV 87121 × JL 24	1.14	1.44	1.52	38.7	44.1	47.4	0.55	0.66	0.71	92	80	78
9	ICGV 87123 × ICGS(E)13	1.14	1.27	1.34	46.8	41.7	41.5	0.53	0.67	0.72	82	99	78
10	ICGV 87123 × Chico	1.01	1.40	1.23	45.3	37.8	32.6	0.47	0.67	0.73	88	80	78
11	ICGV 87123 × J11	1.12	1.15	1.31	46.3	40.2	45.1	0.49	0.53	0.63	88	80	80
12	ICGV 87123 × 55-437	1.06	1.47	1.83	28.0	44.5	50.0	0.68	0.69	0.83	97	80	77
13	ICGV 87123 × JL 24	1.12	1.23	1.42	45.0	43.3	46.7	0.46	0.52	0.69	91	81	77
14	ICGVSM 83005 × TS 32-1	1.16	1.37	1.52	40.7	45.1	47.8	0.55	0.57	0.71	92	81	79
15	ICGVSM 83005 × 796	1.29	1.25	1.67	45.8	43.7	53.0	0.58	0.50	0.75	88	82	77
16	ICGVSM 83005 × JL 24	1.19	1.31	1.91	35.3	46.4	59.3	0.57	0.50	0.75	95	80	76
17	ICGVSM 83005 × ICGV 86015	1.24	1.15	1.53	43.7	40.1	50.8	0.54	0.50	0.65	96	81	79
18	ICGMS 42 × J11	1.10	1.00	1.40	38.8	40.7	51.7	0.48	0.46	0.61	94	80	79
19	ICGMS 42 × Chico	0.85	1.05	1.18	32.5	39.2	42.3	0.47	0.47	0.65	96	80	78
20	ICGMS 42 × TS 32-1	1.03	1.05	1.39	44.0	41.0	53.3	0.44	0.59	0.60	92	80	78
21	ICGMS 42 × JL 24	0.90	1.22	1.68	36.2	41.7	58.3	0.44	0.48	0.63	97	82	81
22	M 13 × ICGS(E) 13	1.23	1.28	1.54	17.2	40.8	47.0	0.55	0.59	0.73	88	79	79
23	M 13 × 55 - 437	1.06	1.36	1.41	33.0	45.7	45.7	0.66	0.59	0.72	94	78	78
	<i>Yield</i>												
24	M 13 × TS 32 - 1	1.46	1.43	1.23	45.3	46.0	41.6	0.62	0.55	0.66	93	78	79
25	M 13 × JL 24	1.30	1.24	1.45	57.8	45.7	48.0	0.49	0.52	0.68	85	78	78
26	M 13 × 796	1.26	1.43	1.53	49.2	44.9	46.6	0.58	0.65	0.78	82	78	77
27	JCGV 86015 × 796	1.16	1.54	1.85	29.5	45.3	51.0	0.64	0.70	0.81	92	78	76
28	JCGV 86015 × JL 24	1.14	1.53	1.94	30.5	47.4	53.0	0.68	0.72	0.77	95	78	78
29	ICGV 56015 × 796	1.26	1.31	1.63	52.3	49.0	49.0	0.51	0.57	0.76	83	79	78
30	ICGV 86015 × TS - 32-1	1.02	1.29	1.37	39.5	45.8	45.3	0.53	0.55	0.71	83	79	78
31	ICGV 86015 × Chico	1.17	1.18	1.38	44.2	46.0	43.3	0.56	0.56	0.75	86	79	78
32	ICGV 86015 × 55 - 437	0.92	1.19	1.37	40.7	42.0	45.6	0.42	0.50	0.68	84	79	78
33	J 11 × TS 32-1	1.23	1.37	1.46	52.0	47.7	49.3	0.49	0.55	0.72	86	79	77
34	J 11 × 55 - 437	1.30	1.25	1.50	49.5	41.7	49.9	0.56	0.68	0.74	83	78	76
35	796 × J 11	1.00	1.29	1.12	38.8	50.3	48.7	0.44	0.49	0.53	96	80	79
36	796 × ICGMS 42	1.22	1.07	1.48	45.0	40.0	51.7	0.49	0.52	0.66	93	80	79
37	JL 24 × 796	1.22	1.40	1.65	47.8	42.2	52.8	0.54	0.65	0.74	85	79	77
38	55-437 × J 11	1.73	1.31	1.58	64.3	49.3	49.2	0.59	0.57	0.76	83	78	78
39	55-437 × 796	1.29	1.25	1.41	49.8	42.7	47.2	0.51	0.55	0.71	83	78	76
40	55-437 × Chico	0.96	1.12	1.12	29.0	38.7	39.8	0.56	0.52	0.55	94	80	80
	<i>Parents</i>												
41	ICGV 87123	1.34	1.54	1.72	39.0	43.3	46.4	0.67	0.75	0.82	87	78	78
42	J 11	1.22	1.41	1.54	49.0	47.0	47.9	0.51	0.65	0.77	84	79	78
43	ICGMS 42	1.28	1.39	1.78	49.2	47.0	54.9	0.46	0.47	0.65	94	80	81
44	M 13	1.05	1.47	1.64	36.8	44.3	50.3	0.52	0.65	0.76	86	79	77
45	ICGV 86015	1.24	1.52	1.58	39.0	44.2	42.8	0.65	0.70	0.82	89	79	78
46	TS 32-1	1.39	1.38	1.55	51.7	46.3	47.2	0.55	0.56	0.77	81	80	77
47	55 - 437	1.21	1.40	1.44	50.0	51.3	45.7	0.53	0.59	0.76	81	79	77
48	796	1.23	1.55	1.76	49.0	47.8	53.4	0.53	0.60	0.77	82	79	77
49	ICGV 87121	1.24	1.42	1.74	37.8	46.8	52.6	0.59	0.59	0.71	89	78	78
Mean		1.17	1.31	1.53	42.9	44.3	48.3	0.55	0.58	0.72	88	78	72
SED		0.096	0.012	0.032	2.57	2.35	3.50	0.056	0.036	0.062	2.8	1.2	1.3

Table 4

Heritabilities and their standard errors computed from parent–offspring regressions and correlations of F_3 on F_2 , and F_4 on F_3 bulk means at three locations and at Gaya plus Tara alone

Trait	Location	Parent–offspring regression		Parent–offspring correlation	
		$F_2:F_3$	$F_3:F_4$	$F_2:F_3$	$F_3:F_4$
<i>C</i>	Sadore	0.03±0.09	0.05±0.18	0.06	−0.04
	Gaya	0.10±0.11	0.10±0.20	0.15	0.08
	Tara	—	0.13±0.16	—	0.13
	Combined-Sadore	0.10±0.08	0.12±0.23	0.20	0.08
<i>p</i>	Sadore	—	0.20±0.11	—	0.28
	Gaya	0.14±0.11	0.18±0.24	0.20	0.11
	Gaya	0.18±0.31	0.17±0.07	0.14	0.20
	Tara	—	0.60±0.06**	—	0.87
D_R	Combined-Sadore	0.45±0.17**	0.24±0.17	0.39	0.22
	Sadore	—	0.46±0.17*	—	0.40
	Gaya	0.00±0.07	0.05±0.14	0.01	0.05
	Gaya	0.06±0.10	0.31±0.11**	0.09	0.41
Pod yield	Tara	—	0.08±0.14	—	0.09
	Combined-Sadore	0.10±0.03	0.59±0.24**	0.47	0.39
	Sadore	—	0.14±0.10	—	0.22
	Sadore	−0.10±0.19	0.09±0.15	−0.16	0.10
	Gaya	0.17±0.12	0.20±0.37	0.23	0.19
	Tara	—	0.53±0.09**	—	0.69
	Combined-Sadore	0.16±0.14	0.07±0.28	0.19	0.04
		—	0.57±0.11**	—	0.62

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

in F_3 and F_4 . The effects of locations were highly significant for all traits studied in all generations. Interactions of locations and populations were also highly significant for yield and model components in F_2 and F_3 . In F_4 the interaction was only significant for p and D_R . The interaction of locations and populations are due in part to the variable growth and low yields at Sadore. For example, the coefficients of variation (%) for pod yield at Sadore were 43 in F_2 , 48 in F_3 and 45 in F_4 compared to 13, 17, and 10, respectively at Gaya. At Tara the values were 13 in F_3 and 12 in F_4 .

Heritabilities of C , p , D_R , and pod yield from $F_2:F_3$ and $F_3:F_4$ regressions are presented in Table 4. The C heritability estimates were low and nonsignificant at all locations and combined over locations. When data from Gaya and Tara were combined, heritability of C determined from $F_3:F_4$ regression slightly improved from 0.12 to 0.20.

Partitioning heritabilities were low and similar for $F_2:F_3$ and $F_3:F_4$ at Gaya and Sadore but moderate and significant at Tara (Table 4). Combined over locations, heritability values for p were similar and sig-

nificant only when Sadore data was excluded from the analysis in the $F_3:F_4$ regression. Heritability estimates for D_R were significant only when estimated by $F_3:F_4$ regression at Gaya and when combined over locations. Exclusion of Sadore data from the regression resulted in a decrease in heritability (Table 4).

Pod yield heritability estimates were low and only significant when determined from $F_3:F_4$ regression at Tara. When Sadore data were excluded from the $F_3:F_4$ regression, heritability for pod yield was moderate and significant.

The parent–offspring correlations were, in most cases, similar to the regression values (Table 4). The standard unit heritabilities may have an advantage compared to the regression coefficients, because they free the estimates from differential environmental effects on parents and offspring.

The effectiveness of isolating high-yielding populations was evaluated based on a combination of above-average pod yield and partitioning (data not shown). On this basis, 9 populations would have been selected in the F_2 , 8 in the F_3 and 12 in the F_4 . Of the

nine selected in F_2 , only three (or 33%) would have been selected in the F_3 and F_4 . Of those selected in F_3 , five (or 63%) would have been selected in the F_4 .

4. Discussion

The phenotypic data in the present study represent the combined effect of genetic and environmental factors influencing yield and the physiological traits. Large location effects were apparent. The locations of our study are characterized by variation in amount and timing of rainfall relative to crop phenology (Table 1). Poor soil exacerbated by spatial variability, is known to be responsible for poor crop growth at Sadore (Brouwer et al., 1993). In addition, low rainfall and its poor distribution, high temperatures and hot winds during crop maturation compound the environmental effects (Sivakumar, 1992). Under these conditions, environmental effects override genetic effects leading to low heritabilities.

The low heritability estimates for C indicate greater influence of environment on C and selection based on C would be ineffective in early generations. Heritability for p from individual locations was lower than from combined locations from $F_2:F_3$ regression. Similarly the heritability for D_R estimated from $F_3:F_4$ regression combined over locations was higher than from individual locations. The heritability for p and pod yield from $F_3:F_4$ regression became significant when Sadore was removed from the analysis suggesting that Sadore was responsible for the extremely low heritabilities obtained from the complete data set.

These results highlight the need for a clear definition of target environments for selection between and within populations.

Estimates of heritability in this study could have been influenced by several factors. According to theory, variation in C is dominated by environmental and management aspects (Williams and Boote, 1995). The evidence concerning partitioning indicates that genotypic differences are more important whereas environment is a less significant source of variation (Greenberg et al., 1992; Ndunguru et al., 1995). Various environmental challenges also have different impact on C , p , and D_R . For instance, drought will influence C and p , calcium deficiency will influence p and foliar diseases will mainly influence C by redu-

cing total biomass through defoliation. Foliar diseases were more prevalent at Gaya than the other two locations (data not shown). The distribution of rainfall during crop growth was erratic and amount of rainfall during pod addition and filling was also variable (Table 1). Thus the within-season variability may have interacted with the method of estimation of both C and p . This could occur because the growth of pods depends largely on photosynthesis. The estimation of C using biomass at harvest gives an indication of the seasonal differences in crop resource use and resource-use efficiency. However, the method does not take into account differences in the distribution of that growth within the season. It would have been desirable to have obtained estimates of C during flowering, although this would have been difficult and costly for such a large number of treatments.

The similarity of the heritabilities for p from the $F_2:F_3$ and $F_3:F_4$ regressions indicate that additive effects are important in the expression of p , but when considered with the rather low standard unit heritabilities, progress from selection in early generations would be slow in the populations used. Heritability estimates from the $F_3:F_4$ appeared to be more reliable than those from the $F_2:F_3$. These differences in the parent–offspring regressions could have arisen from both genetic and environmental differences as well as from the method of generation advance. The increase or decrease in heritability estimates could have occurred because parents and offspring were evaluated in successive years. This is in agreement with conclusions reached by other workers (Fernandez and Miller, 1985; Iroume and Knauff, 1987). In addition, when generations are tested in successive years, the individual populations are subjected to different selection pressures which could lead to genetic shifts from generation to generation (Halward et al., 1990). Therefore, the method of generation advance should be considered carefully when using bulk-breeding method.

One of our objectives was to determine the predictive value of yield-model traits for efficient selection in segregating populations. If any trait is to be used as an indirect selection criterion for yield improvement, heritability of that trait must be larger than the heritability for yield (Falconer, 1989). In this study, this requirement was not met by any of the model traits. One problem with the use of early-

generation bulk populations is that measurements are made on a cross bulk rather than on segregates from specific crosses. This points to a limitation that may occur when selecting for yield and physiological traits among bulk progenies in early generations.

The high coefficients of variation and low heritability from a marginal location such as Sadore, point toward optimizing agronomic practices and improved experimental design to decrease the error variance and consequently to increase the selection efficiencies. Selection from early generation material may be more efficient in high-productivity environments.

Results of this study are most relevant to preliminary selection in large populations when the goal is to preserve an elite fraction of the populations for further testing. The assumption that selection of lines in high-fertility intensively managed environments will maximize gains in marginal environments is especially important in breeding programs at International Agricultural Research Centers and in the national breeding programs of developing countries. In west Africa, groundnut is produced by small-scale farmers who have limited resources and rarely use purchased inputs. To breed cultivars for these production systems (low-input) requires more-extensive replicated yield-testing phases than similar programs in high-input environments. Whether the cost of such testing, and the cost of conducting parallel breeding programs in marginal areas can be justified is a political question.

In a breeding program such as that of ICRISAT, several hundred crosses are made each year and high yield needs to be combined with other desirable attributes such foliar diseases resistance and drought tolerance. Thus producing a large quantity of F_2 seed in order to allow replicated trials simultaneously at two or more locations should be carefully weighed against testing at a single site in subsequent generations. Conducting yield trials at two or more sites in the F_3 generation appeared to be more reliable than in the F_2 . The reliability of the tests is increased through replication and increased plot size, thus minimizing environmental variation to the extent possible.

5. Conclusion

Overall, these results reveal that heritability estimates for yield-model traits were not larger than

heritability for yield. Thus, selection for these traits in segregating bulk populations is difficult. This conclusion only applies to the populations used and might be different if other crosses are used and a different methodology for measuring physiological traits is used. Selection from early-generation material may be more efficient in high-productivity environments.

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