Stability of Pod Yields and Parameters of a Simple Physiological Model for Yield Among Peanut Lines in Northern Benin

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ABSTRACT

Cultivar trials comparing nine early maturing and 14 medium maturing peanut (*Arachis hypogaea* L.) lines were conducted over 3 yr at five sites in Northern Benin. Trials were conducted using presently recommended agronomic practices. Pod and biomass yields, defoliation from all causes and phenology were observed. Crop growth rate (C), partitioning (p) and reproductive duration (parameters of a simple physiological model for yield) were estimated. Both C and p contributed to yield differences among lines within a maturity group. The dwarf cultivar MH2 was in all cases lower yielding due to low C. Duration was apparently not an important determinant of yield differences between early and medium maturity trial sets since (with MH2 excluded) the extra time taken by the medium maturity lines only resulted in 50 kg/ha greater yield. Partitioning of the trial entries was high suggesting that selection should focus on traits that maximize C. Across all lines there appears considerable potential for higher yields achieved by improvements of the crop growth rate, and crop management research and breeding should focus on tactics to increase this determinant of the yield. Lines selected for resistances to foliar diseases in India had, on average, lower C than West African lines, and some Southern African lines, but they had greater stability of C across environments. Stability analysis of yield and the parameters of the yield model identified lines with superior stability of p and others with superior stability of C. It is suggested that both phenotypic and physiological yield models should be used in the identification of lines with desirable adaptive attributes.

Key Words: *Arachis hypogaea* L., crop growth rate, groundnut, models, partitioning, stability analysis.

Peanut production in Benin is primarily to satisfy the food and oil requirements of the population. The production has been increasing progressively, but yields per hectare remain low, with a national average of between 500 and 800 kg/ha. The yield potential for peanut in comparable environments is high, which leads us to hypothesize that farmers could achieve much better yields.

The lack of improved cultivars is considered a major constraint to realizing the potential for production (Adomou, 1990). Other perceived problems include foliar diseases, appropriate post-harvest technologies and cultural practices (Adomou, 1993). It is also possible that 'rank growth' under the high humidity conditions may be a limiting factor to productivity (Williams *et al.*, 1975).

Yield differences between lines in multi-site trials may be analysed using the familiar phenotype model [Eq. 1] where yield (Y) is defined as the result of additive effects of genotype (G), environment (E), and their interaction (GxE).

$$Y = G + E + GxE \qquad \text{[Eq. 1]}$$

Yields also may be analysed against the physiological model where Y is defined as the product of mean crop growth rate (C), the duration of the reproductive phase (D_R) and the fraction of C partitioned to fruit (p) (Duncan *et al.*, 1978).

$$Y = C \times D_R \times p \qquad \text{[Eq. 2]}$$

The parameters of this model may be determined by growth analysis (Duncan *et al.*, 1978), or estimated by nondestructive methods from phenological observation and final harvest data (Williams and Saxena, 1991). Where radiation interception is complete, C for peanut is typically between 15-25g/m^2/d (Duncan *et al.*, 1978; ICRISAT, 1983). Primitive germplasm lines have partitioning coefficients of less than 0.5, while advanced cultivars typically have partitioning of 0.9 or more (Duncan *et al.*, 1978; Williams, unpubl. data) .

From resource capture considerations the parameter C should be determined mostly by environmental factors since there is relatively little genotypic variation in radiation or water use efficiency (Monteith, 1990). In contrast, the effects of G and GxE probably dominates the variation in p. Duncan *et al.* (1978) showed that in optimally managed crops the major source of yield variation between lines was in the partitioning coefficient. Like yield, the parameters of the physiological model can be analysed for stability across environments using the method of Finley and Wilkinson (1963).

This paper examines the stability of yield and the physiological model parameters across a range of environments as determined by years and location and interprets the results to guide future research and development strategies.

Materials and Methods

Two separate trial series were conducted between 1991 and 1993 at five sites in northern Benin. The first trial was composed of nine early maturing lines (90-100 d) while the second set had 14 lines of medium/long duration (110-140 d). The lines were obtained from the ICRISAT and were derived from germplasm and advanced breeding lines from India, Malawi, and Niger. The early maturing trial included

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a dwarf cultivar, MH2, which was of physiological interest because it offered a chance to evaluate the possible effect of high humidity-induced rank growth on partitioning. Cultivars 55-437 and TS 32-1 are standard early maturing peanut types widely grown in West Africa, while cultivar Te 3 is a local check. In the medium/late maturity group, 69-101 and RMP 12 are late-maturing released cultivars in Benin. Lines with the prefix ICG are germplasm lines and those with the prefix ICGV and/or SM are advanced breeding lines of diverse pedigrees developed by ICRISAT in India and Malawi, respectively.

The soils at the five locations are mainly Alfisols, only varying in the amount of clay and gravel. The main characteristics of the test sites are as follows:

Guinirou—Situated 50 km south of Parakou in the northern Guinean Savanna. The site has an annual rainfall of 1000 to 1200 mm during the season with a mean length of 210 d.

Ina—This is the main research station for the savanna region in Benin situated 70 km north of Parakou. Annual rainfall varies from 900 to 1300 mm during a season with a average duration of 170 d.

Bagou and Angaradebou are both in the moist savanna zone and only 70 km apart. They have an annual rainfall of 800 to 1100 mm during 145 to 155 d.

Guene is in the dry savanna zone and receives 600 to 800 mm rainfall annually in 125 d.

Land preparation was done by ploughing with either tractor or animal-drawn implements, with 40 kg ha^{-1} P_2O_5 as triple super phosphate being applied and incorporated before sowing. All experiments were conducted in a randomized complete block design with three to four replications depending on the site and year. Plots were each of 18 m^2. Seeds were sown in rows 60 cm apart with a within row spacing of 10 cm for the early maturing lines and a 15 cm spacing for the medium/late maturing lines. Sowing dates varied by location and year depending on the onset of the rains, but was generally between (mid-June to early July). No crop protection measures were employed.

The data collected included the time to flowering, maturity, the incidence of foliar diseases, and defoliation at harvest. The mass of vegetation and pod was determined after these had dried. The C and reproductive growth rates were calculated by dividing the energy adjusted biomass (after adjusting for defoliation observed at final harvest) and pod mass by the duration of the respective phenological phases to estimate the mean rates of growth. The adjustment for defoliation was based on the assumption that 50% of the vegetation was leaf. The total disease (D_T) was calculated as :

$$D_T = (100 - L_D)/100) \times (L_C + L_R) + L_D \qquad [Eq. 3]$$

Where L_D = the defoliation percentage at 90 d after sowing (DAS), L_C = the leaf spot damage, and L_R = the rust damage on existing leaf at 90 DAS. The p was estimated as the ratio of reproductive growth rate to C (Williams and Saxena, 1991).

Analysis of variance was done using the GENSTAT statistical program (Numerical Algorithms Group, Rothamstead, UK). A separate analysis was done for each environment followed by a combined analysis involving all 15 environments for yield. The data for Y, C, and p across sites and years were used for stability analysis (regression of line in environment on mean of all lines in the environment) according to Finley and Wilkinson (1963). Number of environments for Y was greater than that for C and p since the estimation of the model parameters depended on the availability of a full data set which was only available for nine cases for the early maturity group and seven for the medium/late maturity group.

The stability analysis was conducted within the framework of the multi-location analysis of variance (ANOVA) by examining the contributions of a linear model and deviations from this to the sums of squares (SS) for environments and GxE (Table 3). Effectively this compares the performance of a single line in an environment with the mean of all lines in that situation.

Results and Discussion

Two aspects of the results are worthy of discussion. Firstly, there is the analysis of yield and its determination in these multiple environments and the implications that they have for crop improvement. Secondly, there is the need to consider what additional value the use of estimates of the physiological model parameters had in the interpretation of the results.

General Performance Across Sites

Pod Yields. The average yields achieved across the sites in the two trial series are presented in Tables 1 and 2. For the early maturity group, mean pod yield over sites and years ranged from 1.07 t/ha for MH2 to 2.07 t/ha for ICGV-SM 83011. For the medium maturity group, pod yields ranged from 1.72 t/ha for ICGV 87123 to 2.21 t/ha for ICGV-SM 83708. Only in the medium maturity trial series were yields generally lower at Guene than the other locations, suggesting that this may be the only site where yield was influenced by the season length/rainfall amount available.

Crop Growth Rate. Except for MH2 with the lowest mean C, all the lines in the early maturity group had similar crop growth rates (Table 3). In the medium/late group, the lowest C was recorded for ICGV 87123 while ICGV 83708 recorded the highest.

Partitioning. The dwarf line had the highest p while the other lines in both maturity groups had comparable partitioning (Table 3).

Stability Analysis

The ANOVA showed highly significantly ($P = 0.001$) differences among genotypes for pod yield, C and p in both trial sets (Table 4). Variance due to GxE interactions also was highly significant. The linear component of the GxE was significant for these three parameters. The nonlinear component of the GxE interaction was significant for pod yield and C in the early maturity group. In the medium/late maturity group, the nonlinear term was significant for all three parameters.

Pod Yield. In both trials the stability of pod yield could be attributed to the linear component of the environment sums of squares in the regression analysis. This is supported further by the high values of R^2 of individual lines when regressed on the environmental mean (Table 3). In the early maturity group the regression coefficients ranged from 0.62 to 1.16, reflecting the significant differences in response to different environments (Table 4). ICGV-SM 83011 was consistently above average and had a b_i value close to unity which provides a desirable

Table 1. Pod yield (t/ha) of early maturing lines averaged over years at five sites.

Line	Site					Mean
	Guinirou	Ina	Bagou	Angaradebou	Guene	
	t/ha					t/ha
ICGV-SM 85045	1.53	2.07	2.00	2.00	1.67	1.86
ICGV-SM 83011	1.86	2.30	2.40	2.21	1.61	2.07
ICG 8361	1.29	2.01	2.00	2.12	1.93	1.87
ICGV 86072	1.55	1.99	2.25	2.31	2.02	2.02
JL 241.47	1.96	1.89	2.14	1.66	1.82	
55-437	1.50	2.11	1.96	2.04	2.01	1.92
MH-2	0.90	0.91	1.10	1.39	1.03	1.07
TE 3 1.63	2.10	2.12	1.92	1.78	1.91	
TS 32-1	1.41	2.01	2.11	2.08	1.92	1.91
Mean	1.46	1.94	1.98	2.02	1.74	1.83
SE (mean)	0.152	0.104	0.133	0.159	0.191	0.880
CV (%)	18	9	12	14	19	14

Table 2. Pod yields (t/ha) of medium maturing lines averaged over 3 yr at five sites.

Line	Site					Mean
	Guinirou	Ina	Bagou	Angaradebou	Guene	
	t/ha					t/ha
ICGV-SM 83708	2.26	2.29	2.57	2.85	1.11	2.21
ICGV-SM 83709	1.97	1.85	2.69	2.44	1.00	1.99
ICGV-SM 85038	1.49	1.86	2.31	2.71	1.45	1.97
ICGV-SM 85764	1.99	2.13	2.70	2.95	0.81	2.12
ICGV-SM 87707	1.61	1.92	2.26	2.77	1.08	1.93
ICGV-SM 85005	1.81	1.75	2.32	2.76	1.03	1.93
ICGV 86024	2.01	1.77	2.39	2.50	0.98	1.93
ICGV 86028	2.26	2.08	2.62	2.78	0.92	2.13
ICGV 87141	1.56	1.56	1.96	2.45	1.22	1.75
ICG(FDRS)4	1.92	1.98	2.13	2.29	0.98	1.86
ICG(FDRS)10	1.83	1.97	2.33	2.63	1.14	1.98
ICGV 87123	1.61	1.66	1.22	1.84	2.27	1.72
69-101	1.66	2.25	2.59	2.87	1.13	2.10
RMP 12	2.24	1.84	2.58	2.35	0.84	1.97
Mean	1.87	1.92	2.38	2.62	1.06	1.97
SE (mean)	0.14	0.117	0.142	0.168	0.115	0.081
CV (%)	13	11	11	11	19	12

combination of high performance and stability (Fig. 1). On the other hand, MH2 was consistently below average and had a b_i value less than unity. All the other cultivars responded similarly to improved environment. For the medium maturity group the b_i values ranged from 0.57 to 1.22. ICVG 87123 with below average performance and ICGV-SM 83708 with consistently above average performance were the only exceptions. The other genotypes responded similarly across environments (Fig. 1). Although the sample is small the better adaptation of lines selected in Malawi (relative to those from India) to the West African savanna is of particular significance as it indicates wide adaptation of lines within Africa.

Although the pod yields from the two trial series cannot be compared in a statistical sense, the differences depended mostly on the inclusion of MH2 in the early maturity trials. However, the lines in the two trial series differed in time to harvest by only 5 d probably due to the overwhelming effect of the foliar disease epidemics.

Crop Growth Rate. The crop growth rates observed across all these lines, sites and years show relatively small variation (except MH2, which had a C approximately 50% of that observed for other lines) (Table 3). The rates of C observed in these trials are considerably lower than potential, since peanut has a potential C of 15 g/m²/d in comparable conditions in India (ICRISAT, 1983). The

Table 3. Pod yield (t/ha), crop growth rate (t/ha/d) (CGR), partitioning (*p*) and stability parameters of short and medium duration peanut cultivars.

Lines	Pod yield			CGR			*p*		
	Mean	b_i[a]	R^2[b]	Mean	b_i[a]	R^2[b]	Mean	b_i[a]	R^2[b]
	t/ha			t/ha/d					
Early maturing lines									
ICGV-SM 85045	1.86	1.16	0.88	0.080	-0.043	-	0.81	0.82	0.55
ICGV-SM 83011	2.07	1.03	0.65	0.087	0.005	-	0.94	0.86	0.78
ICG 8361	1.87	1.09	0.91	0.088	0.016	-	0.82	0.93	0.86
ICGV 86072	2.02	1.16	0.82	0.080	-0.024	-	0.94	0.38	0.26
JL 24 1.82	1.01	0.87	0.083	0.023	-	0.92	1.40	0.92	
55-437	1.92	0.98	0.88	0.086	0.014	-	0.89	1.15	0.84
MH-2	1.07	0.62	0.57	0.042	-0.007	-	1.15	1.75	0.46
Te 3 1.91	0.87	0.71	0.086	0.011	-	0.85	0.96	0.71	
TS 32-1	1.91	1.08	0.93	0.081	-0.031	-	0.84	0.76	0.50
Medium and late maturing lines									
ICGV-SM 83708	2.21	0.98	0.81	0.091	-0.0057	0.59	0.90	0.0162	0.54
ICGV-SM 83709	1.99	1.05	0.91	0.086	-0.0048	0.52	0.83	0.0001	-
ICGV-SM 85038	1.97	0.89	0.72	0.071	-0.0061	0.57	0.83	0.0045	-
ICGV-SM 85764	2.12	1.19	0.93	0.090	-0.0069	0.56	0.88	0.0047	0.12
ICGV-SM 87707	1.93	1.22	0.77	0.082	-0.0071	0.53	0.76	0.0164	0.39
ICGV-SM 85005	1.93	1.10	0.95	0.075	-0.0068	0.54	0.91	0.0086	0.27
ICGV 86024	1.93	1.00	0.91	0.080	-0.0061	0.72	0.86	0.0161	0.28
ICGV 86028	2.13	1.20	0.88	0.073	-0.0048	0.54	0.97	0.0173	0.41
ICGV 87141	1.75	0.80	0.82	0.072	-0.0062	0.65	0.86	0.0115	0.29
ICG(FDRS)10	1.98	0.91	0.89	0.073	-0.0052	0.55	0.90	0.0042	-
ICGV 87123	1.72	0.57	0.50	0.066	-0.0059	0.56	0.94	0.0155	0.23
69-101	2.10	1.18	0.89	0.085	-0.0059	0.58	0.81	0.0082	-
ICG(FDRS)4	1.86	0.81	0.85	0.077	-0.0048	0.46	0.88	0.0123	-
RMP 12	1.97	1.10	0.80	0.084	-0.0049	0.30	0.77	0.0040	-

[a]Slope term (b_i) of the regression of the line in that environment on the mean of all lines in that environment.
[b]R^2 percentage variation accounted for by the regression.

Table 4. Analysis of variance for yield and yield components of early to late maturing peanut cultivars.

Source of variation	Mean squares					
	df	Yield	df	Crop growth rate	df	Partitioning
Early maturing lines						
Total	404		242		239	
Genotype (G)	8	3.964 **	8	0.00568 **	8	0.17041 **
Environment (E)	14	6.458 **	8	0.01733 **	8	0.41948 **
Linear	1	90.410 **	1	0.00001	1	3.34617 **
Deviations	12	0.000	6	0.02289 **	6	0.00145
GxE	112	0.195 **	64	0.00038 **	63 (1)	0.02158 *
Linear	8	0.286 **	8	0.00026 *	8	0.03004 *
Deviations	96	0.198 **	48	0.00044 **	47 (1)	0.02047
Error	268	0.069	160	0.00012	158 (2)	0.01532
Medium and late maturing lines						
Total	629		293		293	
Genotype	13	0.881 **	13	0.00123 **	13	0.07747 **
Environment	14	19.631 **	6	0.06565 **	6	0.16253 **
Linear	1	274.841 **	1	0.25644 **	1	0.26967 **
Deviations NS	12	0.000	4	0.02449 **	4	0.17174 **
GxE	182	0.316 **	78	0.00031 **	78	0.03488 **
Linear	13	0.706 **	13	0.00037 **	13	0.05699 **
Deviations	156	0.284 **	52	0.00033 **	52	0.03307 **
Error	418	0.059	194	0.000074	194	0.00747

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

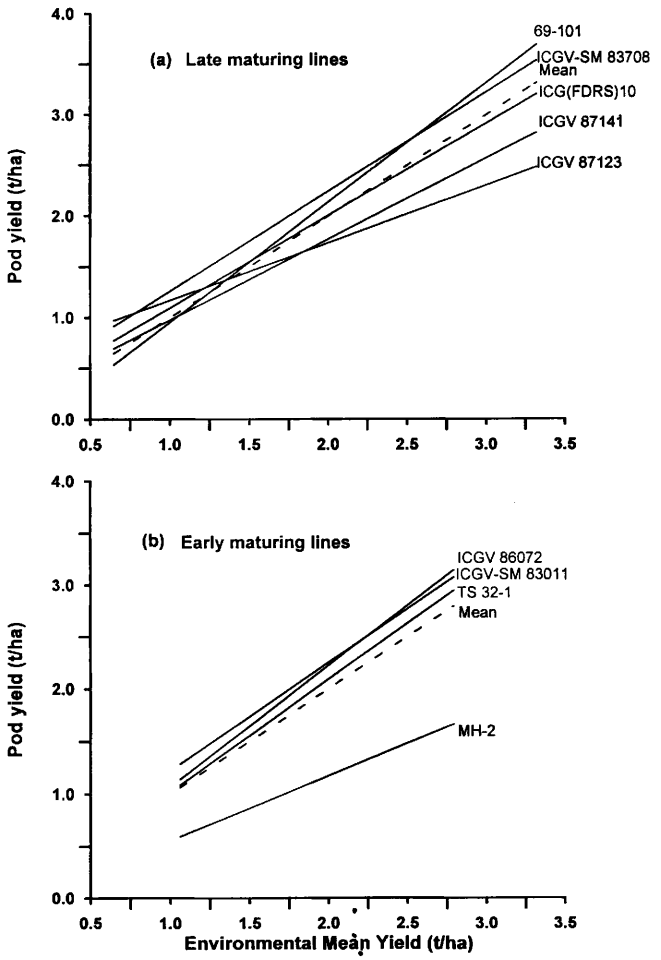

Fig. 1. Pod yield stability across sites and years for (a) medium/late maturing and (b) early maturing lines for selected lines of peanut in Benin (West Africa), 1991, 1992, and 1993.

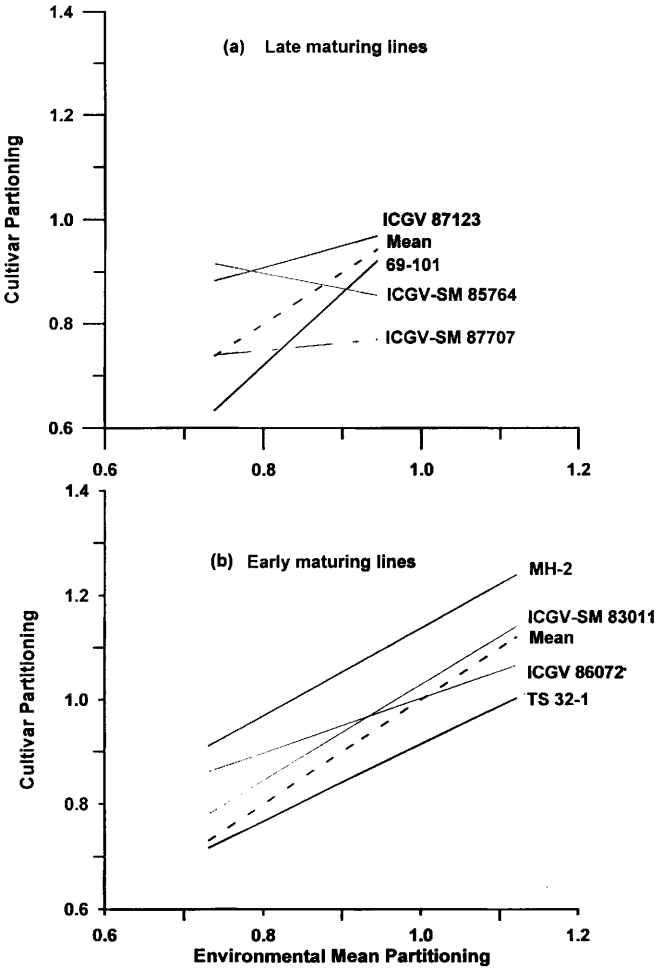

Fig. 2. Stability of crop growth rate across sites and years for (α) medium/late maturing and (b) early maturing lines for selected lines of peanut in Benin (West Africa), 1991, 1992, and 1993.

role of foliar disease in influencing the growth rates was investigated by regression analysis. This showed that the total disease index was significantly ($P \leq 0.001$) related to variation in both the C and p. However, there remained a large fraction of the sums of squares associated with other aspects of the environment. In separate trials at INA with fungicide protection, ICGV 87123 gave pod yield of about 3 t/ha and C was approximately double that observed in this trial series (Adomou, unpubl. data). There was no consistent influence of crop duration on C.

The stability analysis for C shows little interaction of lines with environment since the slope terms of the regressions are all very close to unity (Table 3). If there was consistent light use efficiency, the differences in C across environments may be attributed to differences in energy interception. This mechanism is very clearly the reason for the low C of MH2, and is likely also to be responsible for the advantage of lines with consistently higher than average C (such as ICGV-SM 83708 and ICGV-SM 85764) in the medium maturity group (Fig. 2). However, direct observations of light use efficiency would be valuable to confirm this supposition.

One interesting observation was the relative failure of the lines selected for foliar disease resistance in India [ICG(FDRS) 4, ICG(FDRS)10] to have advantage for C (Table 3). In contrast, the relatively high C of lines selected in Malawi is of particular interest. These differences could be due to more appropriate resistances to foliar diseases, particularly early leaf spot, or due to the need for more leafy cultivars in both the African environments. While it is possible that this problem could be rectified by agronomic adjustments, more detailed study of their growth and light interception is needed to determine future strategy.

Partitioning. The general levels of p observed in the lines show that partitioning of the entries in both maturity groups is comparable with that of most modern cultivars, and better than the product of previous generations of cultivar improvement (TS 32-1, 69-101 and RMP 12). Breeding for further yield advances using the partitioning avenue (Duncan *et al.*, 1978) as a basis for improvement will therefore achieve only slow progress.

Some lines such as ICGV 86072 with relatively high and stable p (Fig. 3) are of particular interest for the physiological basis of this stability of p. Most commonly, stable p across environments is associated with below average levels of p. MH2 was included in the trials to test the potential of its dwarfing gene to control excessive

stem growth associated with high temperatures and humidity (Williams *et al.*, 1975). The partitioning of MH2 was higher than other lines, but this could have been a result of the assumption of 50% of vegetative growth being into stems. However, with the environments encountered, the partitioning of other lines apparently was not limited by excess stem growth so there is little need to investigate this option further.

The additional information resulting from the use of nondestructive estimations of the model parameters was substantial. The similarity of partitioning of these experimental lines with that of contemporary lines from other locations and the importance of crop growth rate as a source of variation suggests that both breeding and management need to focus on changes that will increase this determinant of yield. Essentially, the experimental lines all have good yield potential, and the goal of further crop improvement must be the realization of that potential. The model parameters pointed to the need for additional work to confirm some of the origins of differences in C and p between lines and environments. However, this study can be achieved with relatively little cost since the question is largely whether the differences were due to canopy establishment and retention or light use efficiency. Measurement of the fractional interception at intervals (Williams *et al.*, 1976) should achieve the needed information.

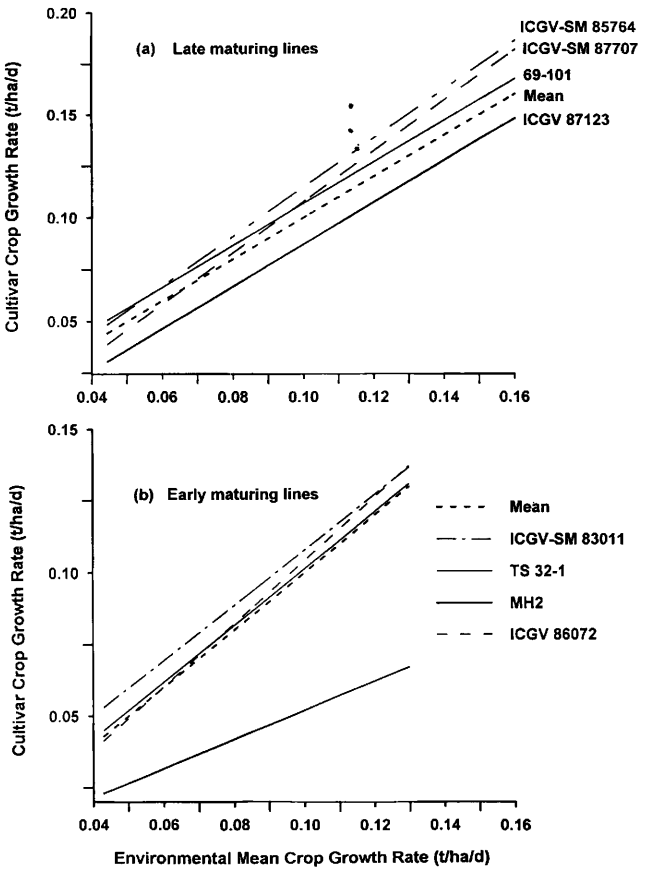

Fig. 3. Stability of partitioning across sites and years for (a) medium/late maturing and (b) early maturing lines for selected lines of peanut in Benin (West Africa), 1991, 1992, and 1993.

Conclusions

The partitioning of the test entries in these trials was better than that of the established traditional cultivars, and was comparable to that observed in the high yield potential lines adopted in other environments suggesting that yield improvement is most likely from manipulating other determinants of yield. The C was the obvious limiting factor to production, and should be targeted for improvement since the levels were very much lower than in other regions. Defoliation due to disease apparently resulted in the duration of the reproductive phase being similar in both the early and medium maturing groups of materials, and probably contributed significantly to variations in C between lines and across environments. Some lines with higher C in all environments were identified and could be used in breeding for greater stability of higher levels of C. In this agro-ecological zone, lines from African breeding programs were more stable for partitioning and crop growth rate than were lines from India. The available season length apparently was not a limitation to the achievement of yield in all but the most northern site, but the expected benefits of longer duration were not realized due to the premature defoliation of the crops by disease.

The use of the model and nondestructive estimates of its parameters provided substantial information to the results and focused both breeding and management onto the most limiting determinant of yield. Additional research to better understand the basis of high and stable C by selected lines is indicated.

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