



Early generation testing for yield and physiological components in groundnut (*Arachis hypogaea* L.)

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Summary

Selection of superior crosses of groundnut (*Arachis hypogaea* L.) in early generations would increase the probability of identifying superior lines. The objective of this study was to determine the potential of selecting for physiological traits identified in a yield model [crop growth rate (C), reproductive duration (D_R) and partitioning (p)] in segregating populations. Forty populations and nine parental lines were evaluated in replicated trials in 1992 (F_2), 1993 (F_3) and 1994 (F_4) at three locations in Niger. Physiological traits were estimated from final yield and biomass as well as data on flowering and maturity. Regressions from two different parent-offspring generations (F_2 : F_3 and F_3 : F_4) were calculated. The results were compared to determine if early generation performance accurately predicts the performance of cross bulks in later generations. Differences were observed among populations and parents for all traits. Effects of locations were significant for C, p and D_R in F_2 and F_3 but nonsignificant for yield and C in F_4 . Regression coefficients from F_3 : F_2 were 0.10 ± 0.08 for C, 0.45 ± 0.17 for p, 0.10 ± 0.03 for D_R and 0.16 ± 0.03 for pod yield. Based on F_3 : F_4 regression, the coefficients were 0.12 ± 0.23 for C, 0.46 ± 0.17 for p and 0.57 ± 0.17 for yield. Parent-offspring correlations were in most cases similar to the regression values. It was concluded that selection for yield and model components in early generation bulks may be ineffective.

Abbreviations: C – crop growth rate; D_R – reproductive duration; p – partitioning; R – pod growth rate; tm – time to maturity; tv – time to flowering; W – adjusted biomass; W_R adjusted pod weight

Introduction

Evaluation of new genetic material is one of the most important and expensive facets of most plant breeding programs. Large numbers of genotypes are advanced through segregating generations before superior cultivars are identified. If performance of progenies in early generations accurately reflects the genetic potential of the cross, then identification and selection of superior crosses in early generations will allow the breeder to increase the number of selections per cross retained, thereby increasing the probability of identifying superior lines. This is especially important when resources are limited and/or a large number of lines must be evaluated.

Selection for yield *per se* has been the basis for improving groundnut productivity in semi-arid environments (Nigram et al., 1991), but gain from such selection is slow due to large environmental effects. Additional or improved selection criteria and procedures are needed.

Use of physiological models offer a means of identifying traits linked with yield and may contribute to improvements in the efficiency of breeding (Williams, 1992). The exploitation of this approach in segregating populations has been hampered by the difficulties of measuring physiological traits on individual plants without either destroying the plant or incurring great cost. A simple yield model such as that proposed by Duncan et al. (1978), provides a framework for the understanding of yield variation among

different genotypes in different environments. This model defines yield (Y) as a product of crop growth rate (C , in g dry matter $m^{-1} day^{-1}$), the length of the reproductive period (D_R , in days) and the partitioning (p , coefficient) of new material to reproductive structures. Thus,

$$Y = C \times D_R \times p \quad (1)$$

The model components integrate many physiological processes. Wallace et al. (1993) suggested that indirect selection for yield will be most effective when applied to traits that already integrate most of the genetic and environmental effects that lead to yield.

The growth analysis measurements summarized in eqn. 1 must be economically feasible for the large number of genotypes, progenies and environments required for effective selection. Fortunately, methods have been developed which allow largely nondestructive growth analysis on the necessary scale and accuracy (Williams & Saxena, 1991; Williams et al., 1996).

The effectiveness of early generation testing for yield in groundnut has been disputed (Wynne, 1976; Mohammed et al., 1978; Halward et al., 1990). In contrast, Coffelt & Hammons (1974), based on yield tests involving high yielding F_2 families in the F_3 , F_4 , F_5 and F_6 generations, concluded that early generation testing for yield should be an acceptable procedure for groundnuts. In their study, selection was practiced each generation with only those families that outyielded parental lines being advanced each generation, rather than advancing the population in bulk, as was practiced by Wynne (1976), Mohammed et al. (1978) and Halward et al. (1990). This could account for the differences in opinion as to the usefulness of early generation tests in groundnuts. The effectiveness of such tests appears limited to those cases in which selection is practiced as each generation is advanced. For example, Bandyopadhyay et al. (1985) evaluated the genetic potential of F_2 progeny from single and three-way crosses using both physiological traits and components of yield. They found that F_3 families derived from the top 25% of F_2 plants provided a higher frequency of selections for increased pod number than those derived from the top 50, 75 and 100%. In addition, they found the frequency of superior selections to be higher in three-way crosses than single crosses, and a selection index based on physiological and yield components to be more effective than an index based on yield components alone. The researchers concluded

that, with appropriate selection intensities and the use of selection index based on both physiological and yield components, effective selection for yield improvement in groundnut can be made as early as F_2 generation.

Iroume & Knauft (1987) investigated early generation selection methods for the identification of peanut crosses with both high yield and resistance to leaf spot diseases. Their results suggested that in F_2 , selection among crosses would be advantageous over individual plant selection or within family selection. Selection of genotypes within crosses was the poorest strategy for selection in early generation. The effectiveness of early generation selection in peanut appears to be enhanced by limiting its use to traits of high heritability or to indirect selection for yield, based on selection for correlated traits.

The objective of this study was to determine the selection potential for physiological components associated with yield in segregating populations. This information will provide guidance as to the usefulness of using physiological traits in cultivar development in semi-arid environments.

Materials and methods

Experimental sites

Field experiments were conducted at three locations in Niger from 1992 to 1994: the ICRISAT Sahelian Center, Sadore (lat $13^\circ 15'N$, long $2^\circ 17'E$, alt 240 m) near Niamey; where the mean annual rainfall is 580 mm from June to September. The soil at Sadore is sandy loam classified as sandy, silicious, Isohypothermic Psammentic Paleustalf. The top soil is 94% sand and 3% clay. The second location was Gaya (lat $11^\circ 59'N$, long $3^\circ 30'E$, alt 160 m) where the annual average rainfall is 850 mm. The soil is an alfisol (clayey-skeletal, mixed isohypothermic family of Udic Rhodastalf) with 12% clay, 70% sand in the top soil. The third location was Tara (lat $11^\circ 59'N$, long $3^\circ 30'E$, 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. Gaya and Tara are 30 km apart. Monthly rainfall, dates of sowing, flowering and last harvest date are presented in Table 1.

Genetic resources and hybridization techniques

During the dry season of 1991 single crosses were made between spanish (subsp. *fastigiata* Waldron var.

Table 1. Monthly rainfall (mm) and dates of sowing, flowering and last harvest at three locations in 1992–1994

Variable	Sadore			Gaya			Tara		
	1992	1993	1994	1992	1993	1994	1992	1993	1994
Rainfall									
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
September	53	21	126	93	121	0	66	133	18
Total	629	553	730	547	591	689	558	594	759
Phenology									
Sowing	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
Last harvest	30 Sept	10 Oct	10 Oct	15 Oct	5 Oct	30 Sept	–	20 Oct	30 Sept

Table 2. Parents and population combinations used in the study

Females	Males							
	796	55–437	TS32–1	Chico	J11	JL24	ICGVSM87003	ICGV86015
ICGV87121	x	x	x	x	x	x	x	x
ICGV87123	–	x	x	x	–	x	–	–
ICGV SM83005	x	x	–	–	x	x	–	x
ICGMS42	x	–	x	x	x	x	–	–
M13	x	x	x	–	–	x	x	–
ICGV86015	x	x	x	x	x	x	–	–
J11	x	x	x	–	–	–	–	–
JL24	x	–	–	–	–	–	–	–
55–437	x	–	–	x	x	–	–	–
Total	8	6	6	5	5	6	2	2

vulgaris Harz) and virginia (subsp. *hypogaea* var. *hypogaea*) botanical types in a glasshouse at Sadore for an on-going breeding program for yield and adaptation in West Africa. The parental lines were predominantly spanish and cross combinations are presented in Table 2. The virginia lines were ICGV 87121, ICG MS 42 and M13 (introduced from India) and mature in 120 days. Lines 796, 55–437, and TS 32–1 are early (< 100 days sowing to maturity), widely grown in the Sahel, and have high partitioning (Greenberg et al., 1992). Chico, a germplasm line, is extra-early maturing (< 90 days). J11 and JL 24 are early-maturing lines popular in India. ICGV 86003, ICGV 86015, ICGV SM 83005 and ICGV 87123 are advanced medium duration (110 days) lines developed by ICRISAT. These materials are representative of those that would be used by groundnut breeders in semi-arid environments in Africa. The F₁ was grown

in the field at Sadore and checked for hybridity to produce F₂ seed.

Field experiments and data capture

In 1992 forty F₂ populations plus nine parental lines (excluding Chico, ICGV 87047, and ICGV 87005) were grown at Sadore and Gaya. A basal dose of 100 kg ha⁻¹ of single superphosphate was incorporated into the soil by broadcasting during land preparation. Seed was hand sown at each location. Individual plots were 3 rows, 3 m long and 0.5 m apart. Within-row spacing was approximately 10 cm at all locations. The experimental design was a 7 × 7 lattice with three replications. Fields were kept weed free by regular manual weeding. The trials were strictly rainfed and no fungicides were applied to control foliar diseases.

The data collected included the time to flowering, maturity, incidence of foliar diseases and defoliation

Table 3. 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
F₂ Generation					
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 × 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
F₃ Generation					
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 × 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
F₄ Generation					
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 × 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.

at harvest. 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. Maturity was determined by pulling out random plants and examining the internal pod wall. Mature pods are indicated by the blackening of internal pod wall (Williams & Drexler, 1981). Defoliation due to diseases was determined on five randomly selected plants before harvesting. At harvest, all plants in a plot were hand-lifted. First three two-seeded mature pods were picked from each plant without selection to constitute seed for F_3 trials. The remaining pods (including immatures) were separated from the haulms and bulked together with pods recovered from the soil. Pods and haulms (including recoverable fallen leaves) were sun-dried separately.

The trials were repeated in the F_3 in 1993 using seed obtained by bulking three pods/plant in the F_2 trials. Similarly seed for the F_4 trials in 1994 was obtained by bulking three pods per plant without selection from F_3 trials. The F_3 and F_4 trials were planted at Sadore, Gaya and Tara. Each plot consisted of four rows, 4 m long and 0.50 m apart. Within-row spacing

was approximately 10 cm. The experimental design was as in F_2 generation (7×7 lattice with three replications). Agronomic management, observations and harvesting procedures were similar to those in F_2 generation.

The dried pods and vegetative weights were added to calculate the final harvest biomass. Crop growth rate (C, $\text{kg ha}^{-1} \text{ day}^{-1}$), pod growth rate (R, $\text{kg ha}^{-1} \text{ day}^{-1}$) and partitioning (p , coefficient) were estimated from each plot using final harvest biomass adjusted for defoliation at final harvest and the timing of flowering and maturity. The adjustment for defoliation was based on the assumption that 50% of the vegetative parts was leaf. Pod dry matter was multiplied by 1.65 (Bell et al., 1992), a value reflecting the ratio for the differences in energy requirement for producing vegetative vs. pod dry matter. C and R were computed as:

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

$$R = W_R/(tm - t_v + 15) \quad (3)$$

Table 4. Mean pod yield (t/ha^{-1}), crop growth rate (C, $kg\ ha^{-1}\ day^{-1}$), partitioning (p) and reproductive duration (D_R , days) for parents and crosses at three locations in 1992 to 1994

Generation	Pod yield		C		p		D_R	
	Parents	Crosses	Parents	Crosses	Parents	Crosses	Parents	Crosses
F ₂ Sadore	0.36	0.32	20.1	16.5	0.31	0.33	95	100
F ₂ Gaya	2.13	1.99	69.0	68.5	0.81	0.75	77	78
F ₃ Sadore	0.29	0.24	13.8	12.3	0.50	0.46	71	72
F ₃ Gaya	2.36	2.13	76.7	72.3	0.59	0.57	86	87
F ₃ Tara	1.71	1.47	48.7	46.6	0.77	0.69	76	75
F ₄ Sadore	0.91	0.94	27.7	30.0	0.71	0.68	76	75
F ₄ Gaya	1.98	1.78	62.9	61.6	0.73	0.68	71	71
F ₄ Tara	2.03	1.77	56.1	53.0	0.85	0.77	70	71

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

where t_m is the time in days from sowing to maturity, t_v is the time in days from sowing to 50% flowering and 15 represents the days between flowering and start of podding. W is the adjusted biomass (haulm yield + (pod weight \times 1.65)) and W_R is the adjusted pod weight. Reproductive duration was the difference between maturity and flowering dates.

Data analysis

Separate analyses of variance were done for each generation and location using GENSTAT procedures (Genstat 5.3 Committee, 1993). Populations and locations were considered to be random. Adjusted means from the lattice were used in the combined analysis of variance across locations. Parent-offspring regression (b) coefficients were obtained by regressing means of F₃ bulks on F₂ bulk and F₄ bulks on F₃ bulks. Parent-offspring correlation (r) were also calculated. These eliminate phenotypic variation caused by evaluating two generations in different years and are computationally equivalent to parent-offspring regression for data coded in terms of standard deviation units (Frey & Horner, 1957).

Results

Mean performance

Populations and parents differed for yield and model components (Table 3). The effects of locations were highly significant indicating that the three sites were

contrasting as indicated by the wide range in mean yields and crop growth rate (Table 4). Location \times population interaction was significant for all traits except for yield and C in the F₄ generation. In both F₂ and F₃ generations, pod yield at Gaya and Tara were more than five times greater than at Sadore. These large differences could be attributed in part to differences in soil pH and organic matter contents as well as the seasonal variation in rainfall (Table 1).

Parent-offspring regression

Parent-offspring regression and correlation coefficients for C, p , and D_R , and pod yield are presented in Table 5. The regressions for C were nonsignificant at all locations and when combined over locations. When F₃ and F₄ data from Gaya and Tara were combined, regression for C slightly improved from 0.12 to 0.20, but was still nonsignificant.

Regression coefficients for partitioning ranged from 0.14 to 0.60 and were similar for F₂ vs. F₃ and F₃ vs. F₄ at Gaya and Sadore (Table 5). When combined over locations, regression values for p were similar and significant only when Sadore data was excluded from the analysis in the F₃: F₄ regression.

For D_R only the F₃: F₄ regression was significant at Gaya and when combined over locations. Exclusion of Sadore data from the regression resulted in a smaller regression coefficient (Table 5).

F₃: F₄ regression for pod yield were significant only at Tara. When Sadore data was excluded from the regression analysis, the regression for pod yield was significant.

F₂: F₃ regression for p was significant indicating that selection for p in F₂ generation would be possible. On the other hand, when Sadore data was excluded

Table 5. Parent-offspring regression and correlations of F₃ on F₂, and F₄ on F₃ bulk means at three locations

Trait	Location	Parent-offspring regression (b)		Parent-offspring correlation (r)	
		F ₂ : F ₃	F ₃ : F ₄	F ₂ : F ₃	F ₃ : F ₄
C	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
	<i>Combined</i>	<i>0.10 ± 0.08</i>	<i>0.12 ± 0.23</i>	<i>0.20</i>	<i>0.08</i>
	-Sadore	–	0.20 ± 0.11	–	0.28
C	Sadore	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
	<i>Combined</i>	<i>0.45 ± 0.17**</i>	<i>0.24 ± 0.17</i>	<i>0.39</i>	<i>0.22</i>
	-Sadore	–	0.46 ± 0.17*	–	0.40
C	Sadore	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
	Tara	–	0.08 ± 0.14	–	0.09
	<i>Combined</i>	<i>0.10 ± 0.03</i>	<i>0.59 ± 0.24**</i>	<i>0.47</i>	<i>0.39</i>
	-Sadore	–	0.14 ± 0.10	–	0.22
C	Sadore	0.00 ± 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
	<i>Combined</i>	<i>0.16 ± 0.14</i>	<i>0.17 ± 0.28</i>	<i>0.19</i>	<i>0.24</i>
	-Sadore	–	0.57 ± 0.11**	–	0.62

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

from the F₃: F₄ regression analysis, the regression for yield was significant and larger than for any of the physiological components.

The parent-offspring correlations were, in most cases, similar to the regression values (Table 5), indicating that the scale did not greatly influence the regression coefficient estimate.

Discussion

Differences between locations were apparent. There was considerable variation in amount and timing of rainfall relative to crop phenology (Table 1). Soil spatial variability is also known to be responsible for poor crop growth at Sadore (Brouwer et al., 1993). Therefore, these factors could account for the significant mean squares due to locations and their interactions with populations (Table 3).

The nonsignificant F₂: F₃ regression showed that selection for yield and physiological traits in early generations would be ineffective. This is typical of complexly inherited traits. For *p*, however, parent-offspring regression was significant indicating that

selection for this trait in F₂ was possible. Exclusion of data from Sadore in the F₃: F₄ regression, improved the relationships among generations for C, *p* and pod yield (Table 5). This suggested that Sadore is not a suitable site for groundnut breeding as it lies at the margin of groundnut production belt in West Africa.

The similarity of the regressions for *p* calculated from the F₂: F₃ and F₃: F₄ regressions indicated absence of significant nonadditive genetic effects, but when considered with the rather low parent-offspring correlations, selection progress in early generations is likely to be slow. Regressions from two different parent-offspring generations offer more precise determination of the significance of nonadditive genetic variance, because if this variance is relatively large, estimates of heritability may be biased upwards. The significant regression coefficient from F₃: F₄ generations for yield indicated that selection based on yield alone would be effective. This is contrary to the results of Halward et al. (1990) who reported no relationship between yield of F₃ and F₄ and concluded that pod yields in early generations were ineffective in predicting the yield potential of crosses grown in bulk in later generations.

The differences in parent-offspring regressions from two different parent-offspring (F_2 : F_3 and F_3 : F_4) generations could be due to both genetic and environmental effects. The increase or decrease could have occurred since parents and offspring were evaluated in successive years. This is in agreement with conclusions reached by other researchers (Fernandez & Miller, 1985; Iroume & Knauff, 1987).

Comparisons of F_2 , F_3 and F_4 via correlations indicated that the physiological components C , p and D_R were not effective in predicting yield in early generations. A number of sources of bias could have affected the regression values obtained in this study. 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). Interaction among crosses, generations and years may be confounded thus reducing the accuracy with which later generations performance can be predicted based on early generation testing. Other potential sources of bias include handling segregating populations and the methodology used in measuring physiological traits. Therefore, the method of generation advance should be considered carefully when using the bulk-breeding method.

Some caution should be exercised, however, regarding the generality of the results of this study. There are various environmental and agronomic factors that impact physiological traits. These factors were not controlled in this study. Different results may be obtained, if for instance supplementary irrigation to alleviate drought stress and fungicides to control foliar diseases are applied. The impact of loss of material at final harvest is potential source of error in estimating growth. Thus, with better description of growth and phenological observations more reliable estimates of partitioning to reproductive structures should be achieved. The ability to describe growth and partitioning more reliably has theoretical significance to the breeders' ability to select for yield with more confidence. This should reduce substantially the cost of varietal development.

References

- Bandyopadhyay, A., V. Arunachalan & K. Venkajah, 1985. Efficient selection intensity in early generation index selection in groundnut (*Arachis hypogaea* L.). *Theor. Appl. Gen.* 71: 300–304.
- Bell, M.J., G.C. Wright & G.L. Hammer, 1992. Night temperature affects radiation use efficiency in peanut. *Crop Sci.* 32: 1329–1335.
- Brouwer, J., L.K. Fussel & L. Herrmann, 1993. Soil and crop growth variability in West African semiarid tropics: a possible risk reducing factor for substance farmers. *Agriculture, Ecosystems and Environment* 45: 229–238.
- Coffelt, T.A. & R.O. Hammonds, 1974. Correlation and heritability studies of nine characters in parental and intra-specific cross populations of *Arachis hypogaea*. *Oléagineux*. 29: 23–37.
- Duncan, W.G., R.L. McGraw & K.J. Boote, 1978. Physiological aspects of peanut yield improvement. *Crop Sci.* 18: 1015–1020.
- Fernandez, G.C.J. & J.C. Miller, 1985. Estimation of heritability by parent-offspring regression. *Theor. Appl. Genet.* 53: 650–654.
- Frey, K.J. & T. Horner, 1957. Heritability in standard units. *Agron. J.* 49: 59–62.
- Genstat 5 Committee, 1993. *Genstat 5 release 3 Reference manual*. Oxford Science Publications.
- Greenberg, D.C., J.H. Williams & B.J. Ndunguru, 1992. Differences in yield determining processes of groundnut (*Arachis hypogaea* L.) genotypes in varied drought environments. *Ann. Appl. Biol.* 120: 557–566.
- Halward, T.M., J.C. Wynne & E.J. Monteverde-Penso, 1990. Effectiveness of early generation testing as applied to a recurrent selection program in peanut. *Peanut Science* 17: 44–47.
- Iroume, R.N. & D.A. Knauff, 1987. Heritabilities and correlations for pod yield and leafspot resistance in peanut (*Arachis hypogaea* L.): Implications for early generation selection. *Peanut Science* 14: 46–50.
- Mohammed, J.J., J.C. Wynne & J.O. Rawlings, 1978. Early generation variability and heritability estimates in crosses of virginia and spanish peanuts. *Oleagineux* 33: 81–86.
- Nigam, S.N., S.L. Dwivedi & R.W. Gibbons, 1991. Groundnut breeding, constraints, achievements and future possibilities. *Plant Breeding Abst.* 61: 1127–1136.
- Wallace, D.H., J.P. Baudoin, J. Beaver, D.P. Coyne, D.E. Halseth, P.N. Masaya, H.M. Munger, J.R. Myers, M. Silbernagel, K.S. Yourstone & R.W. Zobel, 1993. Improving efficiency of breeding for higher crop yield. *Theor. Appl. Genet.* 86: 27–40.
- Williams, E. & J.S. Drexler, 1981. A nondestructive method for determining peanut pod maturity. *Peanut Science* 8: 134–141.
- Williams, J.H., 1992. Concepts for the application of crop physiological models to crop breeding. In: S.N. Nigam (Ed.), *Groundnut – A Global Perspective: Proceedings of an International Workshop ICRISAT Center, India, 1991, November 25*. ICRISAT Patancheru, India, pp. 345–352.
- Williams, J.H. & N.P. Saxena, 1991. The use of non-destructive measurement and physiological models of yield determination to investigate differences in seed yield between genotypes of desi chickpeas (*Cicer arietinum*). *Annu. Appl. Biol.* 119: 105–112.
- Williams, J.H., R.C. Nageswara Rao, F. Dougbedji & H.S. Talwar, 1996. Radiation interception and modelling as an alternative to destructive samples in crop growth. *Ann. Appl. Biol.* 129: 152–160.
- Wynne, J.C., 1976. Evaluation of early generation testing in peanuts. *Peanut Sci.* 3: 62–66.

