Theor Appl Genet (1991) 82:784–792

Generation means analysis for productivity in two diverse peanut crosses*

T.M. Halward** **and J.C. Wynne**

Crop Science Department, North Carolina State University, Raleigh, NC 27695-7629, USA

Received January 8, 1991; Accepted May 16, 1991
Communicated by A.R. Hallauer

Summary. Utilization of exotic germplasm resources for population improvement in peanut (*Arachis hypogaea* L.) has increased as the need to increase genetic diversity among peanut cultivars was recognized. Progeny of crosses of two unadapted germplasm lines (GP-NC 343 and FESR-11-P11-32) with an adapted cultivar ('NC-V11') of peanut were evaluated for the genetic factors influencing the inheritance of yield and fruit characters in crosses among diverse lines. Objectives were to (1) estimate the relative importance of additive and nonadditive genetic effects in the inheritance of yield and fruit characters in two diverse peanut crosses; (2) determine the proportion of exotic germplasm that gave the optimum combination of mean productivity and genetic variability for each of the crosses; (3) relate the results to theories regarding the transfer of desirable alleles from exotic germplasm into adapted breeding populations. Crosses and backcrosses were made to generate germplasm lines (ten generations) ranging from 0 to 100% exotic germplasm for each cross. The populations were evaluated in replicated field trials. Yield and six fruit characters were measured, and a weighted analysis of variance was conducted to determine if significant differences existed among generations. Generation means analyses were performed for each trait measured in each of the crosses using both three- and six-parameter models, which were tested for goodness-of-fit with a joint-scaling test. Significant differences were detected among generations for most traits measured in both crosses. Estimates of additive genetic effects were significant for pod weight and seed weight in cross 1 ('NC-V11' × GP-NC 343) and for all traits in cross 2 ('NC-V11' × FESR-11-P11-32) except seed:pod ratio. Significant estimates of dominance effects were found for pod length, pod width, and pod weight in cross 1 and for pod length in cross 2. No significant estimates of digenic effects were observed in cross 1, whereas in cross 2 estimates of additive × dominance epistatic effects were significant for yield and pod length, while estimates of additive × additive effects were significant for seed number. Regression of trait means on generations showed a curvilinear response for all traits in cross 1 except seed weight, which gave a linear response. For all traits in cross 2, the relationship between productivity and proportion of unadapted germplasm was effectively linear. Based on generation means and variances, progeny from the first or second backcross generation to the recurrent parent should be expected to give an optimum combination of mean productivity and relative variability in the population.

Key words: Germplasm – Genetic diversity

Introduction

Peanut (*Arachis hypogaea* L.) breeding programs aimed at rapid cultivar improvement have generally relied on the use of established cultivars and elite lines in the development of breeding material. The result has been a narrowing of the germplasm base of the cultivated peanut. To broaden the germplasm base and maintain genetic diversity in the crop, breeders have considered incorporating exotic germplasm lines into their cultivar development programs.

While many of the available germplasm lines have been screened for pest resistance and nutritional quality,

---

* The research reported in this publication was funded in part by the North Carolina Agricultural Research Service

** To whom correspondence should be addressed fewer efforts have been directed toward the identification of lines with potential for improving yield or the fruit characters considered important for acceptance by industry or the consumer. Taking advantage of useful quantitative genes in an exotic line or related wild species requires a different approach than the introgression of specific qualitative traits into the adapted population, and is often done as part of a germplasm enhancement project per se, independent of the general breeding program (Bramel-Cox and Cox 1989). An independent germplasm enhancement program allows for the retention of progenies with favorable alleles for quantitative traits that would otherwise be discarded in a breeding program as being unproductive or undesirable. Genetic studies to determine combining abilities, heritabilities, and relative importance of additive, dominance, and epistatic gene effects in controlling traits of interest can be valuable in deciding the most appropriate germplasm lines to include in a germplasm enhancement or breeding program. Subsequently, decisions as to the level of exotic germplasm incorporation desirable and the appropriate hybrid generations for testing should be made.

Important traits in peanut, including yield and adaptability, are considered to be quantitatively inherited, and the exploitation of genetic variability of these quantitative traits through hybridization, inbreeding, and selection is the primary focus of most peanut improvement programs. Although methods for characterizing genetic variability in self-fertilizing species are available, information on the types of gene action and their relative importance in peanut has only slowly started to accumulate during the last two decades (Wynne and Halward 1989). Wynne and Coffelt (1982) concluded that heterosis is generally observed in crosses between different subspecific groups, suggesting that gene action may differ in crosses made within and crosses made between botanical varieties. Evidence suggests that heterosis in peanut is related to genetic diversity (Syakudo and Kawabata 1963; Lin 1966; Parker et al. 1970; Layrisse et al. 1980; Isleib and Wynne 1980). Similar results have been obtained in other crop species, both self-pollinated (Fonesca and Patterson 1968; Marani 1963, 1968; Matzinger and Wernsman 1968) and cross-pollinated (Moll et al. 1962; Sriwatanapongse and Wilsie 1968).

Wynne and Coffelt (1982) also concluded that general combining ability was of primary importance for most traits, suggesting that additive variance is the major component of genetic variance in peanut. Various studies also found significant estimates of specific combining ability in peanut crosses, indicating that nonadditive genetic effects may play a role in the inheritance of important traits (Wynne et al. 1970, 1975; Garet 1976; Gibori et al. 1978; Layrisse et al. 1980; Isleib et al. 1978; Mohammed et al. 1978, Sandhu and Khehra 1976). Additive genetic variance seems of primary importance in crosses made between parents from a single botanical variety, but additive and nonadditive genetic variance may be significant in crosses made between parents from different botanical varieties (Wynne and Gregory 1981). Dominance and additive × additive epistasis contributed to the significant estimates of SCA in the various studies. While variation due to dominance cannot effectively be exploited in a self-pollinating species such as peanut, additive × additive epistatic variation is potentially useful to peanut breeders because it can be fixed in the homozygous state.

Additive and nonadditive genetic effects were found to play a significant role in the inheritance of a number of traits in peanut – fruit yield and fruit size (Mohammed et al. 1978; Sandu and Khera 1976), components of partial resistance to *Cercospora arachidicola* Hori (Green and Wynne 1986); and various nitrogen-fixing traits (Phillips et al. 1989).

The primary objective of this study was to estimate the relative importance of additive and nonadditive genetic effects in controlling the inheritance of yield and fruit characters in two crosses between diverse peanut germplasm lines and an adapted cultivar. A second objective was to determine the proportion of exotic germplasm which gave the highest level of productivity while maintaining adequate variability in the population for each of the crosses. A third objective was to relate the results obtained to theories on the effectiveness of using the backcross method for transferring desirable alleles from exotic lines to adapted cultivars.

Materials and methods

Development of the population

Three peanut genotypes were chosen from among 16 lines being used in an ongoing convergent crossing program to initiate a genetic study of the inheritance of yield and fruit characters in two populations derived from crosses between exotic and adapted peanut cultivars. An adapted cultivar, 'NC-V11' ('Florigiant'/'NC 5'//'Florigiant'/'Valencia'), was used as the female parent in the two crosses. GP-NC 343 (NC Bunch/PI 121067), a germplasm line with resistance to early leafspot and several insect pests, and FESR-11-P11-32 (PI 298115/'Valencia'), an exotic line with resistance to late leafspot, were used as the male parents in the study. The appropriate crosses and backcrosses were made in the greenhouse between 1986 and 1988 to generate a series of germplasm lines ranging from 0 to 100% exotic germplasm from each of the initial crosses. The three original parents were used as the male parent in subsequent backcrosses during development of the populations such that all generations were maintained in the adapted cytoplasm background, avoiding any potential confounding reciprocal effects. Ten F_1 plants were used in crosses to obtain BC_1 generation seed; 20 BC_1 plants were used in crosses to obtain BC_2 generation seed.

The following populations were developed for use in a generation means analysis to study the inheritance of yield and fruit characters in crosses between exotic germplasm lines and adapted cultivars:

Cross 1		*Cross 2*
P_1:	'NC-V11'	'NC-V11'
P_2:	GP-NC 343	FESR-11-P11-32
F_1:	$P_1 \times P_2$	$P_1 \times P_2$
F_2:	$F_1\otimes$	$F_1\otimes$
BC_1A:	F_1 × 'NC-V11'	'F_1 × NC-V11'
BC_1B:	F_1 × GP-NC 343	F_1 × FESR-11-P11-32
BC_2A:	BC_1A × 'NC-V11'	BC_1A × 'NC-V11'
BC_2B:	BC_1B × GP-NC 343	BC_1B × FESR-11-P11-32
BC_1AS_1:	$BC_1A\otimes$	$BC_1A\otimes$
BC_1BS_1:	$BC_1B\otimes$	$BC_1B\otimes$

Generation means analysis: experimental design

Ten populations (generations) of each cross were grown in a replicated test at three locations in 1989 – the Peanut Belt Research Station in Lewiston, N.C.; the Upper Coastal Plain Research Station in Rocky Mount, N.C.; the Central Crops Research Station in Clayton, N.C. A randomized complete block design with three replications was used at each of the three locations. Nonsegregating generations (P_1, P_2, F_1) were represented by single-row plots of five plants each, while segregating generations (F_2 and all backcross generations) were represented by three one-row plots with five plants per row in each replication. The use of three times as many observations on segregating generations compensated for the greater variability in error variance typically associated with segregating populations versus nonsegregating populations (Hallauer and Miranda 1988; Mather and Jinks 1977).

The study was planted by hand, after which standard cultural practices were followed throughout the growing season. At maturity, plants were hand-dug keeping individual rows separate for independent observations. Yield (fruit weight in grams) was measured for each row, and the number of plants in the row was recorded. Because of an unusually high amount of rainfall during the growing season and unequal disease pressure, the number of plants per row varied from 2 to 5. Yield data were subjected to analysis of covariance, with number of plants/row as the covariate.

In addition to yield, the following fruit traits were measured for each observation (row):

Length of 20 random pods, in cm;
Width of 20 random pods, in cm;
Weight of 20 random pods, in g;
Number of seed from 20 random pods;
Weight of seed from 20 random pods, in g;
Seed: pod ratio (seed weight ÷ pod weight).

In the statistical analysis a log transformation of seed : pod ratio was used so that the measurement conformed to an additive model that is necessary to obtain meaningful results from the generation means analysis (Mather and Jinks 1977).

Generation means analysis: statistical analysis

Separate analyses were conducted for each cross. The means of the traits for each generation, weighted by the number of observations (rows) making up the means, were analyzed using a General Linear Model procedure (SAS 1985). A Waller-Duncan K-ratio was applied to each trait to determine whether significant differences existed among generation means. Separate weighted analyses of variance were made to obtain estimates of the variation present within generations for use in the variance matrix of the generation means analysis. Generations expected to have similar variances were grouped in the analyses to provide sufficient degrees of freedom for tests of residual mean squares: (P_1, P_2, F_1); (F_2); (BC_1A, BC_1B); (BC_2A, BC_2B); (BC_1AS, BC_1BS).

Generation means obtained from the original weighted analysis of variance were used to estimate the model parameters. Gamble's (1962) notation was used in defining the parameters of the model:

m = midparent value,
a = pooled additive gene effects,
d = pooled dominance gene effects,
aa = pooled additive × additive epistatic effects,
ad = pooled additive × dominance epistatic effects, and
dd = pooled dominance × dominance epistatic effects.

The parameters were defined using F_∞ – the average value of homozygotes – as the base population, as suggested by Mather and Jinks (1977) and Van der Veen (1959).

An additive-dominance (three-parameter) model and a model including epistatic interactions (six-parameter) were applied to the data and tested for goodness-of-fit using the joint scaling test of Cavalli (1952). The joint scaling test uses a chi-square test for adequacy of the model, and it provides the best possible estimates of all the parameters required to account for differences among generation means when the model proves adequate (Mather and Jinks 1977). The joint scaling test works by estimating the model parameters from the means of all types of families available, followed by a comparison of these means as observed with their expected values derived from the estimates of the parameters.

The model parameters (m, a, d, aa, ad, dd) were estimated by the weighted least squares method in matrix notation described by Rowe and Alexander (1980). The use of a weighted least squares analysis reduces the error mean squares associated with segregating generations that contain a greater number of individuals than the nonsegregating generations. The generation means were weighted by the reciprocal of their corresponding variances, obtained from the independent analyses of variance for each generation, and by the number of observations (rows) used in calculating the various generation means.

Results

Significant differences were detected among generation means for all traits measured in both crosses except seed number in cross 1 and seed : pod ratio in cross 2 (Table 1).

The chi-square values obtained from the joint-scaling tests for both the three- and six-parameter models were not significant for any traits measured in either cross except for yield in cross 1, indicating that either model was adequate for explaining the variability observed among the progeny from both crosses for most traits measured. The significant chi-square values (0.05 level) obtained from the joint-scaling tests of both models for yield in cross 1 indicate that neither model was adequate to explain the variability present. Log transformations of the yield data in cross 1 resulted in nonsignificant chi-square values from the joint-scaling tests for both the three- and six-parameter models; however, no significant genetic effects were detected with either model.

Additive genetic effects were found to contribute significantly to the inheritance of pod weight and seed weight in cross 1 (Table 2). In cross 2, significant estimates of additive effects were found for all traits mea-

Table 1. Generation means and variances for yield and six agronomic traits for two peanut crosses

Generation	n[a]	Plot yield (g)	20-Pod length (cm)	20-Pod width (cm)	20-Pod wt (g)	No. seed/ 20 pods	Seed wt (g)	Seed : pod ratio (log)
		$\bar{x}$ $v_{\bar{x}}$[b]	$\bar{x}$ $v_{\bar{x}}$	$\bar{x}$ $v_{\bar{x}}$	$\bar{x}$ $v_{\bar{x}}$	$\bar{x}$ $v_{\bar{x}}$	$\bar{x}$ $v_{\bar{x}}$	$\bar{x}$ $v_{\bar{x}}$ ($\times 100^2$)
					Adapted × exotic cross I			
P_1 (NC-V11)	9	609.3±18,925.5	72.8± 4.22	29.3± 0.47	44.1± 8.96	39.4± 2.33	32.8± 7.06	0.74±0.12
P_2 (GP-NC 343)	9	483.8±18,925.5	68.1± 4.22	28.8± 0.47	36.8± 8.96	39.1± 2.33	26.0± 7.06	0.70±0.12
F_1	9	648.0±18,925.5	75.4± 4.22	30.9± 0.47	44.2± 8.96	38.9± 2.33	31.5± 7.06	0.71±0.12
F_2	27	498.7± 1,046.8	75.2± 0.98	31.0± 0.17	42.0± 1.81	39.2± 0.38	28.9± 1.30	0.68±0.03
BC_1A	27	553.0±14,903.6	75.0±12.03	30.3± 2.14	44.1±34.92	38.8± 3.72	31.5±27.48	0.70±0.69
BC_1B	27	612.5±14,903.6	74.1±12.03	30.8± 2.14	42.9±34.92	39.6± 3.72	30.0±27.48	0.70±0.69
BC_2A	27	639.8±10,435.1	73.5±12.58	29.8±16.95	44.3±33.44	39.2± 3.39	32.5±25.35	0.73±0.51
BC_2B	27	577.1±10,435.1	70.7±12.58	29.7±16.95	39.7±33.44	39.3± 3.39	27.9±25.35	0.69±0.51
BC_1AS	27	620.0±17,822.4	71.5± 7.11	29.6± 1.12	43.5±15.46	39.4± 1.86	32.0±10.01	0.73±0.08
BC_1BS	27	775.8±17,822.4	69.1± 7.11	28.5± 1.12	41.0±15.46	40.7± 1.86	29.8±10.01	0.72±0.08
LSD (0.05)		131.30	18.69	6.40	30.61	–	27.53	0.02
					Adapted × exotic cross II			
P_1 (NC-V11)	9	609.3±10,109.6	72.8± 8.38	29.3± 0.84	44.1±14.81	39.4± 6.22	32.8± 9.74	0.74±0.10
P_2 (FESR-11-P11-32)	9	154.2±10,109.6	53.6± 8.38	23.3± 0.84	25.4±14.81	46.8± 6.22	18.7± 9.74	0.74±0.10
F_1	9	481.1±10,109.6	69.3± 8.38	27.0± 0.84	38.2±14.81	44.3± 6.22	28.4± 9.74	0.74±0.10
F_2	27	401.2± 9,322.7	64.2±28.58	26.3± 2.60	33.2±32.53	41.3± 7.15	24.4±21.94	0.73±0.62
BC_1A	27	476.1±12,262.3	67.1±18.45	27.3± 1.02	37.5±28.15	39.4±11.52	27.9±18.78	0.74±0.26
BC_1B	27	397.7±12,262.3	63.4±18.45	25.2± 1.02	32.3±28.15	44.4±11.52	23.8±18.78	0.74±0.26
BC_2A	27	556.3±18,949.1	70.1±18.06	28.7± 1.76	40.9±28.91	39.6± 7.19	30.3±22.33	0.73±0.69
BC_2B	27	310.9±18,949.1	59.0±18.06	24.3± 1.76	28.7±28.91	45.3± 7.19	20.7±22.33	0.72±0.69
BC_1AS	27	482.8±12,779.2	65.8±25.75	26.7± 3.38	33.4±33.44	39.0± 7.37	24.4±21.30	0.73±0.56
BC_1BS	27	304.6±12,779.2	60.3±25.75	25.5± 3.38	30.7±33.44	42.6± 7.37	22.5±21.30	0.73±0.56
LSD (0.05)		92.43	28.05	8.45	33.36	1.96	26.22	–

[a] n = Number of observations per generation; an observation = a five-plant row

[b] $v_{\bar{x}}$ = Variance of the mean

Table 2. Genetic parameter estimates (±standard error) for yield and six agronomic traits based on the three-parameter model for two peanut crosses

Genetic parameter	Plot yield (g)	20-Pod length (cm)	20-Pod width (cm)	20-Pod wt (g)	No. seed/20 pods	Seed weight (g)	Seed : pod ratio (log)
				Cross I: NC-V11 × GP-NC 343			
m	651.63**± 76.02	70.19**±1.05	29.13**±0.46	40.90**±0.53	39.81**±0.37	29.77**±0.84	0.73**±0.01
a	1.71 ns± 59.99	2.05 ns±1.03	0.34 ns±0.50	3.06**±0.53	−0.41 ns±0.34	2.86* ±0.85	0.02 ns±0.02
d	−254.13 ns±164.47	8.47**±2.32	2.96* ±0.96	2.76* ±1.12	−1.15 ns±0.83	−0.51 ns±1.81	−0.07 ns±0.03
χ^2 (7)	15.45*	8.09 ns	11.31 ns	0.92 ns	2.40 ns	3.16 ns	6.91 ns
				Cross II: NC-V11 × FESR-11-P11-32			
m	384.26**±25.75	62.59**±0.96	26.20**±0.27	33.21**±1.29	41.63**±0.68	24.32**±1.03	0.730**±0.003
a	169.97**±23.05	7.60**±0.89	2.64**±0.24	7.48**±1.19	−3.88**±0.61	5.66**±0.96	0.002 ns±0.003
s	86.02 ns±59.82	5.73* ±2.17	0.44 ns±0.59	3.22 ns±2.97	0.89 ns±1.69	2.71 ns±2.36	0.005 ns±0.006
χ^2 (7)	2.29 ns	3.13 ns	2.44 ns	3.45 ns	2.90 ns	3.28 ns	0.17 ns

*,** Indicates significance at the 0.05 and 0.01 probability levels, respectively; ns = non-significant

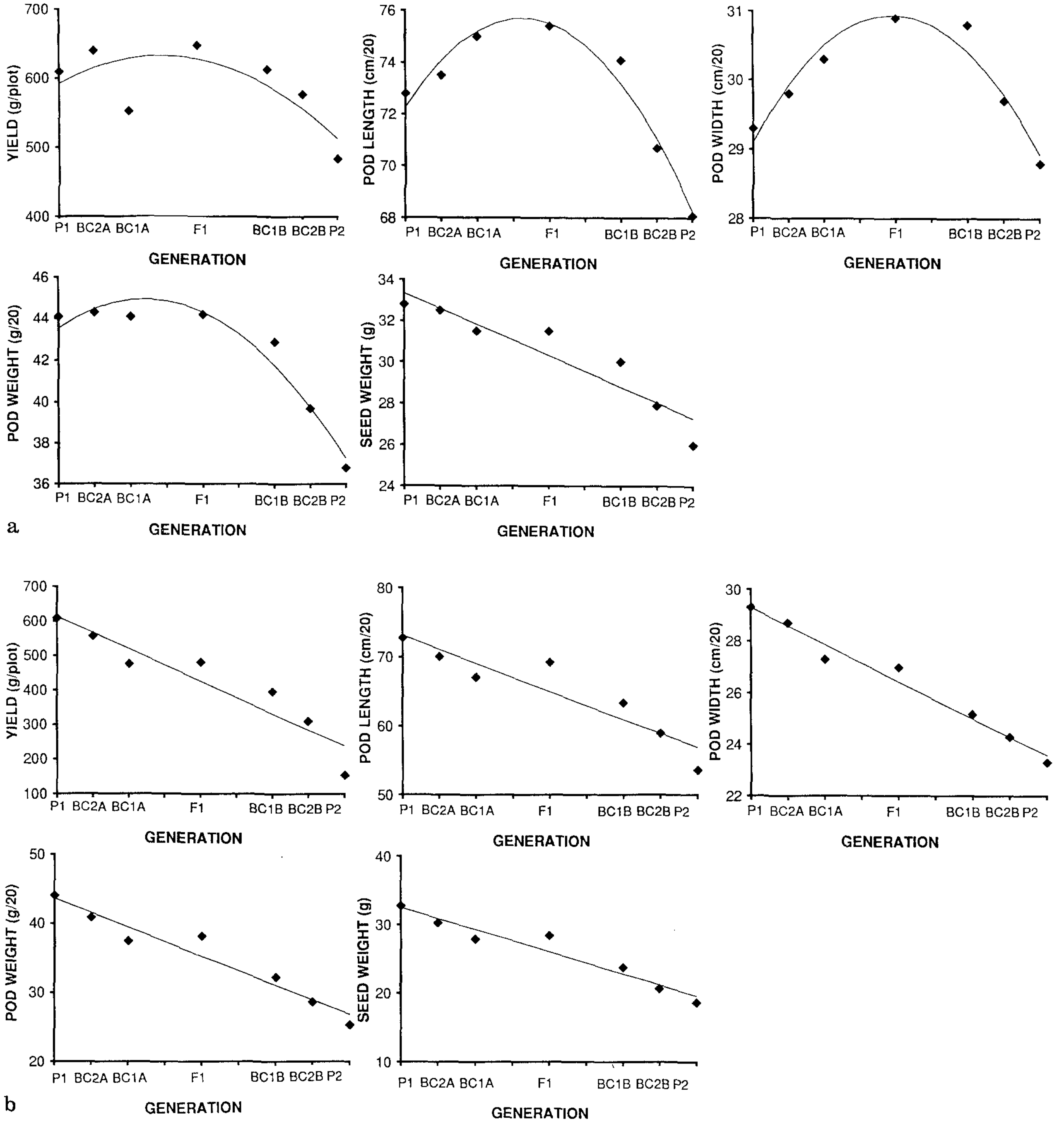

Fig. 1. **a** Productivity (trait means) versus proportion of exotic germplasm remaining in each generation in a cross between an adapted peanut cultivar ('NC-V11') and an unadapted germplasm line (GP-NC 343) (cross 1). **b** Productivity (trait means) versus proportion of exotic germplasm remaining in each generation in a cross between an adapted peanut cultivar ('NC-V11') and an unadapted germ plasm line (FESR-11-P11-32) (cross 2)

sured except seed : pod ratio (Table 2). Dominance effects were significant for pod length, pod width, and pod weight in cross 1, while only pod length showed significant dominance effects in cross 2 (Table 2).

Trends in productivity versus proportion of unadapted germplasm remaining in the population were plotted for yield and fruit characters in both crosses (Fig. 1 a, b). In general, a curvilinear response was observed for most traits in cross 1, especially those traits that were strongly influenced by dominance effects. Only seed weight in cross 1, which was largely controlled by additive effects, showed a linear relationship. For all traits measured in cross 2, a linear relationship was found between productivity and proportion of unadapted germ plasm, corresponding to the greater relative importance of additive effects governing most traits measured.

Discussion

A three-parameter model was fit first because, when no epistasis is present, additive and dominance gene effects are uniquely estimated and unbiased by linkage disequilibrium. However, even when a good fit was indicated using a three-parameter model, a six-parameter model also was applied. Fitting only a six-parameter model would not have provided as meaningful estimates of the main effects. When epistasis is present, estimates of additive and dominance effects are biased and their relative importance to epistatic effects cannot be directly assessed (Mather and Jinks 1977).

Cross 1: 'NC-V11' × GP-NC 343

Failure to detect significant estimates for any genetic effects – additive, dominance, or epistatic – governing yield in cross 1, using either a three- or six-parameter model applied to the original values for yield or to log transformations of yield, suggests the presence of more complex interactions. Lack of fit by a six-parameter model usually indicates the presence of trigenic or high order epistatic interactions and/or linkage of interacting loci. It can indicate also an interaction of main effects with the environment. Based on a highly significant generation-by-location interaction term in the analysis of variance and the large deviation of observed from expected mean for the BC_1BS generation in the generation means analysis, failure of either model to adequately explain the genetic effects governing yield in cross 1 may have been attributable to an interaction of main effects with the environment rather than a complex pattern of linkage or higher order epistatic interactions. Alternatively, the lack of significant estimates of digenic interactions could have resulted from a cancellation of effects. The failure to detect epistasis does not exclude the possibility that interallelic interactions are present (Hayman 1958). A balancing of positive and negative epistatic effects could result in a nonsignificant estimate of epistasis. In addition, significant deviations of backcross generations from their expected means, as was observed for the BC_1BS generation of cross 1, are often an indication of the presence of epistatic interactions (Marani 1968). Although no conclusions can be drawn as to the inheritance of yield in cross 1 from the models tested, the estimate of dominance effects was several magnitudes greater than the estimates of additive effects. The relative importance of dominance effects in cross 1 for a number of fruit characters that contribute to yield (pod length, pod width, pod weight) further suggests that dominance and/or digenic interactions involving dominance are probably operating on yield as well, but are not being detected in the generation means analysis due to some combination of environmental effects, linkage disequilibrium, or cancellation of genetic effects.

The highly significant estimates of dominance effects for pod length and pod width are consistent with previous reports of the importance of dominance effects in controlling the inheritance of agronomic traits among diverse crosses in peanut (Garet 1976; Gibori et al. 1978; Isleib and Wynne 1983a). Most of the previous studies involved intersubspecific hybridizations, whereas in this study both crosses were between lines that could be classified as "intermediate" in botanical type. Both have complex pedigrees involving ancestors from more than one botanical group. The significant estimates of dominance effects obtained for pod length and pod width in cross 1 suggests that dominance may also play an important role in the inheritance of agronomic traits among diverse genotypes that are not as genetically divergent as crosses between intersubspecific hybrids.

The significance of additive effects contributing to pod weight and seed weight in cross 1 suggests that effective selection could be practiced for these traits in early generations. The significant, but somewhat less important, estimate of dominance effects for pod weight can be attributed to the genetic diversity between the two parents of cross 1. The positive value for additive effects suggests that 'NC-V11', the higher parent, is largely responsible for contributing positive alleles for pod weight. The significant estimate of additive effects and the high mean of the F_1 generation for pod weight indicates the potential for selection of superior segregates from among the progeny of cross 1.

The failure to detect significant estimates of any genetic effects for seed number or seed: pod ratio in cross 1 can be explained by a lack of variability among generations for seed number and the importance of environmental effects and relative maturity on seed: pod ratio. Both 'NC-V11' and GP-NC 343 produce a majority of two-seeded pods, and variability for seed number among progeny from crosses between them would not be expected. The variability observed among generations for seed: pod ratio is more likely attributable to differences in maturity and, thus, pod fill at harvest. GP-NC 343, being unadapted to North Carolina, was not able to reach its genetic potential for maturity. Thus, differences in seed: pod ratio among generations in cross 1 are more likely to be of a physiological or environmental nature, and the genetic factors controlling inheritance of this trait cannot be determined from the results obtained in this study.

Cross 2: 'NC-V11' × FESR-11-P11-32

Highly significant estimates of additive gene effects, but no significant dominance effects, detected for yield in cross 2 were not surprising given the relative importance of additive gene effects in controlling yield in peanut. Previous reports of crosses involving diverse lines have indicated the presence of dominance effects also contributing to yield, especially among intersubspecific hybrids (Sandhu and Khehra 1976; Gibori et al. 1978; Mohammed et al. 1978; Layrisse et al. 1980). The two parents in cross 2, while considered genetically diverse, are both "intermediate" botanical types containing a substantial proportion of 'valencia' germplasm in their pedigrees. The relative importance of additive effects governing yield and most agronomic traits measured in cross 2 and the relative importance of dominance effects associated with most traits in cross 1 may be attributable in part to the differences in genetic relatedness of the parents of each cross. The presence of 'valencia' germplasm in the pedigrees of both parents of cross 2 ('NC-V11' and FESR-11-P11-32) and its absence in the pedigree of the male parent of cross 1 (GP-NC 343) is especially noteworthy. It suggests that the failure to detect any main effect of dominance may have been the result of a cancellation of dominance effects due to a balancing of (+) and (–) effects at different loci between the two parents rather than a complete absence of dominance gene action. Both additive and dominance genetic effects were found to contribute to pod length in cross 2.

Pod width, pod weight, seed number, and seed weight were all largely controlled by additive gene effects in cross 2. Failure to detect significant dominance effects may have been due to a balancing of (+) and (–) factors; however, it was more likely attributable to the closer genetic backgrounds of the two parents as compared to the parents of cross 1, in which dominance effects were found to be important in the inheritance of a number of traits. 'Valencia' cultivars typically have three-seeded pods, and the presence of 'valencia' germplasm in their genetic background probably resulted in both parents contributing positive alleles for seed number. The relative importance of additive effects for most traits measured in cross 2 indicates that selection among progeny resulting from crosses between 'NC-V11' and FESR-11-P11-32 for a number of fruit characters would be effective, even in early generations.

Failure to detect significant differences among generation means in the analysis of variance, or significant estimates of gene effects in the generation means analysis for seed : pod ratio in cross 2, is a reflection of the similar levels of maturity and pod fill between the two parents at harvest. No determination as to relative importance of genetic effects governing the inheritance of this trait can be obtained from the generation means analysis.

Productivity over generations

The relationship between productivity and proportion of exotic germplasm present in the population was plotted for yield and fruit characters in both crosses. For most traits in cross 1, the relationship was generally curvilinear, with the F_1 generation giving the highest level of productivity. This general response was consistent with the significant contribution of dominance effects in the trait observed. Only seed weight exhibited a linear relationship between productivity and proportion of exotic germplasm, and for this trait in cross 1 only estimates of additive effects were significant.

Based on the above relationships and the generation means and variances obtained from the weighted analysis of variance, a single backcross generation to the recurrent parent ('NC-V11') appears adequate for obtaining a high mean level of productivity while maintaining adequate variability for most traits measured. Only seed weight and possibly yield appear to benefit from an additional generation of backcrossing to 'NC-V11' to increase productivity to a level comparable to that of the recurrent parent.

In cross 2 the relationship between productivity and proportion of exotic germ plasm was effectively linear for all traits measured, reflecting the relative importance of additive effects in controlling the inheritance of yield and fruit characters. For all traits observed, productivity was greatly enhanced by a second generation of backcrossing to the recurrent parent ('NC-V11'), with no significant loss of variability in the population expected. The advantage of an additional generation of backcrossing in cross 2 as compared to cross 1 can be attributed in part to the greater differences in the means of the two parents of cross 2 for the traits measured than was observed between the parents of cross 1.

Implications for peanut breeding

In peanut, as in any other crop, the effectiveness of selection for any quantitative trait is primarily determined by the nature of the genetic effects controlling its inheritance. Once the relative importance of the contributions from various genetic effects (additive, dominance, epistasis) are estimated for a particular trait in a given cross, the breeding objectives will dictate how the various effects will be exploited in the development of breeding lines or improved cultivars.

When choosing exotic lines for inclusion in a peanut breeding program, a knowledge of the genetic background of the line will be useful in predicting how it will behave in hybrid combinations with particular adapted genotypes. The less divergent the exotic and adapted lines are, the more likely it will be that additive gene effects will play the primary role in the inheritance of quantitative traits (Isleib and Wynne 1983 a). As the diversity between the exotic and adapted lines increases, dominance effects and epistatic variation may have significant roles in the inheritance of quantitative traits. This concept is illustrated by the results of this study. In cross 1, where the two parental lines have relatively diverse genetic backgrounds, dominance gene effects appear to play a significant role in the inheritance of a number of fruit characters. The greater similarity in the genetic backgrounds of the parents of cross 2 – most notably the presence of 'Valencia' germplasm in their ancestry coincides with the predominance of additive gene effects governing the traits studied.

The apparent relationship between genetic diversity and gene action suggests that the more closely related an exotic germplasm line is to the cultivated germplasm base to which it will be introduced, the greater the chance that early generation selection will be effective. The more diverse the exotic germplasm lines are compared with the cultivated germplasm base, the more important later generation selection will be for quantitative traits, due to the greater relative importance of dominance effects and dominance types of epistasis. The extra time required for effective selection progress among progeny from crosses between more diverse lines may be offset by the potential for new gene combinations to come together (Isleib and Wynne 1983b).

Transfer of desirable alleles from exotic to adapted lines using the backcross method

The basic problem associated with utilizing exotic germ plasm is in determining the most efficient method of adding favorable alleles, not currently present, to an adapted population without reducing the frequency of existing favorable alleles in the population or lowering the performance of the population. A number of studies support the idea that at least one backcross to the adapted parent may be useful in incorporating exotic germplasm into adapted populations (Kenworthy and Brim 1979; Lawrence and Frey 1975; Lambert and Leng 1965).

From the results of a simulation study, Dudley (1982) concluded that the level of dominance and the level of diversity between the parents affect the optimum number of backcrosses to use before initiating selection. In general, as level of dominance increases and as the parents become more diverse, the advantages of additional generations of backcrossing prior to initiation of selection increase. In all cases, where one parent contained more favorable alleles than the other parent, at least one generation of backcrossing was advantageous.

Empirical studies have deviated from expectations based on the theoretical and computer simulation studies of Dudley (1982), Reddy and Comstock (1976) and others. Cox and Frey (1984) observed progeny resulting from early backcross generations from crosses with certain wild sorghum [*Sorghum bicolor* (L.) Moench] parents had lower mean yields than expected, based on the proportion of wild germplasm present. Lambert and Leng (1965) found progeny of certain teosinte (*Zea mexicana*) parents that produced higher-than-expected mean yields in early generations of backcrossing to maize (*Z. mays*). Unexpected increases in genetic variance with backcrossing have been reported in sorghum (Cox and Frey 1984), pearl millet [*Pennisetum americanum* (L.) Leeke] (Bramel-Cox et al. 1986), oats (*Avena sativa* L.) (Lawrence and Frey 1976), barley (*Hordeum vulgare* L.) (Rodgers 1982), and soybean [*Glycine max* (L.) Merrill] (Carpenter and Fehr 1986).

The genetic background of the cultivated parent has been shown to have a strong influence on the expression of introgressed genes from wild/weedy relatives. Bramel-Cox et al. (1985) found that the relative proportion of additive and dominance effects between cultivated and wild parents in two pearl millet crosses strongly influenced the grain yield of progeny. Specific interactions between cultivated and wild accessions in sorghum – in the F_1, F_2, and backcross generations – have also been observed (Bramel-Cox and Cox 1989). Such interactions influence decisions regarding which germplasm sources – both wild and cultivated – should be included in a germ plasm enhancement program.

The results from both crosses in the present study indicate some advantage to backcrossing to the recurrent parent ('NC-V11') prior to initiating selection with the population. However, in cross 1, where dominance gene effects were important in controlling most traits measured (pod length, pod width, pod weight), the F_1 outperformed both the recurrent parent and the two backcross generations to it. In spite of the high mean productivity in the F_1 and first backcross generations, it would probably still be advantageous to conduct either a second backcross or a generation of selfing before initiating selection in the population.

For most traits measured in cross 2, there seemed to be an advantage to backcrossing a second time to the recurrent parent ('NC-V11') to increase the population mean to a level compatible with that of the recurrent parent before initiating selection. The results from this study generally support Dudley's theory that increased diversity between the parents (i.e., adapted × exotic hybrid combinations) and level of dominance make it more advantageous to backcross one or more times to the recurrent parent prior to initiating selection in the population.

References

Bramel-Cox PJ, Cox TS (1989) Use of wild germplasm in sorghum improvement. In: Wilkinson D (ed) Proc 43rd Annual

Corn and Sorghum Industry Res Conf. American Seed Trade Assoc, Washington, D.C., pp 13–26

Bramel-Cox PJ, Andrews DJ, Frey KJ (1985) Exotic germplasm for improving grain yield and growth rate in pearl millet. Crop Sci 26: 687–690

Bramel-Cox PJ, Cox TS, Andrews DJ, Frey KJ (1986) Genetic variance within exotic, weedy, and wild populations of pearl millet and crosses with adapted inbreds. Agron Abstr 1985: 49

Carpenter JA, Fehr WR (1986) Genetic variability for desirable agronomic traits in populations containing *Glycine soja* germplasm. Crop Sci 26: 681–686

Cavalli LL (1952) An analysis of linkage in quantitative inheritance. In: Reeve ECR, Waddington CH (eds) Quantitative inheritance. HMSO, London, pp 35–144

Cox TS, Frey KJ (1984) Genetic variation for grain yield and related traits in sorghum introgression populations. Theor Appl Genet 68: 145–153

Dudley JW (1982) Theory for transfer of alleles. Crop Sci 22: 631–637

Fonesca S, Patterson FL (1968) Hybrid vigor in a seven-parent diallel cross in common winter wheat (*Triticum aestivum* L.). Crop Sci 8: 85–88

Gamble EE (1962) Gene effects in corn (*Zea mays* L.). I. Separation and relative importance of gene effects for yield. Can J Planta Sci 42: 339–348

Garet B (1976) Heterosis et apitudes a la combinaison chez l'arachide (*Arachis hypogaea* L.). Oleagineux 31: 435–442

Gibori A, Hillel J, Cahaner A, Ashri A (1978) A 9 × 9 diallel analysis in peanuts (*A. hypogaea* L.): Flowering time, top weight, pod yield per plant and pod weight. Theor Appl Genet 53: 169–179

Green CC, Wynne JC (1986) Diallel and generation means analyses for the components of resistance to *Cercospora arachidicola* in peanut. Theor Appl Genet 73: 118–235

Hallauer AR, Miranda JB (1988) Quantitative genetics in maize breeding. Iowa State University Press, Ames

Hayman BI (1958) The separation of epistatic from additive and dominance variation in generation means. Heredity 12: 371–390

Isleib TG, Wynne JC (1980) Expression of heterosis in test-crosses of exotic peanut (*Arachis hypogaea* L.) genotypes. Proc Am Peanut Res Educ Soc 12: 74 (abstr)

Isleib TG, Wynne JC (1983a) Heterosis in testcrosses of 27 exotic peanut cultivars. Crop Sci 23: 832–841

Isleib TG, Wynne JC (1983b) F_4 bulk testing in testcrosses of 27 exotic peanut cultivars. Crop Sci 23: 841–846

Isleib TG, Wynne JC, Rawlings JO (1978) Estimates of epistasis for diverse peanut cultivars. Peanut Sci 5: 106–108

Kenworthy WJ, Brim CA (1979) Recurrent selection in soybeans. I. Seed yield. Crop Sci 19: 315–318

Lambert RJ, Leng ER (1965) Backcross response of two mature plant traits in certain corn-teosinte hybrids. Crop Sci 5: 239–241

Lawrence PL, Frey KJ (1976) Inheritance of grain yield in oat species crosses (*Avena sativa* L. × *A. sterilis* L.). Egypt J Genet Cytol 5: 400–409

Layrisse AJ, Wynne JC, Isleib TG (1980) Combining ability for yield, protein, and oil of peanut lines from South American centers of diversity. Euphytica 29: 561–570

Lin H (1966) Studies on the genetic behaviour of quantitative characters in the hybrid progenies of virginia and spanish peanut. J Agric Assoc China, NS 54: 17–24

Marani A (1963) Heterosis and combining ability for yield and components of yield in a diallel cross of two species of cotton. Crop Sci 3: 552–555

Marani A (1968) Heterosis and inheritance of quantitative characters in interspecific crosses of cotton. Crop Sci 8: 299–303

Mather K, Jinks JL (1977) Introduction to biometrical genetics. Cornell University Press, Ithaca, N.Y.

Matzinger DF, Wernsman EA (1968) Genetic diversity and heterosis in *Nicotiana* II. Oriental × flue-cured variety crosses. Tob Sci 12: 177–180

Mohammed J, Wynne JC, Rawlings JO (1978) Early generation variability and heritability estimates in crosses of virginia and spanish peanuts. Oleagineux 33: 81–86

Moll RH, Salhuana WS, Robinson HF (1962) Heterosis and genetic diversity in variety crosses of maize. Crop Sci 2: 197–198

Parker RC, Wynne JC, Emery DA (1970) Combining ability estimates in *Arachis hypogaea* L. I. F_1 seedling responses in a controlled environment. Crop Sci 10: 429–432

Phillips TD, Wynne JC, Elkan GH, Schneeweis TJ (1989) Inheritance of symbiotic nitrogen fixation in two peanut crosses. Peanut Sci 16: 66–70

Reddy BVS, Comstock RE (1976) Simulation of the backcross breeding method. I. Effects of heritability and gene number on fixation of desired alleles. Crop Sci 16: 825–830

Rodgers DM (1982) Improvement of cultivated barley (*Hordeum vulgare*) with germplasm introgressed from *A. spontaneum*. PhD thesis, Iowa State University, Ames

Rowe KE, Alexander WL (1980) Computations for estimating the genetic parameters in joint-scaling tests. Crop Sci 20: 109–110

Sandhu BS, Khehra AS (1976) The role of epistasis in the inheritance of yield and its components in groundnut. Crop Improv 3: 9–17

SAS (1985) SAS user's guide: statistics, version 5. SAS, Inc, Cary, N.C.

Sriwatanapongse S, Wilsie CP (1968) Intra- and inter-variety crosses of *Medicago sativa* L. and *Medicago falcata* L. Crop Sci 8: 465–466

Syakudo K, Kawabata S (1963) Studies on peanut breeding with reference to the combinations of some main characters. I. On pod setting percentage in the crossing among varieties and characteristics of F_1 plants. Jpn J Breed 3: 137–142

Van der Veen JH (1959) Tests of non-allelic interaction and linkage for quantitative characters in generations derived from two diploid pure lines. Genetica 30: 201–232

Wynne JC, Coffelt TA (1982) Genetics of *Arachis hypogaea* L. In: Pattee HE, Young CT (eds) Peanut science and technology. Am Peanut Res Educ Soc, Yoakum, Tex., pp 50–94

Wynne JC, Gregory WC (1981) Peanut breeding. Adv Agron 34: 39–72

Wynne JC, Halward TM (1989) Cytogenetics and genetics of *Arachis*. Crit Rev Plant Sci 8: 189–220

Wynne JC, Emery DA, Rice PW (1970) Combining ability estimates in *Arachis hypogaea* L. II. Field performance of F_1 hybrids. Crop Sci 10: 713–715

Wynne JC, Rawlings JO, Emery DA (1975) Combining ability estimates in *Arachis hypogaea* L. II. F_2 generation of intra- and intersubspecific crosses. Peanut Sci 2: 50–54