Combining Ability Estimates in **Arachis Hypogaea** L. III. F_2 Generation of Intra- and Intersubspecific Crosses[1]

J. C. Wynne, J. O. Rawlings, and D. A. Emery[2]

ABSTRACT

A hybridization program was initiated to investigate the breeding potential of crosses among diverse peanut (**Arachis hypogaea** L.) lines. Fifteen crosses in F_2 generation generated by crossing six peanut lines representing Valencia, Virginia, and Spanish botanical varieties in diallel without reciprocals were used to estimate combining ability in drilled and space-planted tests.

Estimates of both general (GCA) and specific (SCA) combining ability were significant for percent extra large kernels, percent sound mature kernels, kernels/kg, pod length, and yield measured in the drilled test. The GCA estimates were also significant for all characters measured in the space-planted test, while estimates of SCA were significant for five of the six characters. Estimates of GCA were of greater magnitude than SCA estimates for all characters except one.

A Spanish line, C_2, had the highest GCA effects for yield and sound mature kernels in both drilled and space-planted tests.

Although most F_2 cross means, especially for the intersubspecific crosses, were less than the midparent value, the presence of transgressive segregants indicated an opportunity for breeding improvement. The depression of F_2 means probably resulted from recombination of genes responsible for adaptation of the parental lines.

Comparison of results from the space-planted and drilled tests indicates that data from space-planted tests can provide useful information on the performance of crosses in early generation.

Additional index words: Peanuts, Groundnuts, General and Specific Combining Ability, Diallel.

The variation of peanuts (*Arachis hypogaea* L.) has been classified into two subspecies, each of which is subdivided into two botanical varieties (7). Crosses between these subspecies have not been fully utilized in the development of cultivars. Hammons (5) concluded that commercial cultivars with new characters can be developed through intersubspecific (crosses between subspecies) hybridization. Over 1,000 accessions collected from the five major centers of diversity for peanuts in South America are available for improving cultivated types (3).

An intersubspecific hybridization program was initiated to investigate the breeding potential of crosses among these diverse types. Estimates of general and specific combining ability for intra- and intersubspecific crosses in the F_2 generation for spaced and drilled experiments will be presented in this paper. Estimates of combining ability for F_1 hybrids grown in a controlled environment and in a space-planted field test were previously reported (10,13). General combining ability (GCA) estimates were found to be of larger magnitude than estimates of specific combining ability (SCA) for 14 of 17 seedling characters measured in a controlled environment (10). For F_1 hybrids grown in space-planted field plots,

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[2] Assistant Professor of Crop Science; Professor of Statistics; and Professor of Crop Science, North Carolina State University, Raleigh, N. C.; respectively.

estimates of SCA were greater than GCA for yield and most fruit characters when the lines were assumed to be a random sample from a larger population (13).

Materials and Methods

Six lines representing three botanical varieties of the cultivated peanut were crossed in diallel without reciprocals (13). Two lines designated A_1 and A_2, collected in Peru, were classified as Valencia (ssp. **fastigiata** var. **fastigiata**). Lines B_1 and B_2 from Bolivia were Virginia types (ssp. **hypogaea** var. **hypogaea**) and C_1 from Argentina and C_2 from Paraguay were Spanish types (ssp. **fastigiata** var. **vulgaris**).

Equal numbers of F_2 seeds from 30 F_1 plants from each of the 15 crosses were bulked and used to plant the F_2 tests. The six parents were included in both experiments. Two types of F_2 tests, drilled and space-planted, were conducted. A plot for each entry in the drilled test consisted of two rows spaced 0.91 m apart with 50 plants each 25.4 cm apart. They were planted at the Peanut Belt Research Station at Lewiston on May 11 and the Upper Coastal Plain Research Station, Rocky Mount, N. C. on May 13, 1970, Each entry was replicated four times at each location. Plots were dug and harvested mechanically on September 16 at Rocky Mount and September 17 at Lewiston.

In the space-planted test, planted at Lewiston on May 12, each plot consisted of a single row of 10 plants spaced 50.8 cm apart. Individual plants were dug and harvested by hand on September 17. Data were taken on all plants of a plot and plot averages were used in all analyses.

Characters measured for the drilled tests were (a) percent extra large kernels, XLK (kernels which ride a 0.85 x 2.54-cm screen), (b) percent sound mature kernels, SMK (kernels which ride a 0.60 x 2.54-cm screen), (c) number of kernels per kg, (d) length of 20 randomly drawn pods in cm, and (e) yield (kg/ha). Days to first flower, number of pods per plant, length of 20 randomly drawn pods per plant (cm), weight of XLK per plant (g), weight of SMK per plant (g), and yield of fruit per plant in g were measured in the spaced test.

Combining ability analyses were performed using Griffing's (4) Method IV, Model I. In Model I the experimental material is the population about which inferences are to be made. Location effects were also assumed to be fixed.

Results and Discussion

The mean squares from the analyses of variance combined over both locations for the five characters measured in the drilled tests are given in Table 1. Estimates of GCA and SCA were significant for all five characters. Estimates of GCA were of greater magnitude than SCA for all characters except for percent sound mature kernels.

Mean squares for GCA for the space-planted test at Lewiston were significant for all six characters and SCA was significant for all characters except for the weight of SMK (Table 2). Estimates of GCA were of greater magnitude than SCA for all six characters. Most studies with self-pollinated crops where fixed models have been assumed have indicated that GCA is greater than SCA (6). However, significant estimates of SCA should probably have also been anticipated for this group of crosses. Parents B_1 and B_2 are Virginia types, while the other parents are Valencia and Spanish types. The Virginia plant type is dominant to the fastigiate plant type in the F_1 generation and very few Spanish or Valencia type recombinants are recovered in the F_2 generation of these crosses. Dominance contributes to the SCA estimates.

GCA effects for the six parents for the drilled and space-planted tests are shown in Tables 3 and

Table 1. Mean squares from analyses of variance for five characters measured on parents and their F_2 generation planted in drilled plots at two locations.

Source	df	XLK (%)	SMK (%)	Kernels/kg	Pod length (cm)	Yield (100 kg/ha)
Location	1	1840.1**	0.2	53374**	2.6	222.4*
Reps in locations	6	4.2	13.1	197	16.1	22.6
Entry	20	701.3**	96.7**	6793**	177.5**	86.5**
Among parents	5	1638.9**	42.3**	10882**	374.7**	73.1**
Among crosses	14	408.5**	75.7**	5623**	116.5**	67.6**
GCA	5	746.4**	72.8**	13853**	170.9**	110.5**
SCA	9	220.8**	77.3**	1051**	86.2**	43.8**
Parents _vs_ crosses	1	113.2**	662.5**	2728**	46.7*	418.4**
Entry x Location	20	49.2**	6.2*	303	13.2	28.4**
Parents x Location	5	94.1**	10.4*	345	14.9	9.4
Crosses x Location	14	36.6**	4.3	303	13.0	33.9**
GCA x Location	5	70.0**	8.4*	307	24.5*	55.6*
SCA x Location	9	18.1	2.0	300	6.6	21.8*
Parents _vs_ crosses x Location	1	1.5	13.2	86	7.5	47.3*
Error	120	10.5	3.6	225	10.4	10.7

*, ** Significant at .05 and .01 levels of probability, respectively.

Table 2. Mean squares from the analyses of variance of six characters measured on parents and their F_2 generation grown in spaced test.

Source	df	Days to first flower	No. pods	Pod length (cm)	Weight (g)		
					XLK	SMK	Fruit
Reps	3	8.57**	73.61	6.97	124.96	458.00	386.39
Entries	20	15.12**	1934.74**	102.80**	934.34**	897.75**	1577.28**
Among parents	5	23.82**	2355.49**	182.53**	1922.24**	921.92**	1735.25**
Among crosses	14	12.82**	1914.38**	81.55**	617.42**	830.15**	1567.55**
GCA	5	26.13**	4337.51**	133.45**	998.14**	1332.86**	2566.35**
SCA	9	5.43**	568.19*	52.71**	405.92**	550.86	1012.67**
Parents vs crosses	1	3.80	116.10	1.64	431.72*	1723.44*	923.58
Error	60	1.81	220.65	11.00	84.46	285.60	355.87

*, ** Significant at .05 and .01 levels of probability, respectively.

Table 3. Estimates of general combining ability effects for characters measured in drilled tests.

Parent	XLK (%)	SMK (%)	Kernels/kg	Pod length (cm)	Yield (kg/ha)
A_1	-3.37	-0.42	28.52	2.08	-32.36
A_2	-5.12	-2.04	15.71	3.45	-238.86
B_1	6.49	-0.54	-22.25	-2.04	-208.36
B_2	5.74	-0.42	-18.40	-2.79	103.63
C_1	-1.12	.96	-8.42	1.83	129.64
C_2	-2.62	2.45	4.84	-2.54	246.32
S.E. $(\hat{g}_i-\hat{g}_j)$	2.79	1.34	10.61	2.28	231.45

Table 4. Estimates of general combining ability effects for characters measured in space-planted tests.

Parent	Days to first flower	No. pods	Pod length (cm)	Weight (g)		
				XLK	SMK	Fruit
A_1	-1.05	-9.98	2.90	-5.87	-6.26	-5.01
A_2	-0.70	-13.97	4.44	-6.15	-13.47	-17.24
B_1	0.57	-5.68	-1.75	13.54	4.25	1.76
B_2	2.65	-3.89	-2.30	6.53	-1.36	0.36
C_1	-0.50	1.26	0.72	-4.28	1.78	-1.26
C_2	-0.97	32.26	-4.02	-3.78	15.06	21.40
S.E. $(\hat{g}_i-\hat{g}_j)$	0.77	10.50	2.35	6.50	6.54	12.96

4, respectively. The estimates of GCA for yield and percent SMK were highest for the Spanish type, C_2, in the drilled tests. The estimates of GCA for percent XLK were highest for the Virginia parents, B_1 and B_2, while the Valencia parents, A_1 and A_2, had the highest GCA for number of kernels per kg and pod length. Somewhat similar results for GCA were obtained in the space-planted test (Table 4). The Spanish line, C_2, again had highest GCA estimates for yield, weight of SMK, and number of pods per plant. GCA estimates for XLK and days to first flower were highest for the Virginia lines. GCA estimates for pod length were highest for the Valencia lines. The Valencia lines were lowest in GCA for yield in both tests. Thus estimates of GCA for the six parents were similar in both spaced and drilled tests.

Estimates of SCA constants for the crosses involving the six parents for the characters measured in the drilled test are large for several crosses for each of the traits (Table 5). For yield, SCA constants range from -281.85 for A_1 x B_1 to 401.90 for B_1 x B_2. The two Virginia type lines had negative or small positive SCA constants for yield when they were crossed to lines from the ssp. *fastigiata,* A or C's, while the SCA constant was positive and large when they were crossed to each other (401.90). However, lines within a botanical type also differed in the magnitude of SCA constants. A_1 had large (positive and negative) SCA constants for yield when crossed with all other lines, while SCA constants for A_2 were small except when crossed with A_1. Estimates of SCA constants for the crosses measured in the space-planted test were similar to the estimates obtained in the drilled test. These high SCA constants indicate that crosses do deviate from expectations based upon GCA. Because of the magnitudes of the SCA constants, early generation selection for fruit yield in crosses between the subspecies of peanuts may be impossible.

Few of the crosses significantly exceed the midparent value and most of the crosses have means that are substantially below their midparent value in the drilled experiment. For yield, only A_1 x C_2 and B_1 x B_2 of the 15 crosses equal the midparent value. Both of these are intra-subspecific crosses. Similar results were obtained for the space-planted experiment. Only four of the crosses were equal to or higher than the midparent value for yield. For the drilled experiment, the average value for the parents was significantly higher than the crosses for each of the five traits (Table 1).

The poor performance of the F_2 generation of the intersubspecific crosses when compared with their parents probably occurred because of segre-

Table 5. Estimates of specific combining ability constants ($\hat{s}_{ij}$) for crosses grown in drilled tests.

Parent	Character	Parent A$_2$	B$_1$	B$_2$	C$_1$	C$_2$
A$_1$	XLK, %	0.40	-5.23	-4.98	3.90	5.90
	SMK, %	-0.28	-1.78	-2.40	1.23	3.23
	Kernels/kg	10.10	10.35	8.60	-8.40	20.65
	Pod length, cm	-2.88	0.13	3.88	-2.75	1.63
	Yield, kg/ha	114.65	-281.85	-227.35	124.65	269.90
A$_2$	XLK, %		-2.98	-0.23	2.15	0.65
	SMK, %		0.35	1.23	-0.15	-1.15
	Kernels/kg		2.85	-0.90	-1.90	-10.15
	Pod length, cm		2.75	0.00	1.38	1.25
	Yield, kg/ha		-22.10	30.40	-86.60	-36.35
B$_1$	XLK, %			9.15	0.53	-1.48
	SMK, %			5.23	-2.15	-1.65
	Kernels/kg			-6.65	-14.65	8.10
	Pod length, cm			-2.00	0.38	-1.25
	Yield, kg/ha			401.90	-31.10	-66.85
B$_2$	XLK, %				-2.73	-1.23
	SMK, %				-1.28	-2.78
	Kernels/kg				0.60	-1.65
	Pod length, cm				-0.88	-1.00
	Yield, kg/ha				-22.60	-182.35
C$_1$	XLK, %					-3.85
	SMK, %					2.35
	Kernels/kg					24.35
	Pod length, cm					1.88
	Yield, kg/ha					15.65

	S.E. ($\hat{s}_{ij}-\hat{s}_{ik}$)	S.E. ($\hat{s}_{ij}-\hat{s}_{kl}$)
XLK, %	3.97	3.24
SMK, %	2.32	1.90
Kernels/kg	18.37	15.00
Pod length, cm	3.95	3.22
Yield, kg/ha	400.88	327.31

gation and recombination of the genetic factors responsible for adaption of the parental lines to different ecological conditions. Stebbins (11) states that hybridization between subspecies leads to the production of many ill-adapted genotypes and thus to a reduction in performance and yield. The offspring in the F$_2$ generation were observed to be extremely variable due to Mendelian segregation of genetic factors responsible for the differences between the subspecies. Many of the individual F$_2$ plants were variants which represented recombinational types which would not have been predicted from a study of the parents. However, several F$_2$ plants within each cross were similar to the parental types and offer material for selection and utilization. Claussen and Hiesey (2), in crosses between subspecies of *Potentilla glandulosa,* found that 15 of 505 F$_2$ individuals were highly successful at all three locations tested. These few superior individuals were found although most of the F$_2$ individuals were poorly adapted. Perhaps, with extensive testing of F$_2$ segregates from an intersubspecific cross in peanuts, superior performing cultivars can be selected.

Stebbins (12) states that a small proportion of transgressive segregants might be expected in the progeny of hybrids between subspecies. An examination of individual F$_2$ plant data for plants from crosses between the subspecies of the peanut lines showed transgressive segregation. Selection of transgressive segregates would allow peanut breeders to select cultivars with traits superior to the best parent.

A spaced planting of the F$_2$ was included to compare performance of the crosses in spaced and drilled tests. Because of the limited quantity of seed, estimates of heterosis and combining ability for the F$_1$ generation were measured in an earlier experiment using spaced plants (13). Whether estimates of combining ability obtained in the spaced experiment would be comparable with estimates of drilled experiments was not known. Therefore, both a spaced and drilled F$_2$ generation test were planted at the Lewiston location. Estimates of combining ability for pod length and yield for the two experiments are almost identical (Tables 1 and 2). The correlation for the 21 entry means for yield between the two experiments is also highly significant ($r = 0.62$). The coefficients of variation for pod length and yield were 9.5 and 4.8 for the drilled test and 14.8 and 5.3 for the space-planted test. From a comparison of these tests, it appears that spaced experiments can give useful information on the performance of crosses in early generation. Spaced tests can be utilized whenever seed supplies are limited.

The estimates of heterosis and combining ability for the F$_1$ generation were measured at only one location (13). Thus estimates of combining ability were biased since they did not account for genotype x environment interactions. The F$_2$ drilled tests provided an estimate of the genotype x environment interaction. Percent extra large kernels, number of kernels/kg, and yield were significantly different between the two locations (Table 1). The crosses x location interaction was significant for percent XLK and yield. The GCA x location interaction was significant for XLK, SMK, fruit length, and yield; while the SCA x location interaction was significant for yield. Thus, as expected, estimates of combining ability for characters of the F$_1$ generation were obviously biased in results from only one location.

Although crosses within a subspecies or even within a botanical variety may yield more than crosses between subspecies or botanical varieties, intersubspecific hybridization should still be considered as desirable. As Hammons (5) states, peanut varieties with characters not presently found in commercial varieties can be obtained through intersubspecific hybridization. Although new recombinants may be selected, it should also be realized that several deleterious effects will be obtained after hybridization between the subspecies. It would also appear that sporophytic hybrid sterility similar to that reported for hybrids between rice subspecies (1,8,9) is present in peanuts. Partially sterile and sterile segregates were observed in the F$_2$ from apparently fertile F$_1$ plants. Although this may hinder progress in selection for superior genotypes, the possibility of selecting transgressive segregates makes intersubspecific hybridization a useful breeding procedure for peanuts.

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