Combining Ability for Large Pod and Seed Traits in Peanut[1]

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ABSTRACT

Recently, the peanut (*Arachis hypogaea* L.) industry has expressed a greater need for higher percentages of fancy pods and extra large kernels (ELK), especially for use in large-seeded in-shell products. Genetic control of these traits has been reported to range in complexity from simple inheritance to the inclusion of multiple modifier genes. This study was conducted to determine the general combining ability (GCA) effects of 50 peanut genotypes on pod and seed size. Each genotype was used five times as a female parent and five times as a male parent in a partial diallel crossing program. F_1 hybrids were grown and their pods were harvested for measurements of pod and seed size. The F_2 generation was planted the following year and similar measurements were recorded using the single pod descent procedure. Individual F_2 plants were harvested and pod and seed characteristics measured for segregation information within four crosses. General combining ability effects were not well correlated between generations (r=0.53-0.56) or with the same traits measured on pure-line parents (r=0.32-0.42). PI 298845, PI 314897, PI 325079, Jenkins Jumbo, and Fla 393-8-1-1-1-1-1-2 had consistently large positive GCA effects on pod and seed weight. F_2 segregation patterns indicated that some crosses exhibit predominantly additive gene action while one cross (PI 270818 / PI 269111) showed dominance toward smaller pods. Transgressive segregation occurred for pod and seed size traits in four crosses. Substantial genetic variability for pod and seed size remains in the peanut germplasm collection.

Key Words: *Arachis hypogaea* L., groundnut, general combining ability, jumbo pods, fancy pods, extra large kernels

Producers and processors of virginia peanuts (*Arachis hypogaea* L.) have expressed demand for cultivars with larger pods and seeds than cultivars currently available. Producers whose farmer's stock contains at least 40% fancy pods (FP) measured on a percentage basis at the buying point are paid a premium for extra large kernels (ELK). At present the maximum ELK in peanuts cultivated in the Virginia-Carolina production area is approximately 60% of the raw unshelled sample. It would benefit the peanut industry to develop genotypes that increase the percentage ELK while maintaining or surpassing yield and quality of the present cultivars. Shellers commonly screen farmer's stock peanuts to separate jumbo and fancy size pods for sale as unshelled products.

Reports pertaining to the genetics of peanut pod and seed size are few and conflicting. Large pod and seed size have been reported to be dominant to small pod and seed (1,2,5,7,8). Monogenic inheritance was reported for both pod and seed size by Balaiah *et al.* (2) who also observed transgressive segregation for seed size and suggested possible modifier genes. Martin (8) indicated that five gene pairs control seed size and Badami (1) suggested that three genes control pod size. Dwivedi *et al.* (3) reported that pod and seed traits exhibited largely additive genetic variance and that maternal effects were also often significant. Other

[1]Research supported in part by the North Carolina Agricultural Research Service and by the Peanut CRSP, USAID grant number DAN-4048-G-SS-2065-00. Recommendations do not represent an official position or policy of NCARS or USAID.

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studies have reported primarily additive genetic variance for pod and seed traits (4,7,9,11). Recent crosses between the large-seeded cultivars NC 7 and NC 9 have produced selections with greater 100-seed weights and more ELK than either parent (unpublished data).

An excellent source of genetic variability in peanut exists in the germplasm collection maintained at the USDA's Southern Regional Plant Introduction Station at Griffin, Georgia (12). Information is published in the collection catalog regarding the pod and seed size of the plant introductions. This information was used to selectively obtain the largest peanut genotypes available for the present genetic study. The objectives of this study were: a) to determine the general combining ability effects on pod and seed size of 50 peanut genotypes and b) to determine the amount of phenotypic variability among plants within four selected crosses in the F_2 generation.

Materials and Methods

Twenty-eight parents were selected from the USDA's peanut germplasm collection based on their recorded 100-seed weights. Seeds of parents not extant in the North Carolina State University germplasm collection were obtained from the Southern Regional Plant Introduction Station and from Dr. T.A. Coffelt, USDA-ARS, Tidewater Agricultural Experiment Station, Suffolk, Va. Two small-seeded spanish (*A. hypogaea* ssp. *fastigiata* Waldron var. *vulgaris* Harz) and 20 medium to large-seeded virginia (*A. hypogaea* ssp. *hypogaea* var. *hypogaea*) genotypes were also selected (Table 1). Ten of the medium- or large-seeded parents have been used as cultivars in the U.S. at one time or another. Jenkins Jumbo was used as a source of large seed size by the peanut breeding program at the University of Florida (6). It is a parent of F393-8-1-1-1-1-1-2 and is pervasive in the ancestry of runner and large-seeded virginia cultivars including Florigiant, NC 7, NC 9, NC 8C, NC 10C, NC-V 11, and VA 81B. NC-Fla 14 and NC 17 are sister lines of Fla 393-8-1-1-1-1-1-2. The 50 parents were crossed in a partial diallel mating design that included each parent five times as a female and five times as a male. Two to fifteen F_1 hybrid seeds were produced and evaluated for 202 crosses of the 250 attempted.

Table. Peanut genotypes used in the large pod and seed genetics crossing program.

No.	Parent	Pod Size	Identity	Origin	Crossed as a Female to:
1	PI 221068	Large	Nambyquarae	Brazil	10 20[b] 30 40 50
2	PI 259861	Large	Chalimbana	Nyasaland	1 11 21 31 41
3	PI 268882	Large	Ahmer Mogy	Rhodesia	2 12 22 32 42
4	PI 269080	Large	Smooth Jumbo (AM 1)	Rhodesia	3 13[b] 23 33 43
5	PI 269081	Large	Smooth Jumbo (AM 4)	Rhodesia	4 14 24 34 44
6	PI 269723	Large	Virginia Red	Israel	5 15 25 35 45
7	PI 270818	Large	58-18 Flat Jumbo	Rhodesia	6 16 26 36 46
8	PI 279953	Large	Macrocarpa	Brazil	7[b] 17[b] 27 37 47
9	PI 282706	Large	Giant Sized	Nigeria	8[b] 18[b] 28 38[b] 48
10	PI 288211	Large	A.N.-2	India	9 19 29 39 49
11	PI 289620	Large	Virginia Large Seeded	Israel	1 2 3 4 5
12	PI 290686	Large	Rikkei No. 8	Japan	6[b] 7 8 9 10
13	PI 291985	Large	Virginia Improved IV	Israel	11 12 14 15[b] 16
14	PI 296559	Large	Sel.(Florigiant / Florispan)	Israel	17 18 19 20 21
15	PI 298845	Large	Virginia Giant	S. Africa	22 23[b] 24[b] 25 26
16	PI 314897	Large	Galadi	Nigeria	27[b] 28 29 30[b] 31
17	PI 315616	Large	V 4 (Virginia Bunch Imp.)	Israel	32 33 34 35 36
18	PI 315620	Large	Sel.(PI 315616 / PI 315606)	Israel	37 38 39 40 41
19	PI 315622	Large	Sel.(PI 315616 / PI 315606)	Israel	42[b] 43 44[b] 45[b] 46
20	PI 315626	Large	Sel.(PI 315616 / NC2)	Israel	42 47 48 49 50[b]
21	PI 315629	Large	Sel.(PI 315616 / NC2)	Israel	1 3 5 7 9
22	PI 315630	Large	Sel.(PI 315616 / PI 315605)	Israel	11 13 15 17 19
23	PI 315631	Large	Sel.(PI 315616 / PI 315605)	Israel	21 24 26 28 30
24	PI 318740	Large	E63/84/65/63	S. Africa	32 34 36 38 40
25	PI 325079	Large	A 62	Nigeria	42 44 46 48 50
26	PI 343365	Large	Sel.(PI 315616 / H.G.I.)	Israel	2 4 6 8 10
27[a]	PI 372572	Large	Shulamith	Israel	12 14 16 18 20
28	PI 442604	Large	RG 226	S. Africa	22[b] 24[b] 26 29 31
29	Japan Jumbo	Med. to large		Japan	33[b] 35[b] 37 39 41
30	Jenkins Jumbo	Med. to large		U.S.A.	1 43 45 47 49[b]
31[a]	NC 17	Med. to large	Florispan / Jen. Jumbo	U.S.A.	1 4[b] 7[b] 10 13
32[a]	NC-Fla 14	Med. to large	Florispan / Jen. Jumbo	U.S.A.	16 19 22 25 28
33	4144	Med. to large	Jumbo 101 / Chinese	U.S.A.	31 35[b] 38[b] 41 44
34[a]	GK 3	Med. to large	F416 / F392	U.S.A.	2[b] 6[b] 10 47 50[b]
35	PI 269076	Med. to large	Chalimbana	Rhodesia	3[b] 7[b] 11[b] 15[b] 19[b]
36	Egyptian Giant	Med. to large	RG 370	S. Africa	23 27 31 35 40
37	PI 269111	Med. to large	Jumbo 37	Rhodesia	2[b] 6 13 44 48[b]
38	PI 152113	Med. to large	Jumbo Runner	Brazil	3 8 12 17 21
39	Rhodesia Giant	Med. to large	RG 220	S. Africa	4[b] 8[b] 13 18 22
40	South Africa Jumbo	Med. to large	RG 208	S. Africa	5 9 14 18[b] 23
41	Fla 393-8-1-1-1-1-1-2	Med. to large	Jenkins Jumbo / F334A	U.S.A.	9 11[b] 15 20 24
42	GP-NC 343	Med. to large	F_7 #10 (45073)	U.S.A.	34 38 41 46 49
43[a]	NC 9	Med. to large	NC 2 / Florigiant	U.S.A.	5 12 16 20 25
44[a]	NC 6	Med. to large	GP-NC 343 / Va 61R	U.S.A.	14 17 23 33 39[b]
45[a]	NC 7	Med. to large	NC 5 / Fla 393	U.S.A.	21[b] 25[b] 28 36 40[b]
46[a]	Holland Jumbo	Med. to large		U.S.A.	26 27[b] 30 34 50[b]
47[a]	NC-V 11	Med. to large	NC 5 / Florigiant	U.S.A.	27 32[b] 36 37 39[b]
48[a]	NC 10C	Med. to large	NC 8C / Florigiant	U.S.A.	29 30 33 37 49
49	Chico	Spanish		U.S.A.	32 43 45 47 48
50[a]	Argentine	Spanish		U.S.A.	29 42 43[b] 45 46

[a] Released peanut cultivars.

[b] No F_1 seeds produced, cross not tested.

During the summer of 1988 the parents and F_1 generation were grown in an unreplicated nursery at the Peanut Belt Research Station at Lewiston, N.C., on a Norfolk sandy loam soil (Typic Paleudult, fine-loamy, siliceous, thermic). Plants were spaced 51 cm apart within single 10-plant rows spaced 91 cm apart. Plots were bulk harvested 140 days after planting. Pods were dried under forced air at 11 C above ambient air temperature. Data were recorded on 20-pod length (cm), 20-pod weight (g) and 100-seed weight (g) for each entry.

In 1989, the parents and F_2 generation of each entry were planted in a randomized complete block design with two replications at the Upper Coastal Plain Research Station at Rocky Mount, N.C., on Aycock very fine sandy loam soil (Typic Paleudult, fine-silty, siliceous, thermic). Each plot consisted of two rows with the same plant and row spacing as in 1988. A single mature pod was harvested at random from each plant within plots. Pods were bulked within plots. Pod and seed data were recorded using the same procedure as in 1988.

General combining ability (GCA) effects for pod length, pod weight, and seed weight were calculated for the parents in both the F_1 and F_2 generations. Cross means were subjected to multiple regression analysis (10) using a design matrix with values of 1, 0, and -1 to indicate which GCA effects contributed to each cross. The usual assumption regarding GCA effects, viz. that their sum was zero, was applied. In the F_1, the variance residual after fitting of GCA effects was used as an error term in tests of significance. Correlations were calculated among GCA effects of pod and seed traits over generations.

Four crosses with pod and seed appearance generally approximating the virginia type in the F_2 GCA test were selected to measure F_2 variation. These were PI 269723 / PI 298845, Egyptian Giant / PI 315630, Jenkins Jumbo / NC-V 11, and PI 270818 / PI 269111. Plants of selected crosses were harvested individually, dried, and pod and seed characteristics measured using all pods and seeds harvested from each plant. Pod length and seed weight distributions were graphed to observe the phenotypic variation among F_2 plants within each cross.

Results and Discussion

Significant genetic variability for pod and seed size characteristics was found among the parental lines used for this study. General combining ability was highly significant ($P<.001$) for all traits in both the F_1 and F_2 generations. The GCA effects of the two small-seeded spanish genotypes (Chico and Argentine) were negative and highly significant. Crosses involving these two genotypes were subsequently deleted from further combining ability analyses because they caused a general downward bias of the GCA effects of large-seeded parents with which they were crossed. A number of the plant introductions used in this study produced large-seeded hybrid progeny. Lines among the highest ten for GCA effects on more than one trait or generation included PI 221068, PI 282706, PI 289620, PI 290686, PI 298845, PI 314897, PI 315631, PI 318740, PI 325079, Japan Jumbo, Jenkins Jumbo, NC-Fla 14, Fla 393-8-1-1-1-1-1-2, and NC 7. None of the plant introductions have figured in the pedigrees of large-seeded cultivars released in the U.S. Some of the introductions such as PI 221068 produced F_1 and F_2 progeny with large pods but seed were shriveled and immature. Other genotypes reached full maturity at harvest. PI 221068 had the highest GCA effects for pod length but was not among the highest parents for seed weight (Table 2), perhaps because of its late maturity. The parents with the most consistent positive GCA effects over traits and years were PI 298845, PI 314897, Jenkins Jumbo, and Fla 393-8-1-1-1-1-1-2. Genotypes such as PI 298845, PI 314897 and PI 325078 may be useful for increasing seed size in domestic breeding programs. However, recombination of genotypes such as Jenkins Jumbo, NC 7, and Fla 393-8-1-1-1-1-1-2 may be more useful because they are already adapted to the United States and have seed quality characteristics that match industrial needs.

Rank correlations for F_1 and F_2 GCA effects ranged from 0.53 to 0.56 for pod length, pod weight, and seed weight. The discrepancy between years may be due to either or both of two sources: inbreeding and genotype-by-environment interaction. Generally, correlations of GCA in the F_1 and F_2 with self effects were low (0.32 - 0.42). The low correlations of self effects with GCA effects indicate that parental performance cannot be predicted from the homozygous phenotypes. This result indicates that nonadditive genetic effects are at play in the inheritance of pod and seed

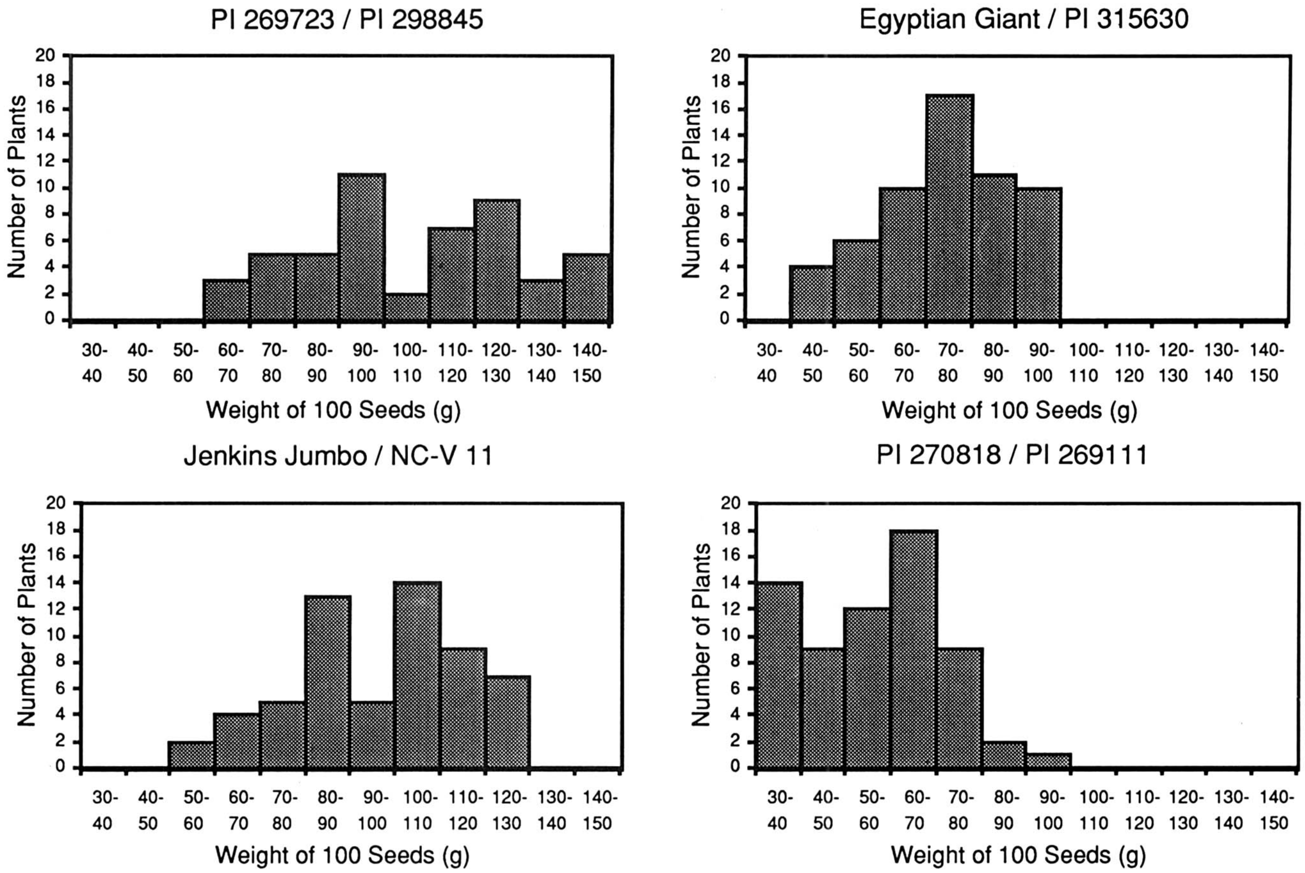

Fig. 1. Distribution of pod length (cm 20 pods^{-1}) in the F_2 generation of four peanut crosses.

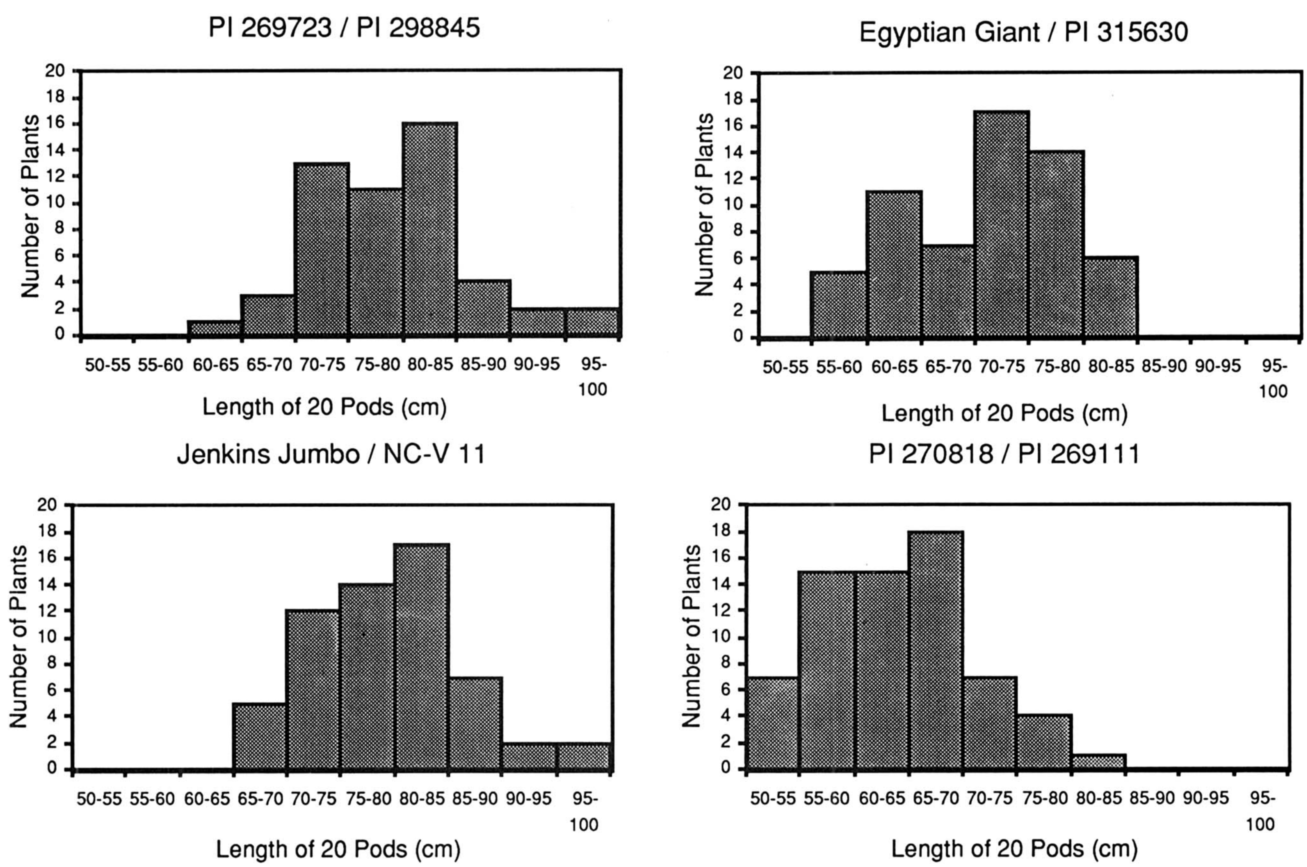

Fig. 2. Distribution of seed size (g 100 seeds^{-1}) in the F_2 generation of four peanut crosses.

size for this group of parents taken as a whole. Rank correlations for GCA of different pod and seed traits within generations were moderate to high (Table 3).

Segregation patterns for pod length and seed size in four selected crosses were generally symmetric, indicating additive gene action (Fig. 1 and 2). Dominance toward the smaller parent was indicated by the skewed distribution of pod length in the crosses Jenkins Jumbo / NC-V 11 and PI 270818 / PI 269111. Transgressive segregation occurred in all four crosses for both pod length and seed weight. A large percentage of the F_2 progeny of crosses PI 269723 / PI 298845 and Jenkins Jumbo / NC-V 11 had larger seed than either parent. Intergenomic interaction in the cross PI 270818 / PI 269111 produced many F_2 plants with smaller seeds and shorter pods than either parent.

Table 2. General combining ability and self effects for pod and seed size traits of 48 large-seeded peanut genotypes (F_1 in 1988 and F_2 in 1989).

Parent	Length of 20 Pods F_1	F_2	Self[a]	Weight of 20 Pods F_1	F_2	Self[a]	Weight of 100 Seeds F_1	F_2	Self[a]
	cm			g			g		
PI 221068	13.8 (1)[b]	8.4 (1)	12.4 (1)	0.1	-1.6	-1.4	9.3 (7)	-3.2	-1.4
PI 259861	-6.3	-4.9	-3.1	-7.9	-4.9	-7.9	-7.5	-8.0	-13.8
PI 268882	-1.0	-3.2	-3.1	1.8	-6.0	2.2	-1.1	-7.9	4.0
PI 269080	-1.2	-0.5	1.4	-3.1	-1.7	2.9	2.5	-4.2	-0.4
PI 269081	2.1	1.7	0.9	1.8	1.1	2.8	-1.8	1.3	1.2
PI 269723	0.7	-3.2	-6.1	2.0	-2.4	-9.3	3.0	-2.3	-4.2
PI 270818	-3.3	-3.1	2.9	0.2	-2.1	9.2 (9)	-9.3	-9.2	5.6
PI 279953	-3.5	-2.3	-2.1	-3.7	-9.3	-0.2	-6.9	-6.6	-5.8
PI 282706	1.0	0.4	4.4	5.2 (9)	3.4 (10)	15.4 (5)	7.3 (9)	3.0	22.2 (2)
PI 288211	2.5 (8)	-0.8	7.9 (8)	-5.9	-12.1	-3.3	-1.9	-23.3	-14.4
PI 289620	9.3 (2)	1.9	10.4 (2)	14.2 (2)	6.5 (8)	26.3 (1)	15.5 (3)	2.4	15.8 (4)
PI 290686	2.2 (10)	3.0 (10)	8.4 (5)	-3.5	0.5	9.5 (8)	0.4	1.3	15.0 (7)
PI 291985	0.4	0.2	8.4 (5)	-2.4	-0.7	3.4	4.1	3.7	10.6
PI 296559	-1.4	-0.4	-6.6	-0.1	0.8	-11.8	0.9	4.8	-10.6
PI 298845	7.6 (3)	3.2 (8)	4.9	14.5 (1)	9.7 (4)	24.2 (2)	21.3 (1)	9.8 (5)	9.0
PI 314897	3.5 (7)	3.2 (8)	-1.1	10.7 (5)	12.9 (1)	13.2 (6)	8.4 (8)	10.5 (4)	26.8 (1)
PI 315616	1.0	0.7	4.4	1.0	-2.4	0.7	-1.2	-1.3	11.2 (9)
PI 315620	1.8	-3.4	3.4	1.4	-5.8	0.6	5.0	-8.4	4.4
PI 315622	-1.1	-0.2	-0.6	-2.0	-0.7	-4.3	-4.0	2.1	4.0
PI 315626	-1.2	0.2	-0.6	-2.4	-3.0	-5.8	2.4	-0.9	-15.6
PI 315629	-1.8	3.9 (4)	5.4 (10)	-5.8	0.8	3.2	-3.2	1.5	7.6
PI 315630	-0.6	-2.0	-8.6	0.4	1.0	-11.7	1.1	1.6	-10.0
PI 315631	-0.1	-5.2	-6.1	5.4 (8)	-3.3	0.2	10.0 (6)	0.8	10.6
PI 318740	2.3 (9)	1.9	3.9	3.7 (10)	1.9	6.1 (10)	5.5	9.6 (6)	10.8 (10)
PI 325079	1.8	-1.2	-9.1	8.6 (7)	8.7 (6)	-5.0	7.0 (10)	12.5 (3)	-7.2
PI 343365	-3.0	-0.8	-2.1	-1.0	-0.4	0.8	-1.1	2.7	5.0
PI 372572	-2.4	-3.7	-1.1	-2.9	-7.7	3.5	-4.3	-8.0	12.4 (8)
PI 442604	-5.5	0.2	-10.6	-6.0	-1.1	-18.3	-9.5	-5.9	-30.0
Japan Jumbo	5.5 (5)	4.2 (3)	5.9 (9)	12.1 (4)	8.8 (5)	10.9 (7)	17.9 (2)	2.9	15.4 (6)
Jenkins Jumbo	6.9 (4)	4.9 (2)	9.4 (3)	13.8 (3)	10.5 (3)	17.4 (3)	13.3 (5)	13.3 (2)	10.0
NC 17	-1.8	-0.6	-6.1	-0.4	2.2	-9.9	-4.5	5.7	-13.2
NC-Fla 14	1.3	3.8 (5)	-2.6	2.7	7.5 (7)	2.6	1.2	7.2 (9)	-1.6
4144	0.2	0.0	9.4 (3)	-2.0	-1.7	16.4 (4)	-5.8	-2.0	15.6 (5)
GK 3	-0.5	-1.1	4.4	-1.7	-1.7	0.6	-4.5	-1.1	3.8
PI 269076	1.9	1.2	0.9	0.6	-3.6	-16.5	-8.3	-12.2	-39.2
Egyptian Giant	-5.0	-0.9	-0.1	-6.7	-3.9	-5.9	-13.0	-1.7	-5.4
PI 269111	-9.7	-7.0	-15.6	-10.3	-10.1	-21.1	-21.1	-14.2	-33.8
PI 152113	-1.8	-0.2	-1.1	-1.9	1.5	-7.6	2.0	3.6	-10.8
Rhodesia Giant	-0.8	-6.7	8.4 (5)	-7.8	-10.0	5.8	-6.8	-12.8	8.4
South Africa Jumbo	-0.5	0.0	2.4	-8.8	-3.3	-12.5	-16.3	-11.0	-35.8
Fla 393-8-1-1-1-1-1-2	3.7 (6)	3.6 (7)	.	9.7 (6)	3.5 (9)	.	15.0 (4)	9.1 (7)	.
GP-NC 343	-0.2	-0.2	-8.1	-3.2	-1.4	-13.4	-2.0	-5.0	-13.8
NC 9	-5.1	-1.1	-10.6	-6.5	-0.3	-5.4	-5.4	6.7 (10)	-0.2
NC 6	-1.6	1.2	-0.6	-2.7	2.0	-4.4	-4.7	6.3	-3.6
NC 7	-8.3	3.7 (6)	-6.1	-2.1	12.3 (2)	2.4	-6.5	16.0 (1)	20.4 (3)
Holland Jumbo	-2.6	0.0	2.9	-6.4	-1.0	3.9	-6.6	-1.0	10.4
NC-V 11	1.5	1.7	-9.1	-0.2	3.3	-9.6	3.0	4.8	7.8
NC 10C	-0.7	-0.8	-4.6	-2.0	3.3	-5.6	0.8	8.1 (8)	-9.6
Mean	80.2	78.9	79.1	55.9	55.1	54.3	103.1	89.9	90.0
Std. Deviation	4.2	3.0	6.5	6.1	5.7	10.4	8.5	8.0	14.9

[a] Self effects were calculated from average values of homogeneous parents in 1989.
[b] Numbers in parentheses indicate rank of the ten highest parents from high to low values.

Table 3. Rank correlation coefficients for GCA and self effects of pod and seed size characteristics within generations.

Parent	Length of 20 Pods F_1	F_2	Self	Weight of 20 Pods F_1	F_2	Self	Weight of 100 Seeds F_1	F_2
	cm			g			g	
Length of 20 Pods (cm)								
F_2	.53**	--	--	--	--	--	--	--
Self	.53**	.42**	--	--	--	--	--	--
Weight of 20 Pods (g)								
F_1	.70**	.37**	.15	--	--	--	--	--
F_2	.37**	.68**	.00	.56**	--	--	--	--
Self	.41**	.37**	.69**	.40**	.32*	--	--	--
Weight of 100 Seeds (g)								
F_1	.74**	.41**	.24	.78**	.55**	.41**	--	--
F_2	.25	.53**	.00	.50**	.91**	.26	.54**	--
Self	.33*	.34*	.47**	.41**	.37**	.86**	.42**	.36*

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

Pod and seed characteristics do not appear to be as simply inherited as previously reported (1,2). The lack of correlation of GCA effects from the F_1 to F_2 generations and self effects and the F_2 segregation patterns of crosses investigated indicated that multiple genes are involved in both pod and seed size. The mean pod length and seed weight from F_1 and F_2 plants of certain crosses exceeded either parent and in other cases the hybrid means were less than either parent. Additive genetic variance was predominant as has been reported (3,4,6,9,11), however modifier genes may also be involved as suggested by Balaiah *et al.* (2).

Genes for maturity may interact with seed size genes. Size genes may be fully expressed only when the growing season allows full maturation of the crop. Therefore, genes for late maturity may mask genes for large seed size if the growing season is not long enough to permit full maturity. PI 221068 consistently produced progeny with large pods but relatively small seeds. Many of these seeds had a shriveled appearance indicative of immaturity. The maturity effect may have been a factor in the inconsistent estimates of GCA's from F_1 and F_2 generations of plants. GCA effects in the F_2 generation for 20-pod weight and 100-seed weight were generally better for U.S. genotypes, especially for released cultivars NC 17, NC-Fla 14, NC 9, NC 6, NC 7, and NC 10C.

Several parents with positive GCA effects on pod and seed size were identified. Some of these parents have already been used as sources of large pod and seed size in U.S. breeding programs, but others have not. Lines of particular interest for seed size were PI 298845, PI 314897, PI 325079, Jenkins Jumbo, and Fla 393-8-1-1-1-1-1-2. Although GCA effects were significant for the three traits measured in the F_1 and F_2 generations, there were some indications that nonadditive genetic effects influenced the traits in the population as a whole and in specific crosses examined for F_2 segregation patterns.

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Accepted March 6, 1993