

The Inheritance of Seed Size and Other Traits in Soybean (*Glycine max* (L.) Merr.)

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Abstract

The heritability of seed size in soybean was studied for the cross Tracy-M x PI 416808 (for large-seeded line improvement), and the reciprocal crosses of Forrest and PI 399007 (for small-seeded line improvement). Means of seed size of the F₂ populations were near the mid-parent value, and the parental seed size was recovered in some F₂ plants. Broad sense heritabilities for seed size (41.7% to 88.8%) were higher than yield and seed number, but lower than plant height, flowering date, maturity, and fruiting period in the F₂ and F₃ populations for all three crosses. The heritabilities of pod length and pod width were lower than that of seed size for the cross Tracy-M x PI 416808. The realized heritabilities were 51.1%, 99.1%, and 68.8% for the cross Tracy-M x PI 416808 and the reciprocal crosses of Forrest and PI 399007, respectively. Means of seed size in the selected F₃ were similar, 9.81g and 9.76g per 100 seeds, for the reciprocal crosses of Forrest and PI 399007.

Introduction

Soybean [*Glycine max* (L.) Merr.] has become a worldwide economically important crop because it is not only processed into animal feed, edible and industrial oils and other industrial products, but also used as a high protein food crop for direct human consumption. The vegetable soybean and soybean sprouts are directly consumed as a high protein food. Proper seed size and high germination are two essential traits for public acceptance as vegetable soybean or soybean sprout. However, seed size is not usually an important selection criterion in soybean breeding, unless cultivars are developed to supply a special demand for unusually small or large seeds⁽¹²⁾. There are only a few studies about the inheritance of soybean seed size, and even fewer concerning the improvement of a large-seeded or small-seeded soybean cultivar. Therefore, the inheritance of soybean seed size and the impact of selection for seed size upon cultivar improvement become important research topics.

Within the cultivated soybean, *G. max.*, the range in 100-seed weight is from 4 to 55g. The wild soybean, *G. soja*, produces seed averaging 1.2 to 1.8 g per 100 seeds. The seed size of widely grown cultivars ranges from about 12 to 18 g per 100 seeds⁽¹⁷⁾. Seed size

in soybean is determined by the rate of seed growth and duration of seed fill, both of which are under genetic control^(8,10,14). Although there are some environmental influences on soybean seed size^(9,11,24), it is, in general, inherited as a quantitative character with a heritability of about 70%⁽⁶⁾. The heritabilities were high for seed size, plant height, flowering, maturity and fruiting period, and low for yield^(2,15,28). Because of relatively high heritability values, it seems that early generation testing and the preliminary evaluation of advanced lines should be effective for seed weight in soybean^(16,20,23).

Materials and Methods

Two highly productive commercial cultivars, Forrest and Tracy-M, and two unadapted germplasm accessions, PI 399007 and PI 416808, selected for differences in seed size, were chosen for this study. The descriptive data of the four soybean parents are presented by Hartwig and Edwards⁽¹⁸⁾. All experiments were conducted at the Delta Branch, Mississippi Agricultural and Forestry Experiment Station, Stoneville, Mississippi.

All crosses were made on field-grown plants. An attempt was made to obtain reciprocal crosses between both sets of commercial cultivar and germplasm accession. However, the PI 416808 x Tracy-M cross was unsuccessful. For ease of discussion, the Tracy-M x PI 416808 cross will be identified as cross 1, Forrest x PI 399007 as cross 2, and PI 399007 x Forrest as cross 3. The F₁ plants were grown in a glasshouse during the winter of 1986-1987. Supplemental light was used to extend the photoperiod. Seed from the F₁ plants were planted in a field nursery with the parents on May 20, 1987. Plantings were made in rows 4 m long with 10 cm between seeds and rows 0.9 m apart. Four hundred eighty seeds of cross 1, 240 seeds of cross 2, and 240 seeds of cross 3 were planted.

In the F₂ generation, the estimate of heritability of quantitative character was determined by utilizing the variability among spaced F₂ plants in relation to the variability among spaced plants of the nonsegregating parents. Such an estimate of the broad sense heritability (H) was obtained, from the formula used by Mahmud and Kramer⁽²²⁾, as follows:

$$H = \frac{V_{F_2} - \frac{V_{P_1} + V_{P_2}}{2}}{V_{F_2}} \times 100$$

where

V_{F_2} = Total variance (genotypic + environmental) of the F₂ Population, or phenotypic variance.

V_{P_1} and V_{P_2} = Phenotypic variances among plants of parents (estimates of environmental variance.)

$\frac{V_{P_1} + V_{P_2}}{2}$ = Environmental variance.

$$V_{F_2} - \frac{V_{P_1} + V_{P_2}}{2} = \text{Genotypic variance.}$$

Expected genetic gain was calculated for 10% selection pressure using the formula of Allard⁽¹⁾.

$$G_s = (K)(\sigma)H$$

where G_s = expected genetic advance under selection,

K = the selection differential expressed in standard deviation units,

σ = standard deviation of the F_2 phenotypic mean for the respective selected character,

H = heritability coefficient.

Only the seed weight was recorded for measuring the realized heritability. The 10% largest-seeded F_2 plants in cross 1, and 10% smallest-seeded F_2 plants in crosses 2 and 3, respectively, were the selected populations. Two F_3 seeds from individual plants of the entire F_2 population from each cross was used to form the unselected bulk populations. The selected and unselected populations were planted on May 25, 1988. There were two replications for each cross.

The values of R and S for the realized heritability in this study on seed size were calculated as follows⁽¹²⁾:

$S = \bar{X}_{s, F_2} - \bar{X}_{F_2}$ = the selection differential in F_2 ,

\bar{X}_{F_2} = the mean performance of all F_2 plants,

\bar{X}_{s, F_2} = the mean of selected F_2 plants;

$R = \bar{X}_{s, F_3} - \bar{X}_{F_3}$ = the realized response from selection,

\bar{X}_{F_3} = the mean of F_3 progeny from selected F_2 plants,

\bar{X}_{s, F_3} = the mean performance of all F_3 progeny from F_2 plants.

Therefore, the realized heritability can be summarized as:

$$H_R = \frac{\bar{X}_{s, F_3} - \bar{X}_{F_3}}{\bar{X}_{s, F_2} - \bar{X}_{F_2}}$$

The experiment for broad sense heritability calculated from variance components was conducted on the F_3 generation. On May 24, 1988, 60 random F_3 lines derived from individual F_2 plants were planted in a randomized complete block design with two replications. Rows were 1 m long with 10 cm between seeds and rows 0.9 m apart. Twenty seeds per row were sown as an experimental plot. Adjustments to plant spacing for 10 cm apart were made after seedlings were 10 cm high. Five random plants from the middle of each row were chosen for measurement of traits. Analyses of variance in the F_3 generation were computed from the mean of five plants per plot. The components of genotypic and environmental variance was obtained from the analyses of variance, and heritability estimates were calculated according to Table 1. All analyses of variance were computed by the Statistical Analysis System⁽²⁶⁾.

Table 1. Form of variance analysis, mean square expectations, formulas for variance components and heritability estimates for the F₃ generation.

Source of variation	d.f.	M.S.	M.S.E.
Replication	R-1		
Genotypes	L-1	M ₁	$\sigma_e^2 + R\sigma_1^2$
Error	(R-1)(L-1)	M ₂	σ_e^2

R and L refer to number of replications and lines, respectively.

$$\text{Genotypic variance } (V_g) = \frac{M_1 - M_2}{R} = \sigma_1^2$$

$$\text{Phenotypic variance } (V_p) = \sigma_1^2 + \sigma_e^2$$

$$\text{Environmental variance } (V_e) = \sigma_e^2$$

$$\text{Heritability per plot basis} = \frac{V_g}{V_g + V_e} = \frac{V_g}{V_p}$$

$$\text{Heritability per family basis} = \frac{V_g}{V_g + \frac{V_e}{R}}$$

Individual plants were tagged and the following quantitative traits were recorded on F₂ and F₃ populations:

1. Flowering date—Recorded every other day as number of days from sowing date to the first flower on the plant.
2. Maturity date—Recorded every 3 days as the day when 95% of the pods had turned brown.
3. Fruiting time—Calculated as the number of days from flowering date to maturity date (maturity date-flowering date).
4. Plant height—Determined as the length of plant in cm from the ground to the top extremity at maturity.
5. Yield—All plants were harvested and threshed individually, and the seed yield recorded in grams per plant after all seed were allowed to reach an uniform moisture level by storing the seed in an air conditioned room for two weeks.
6. Seed size—Measured as the weight of 100 seed from each plant expressed as grams per 100 seeds.
7. No. of seeds per plant—Recorded the number of seeds of each plant.
8. Pod width—Pod width was measured at the widest part of the terminal seed cavity from suture to suture when the green pod reached its full-size. The measurement was made to the nearest 0.1mm with a caliper.
9. Pod length—Pod length was measured from the tip of the pod to the point of attachment of the sepals. Pod width and length were only recorded in cross 1. One random two-seeded pod was measured from the top nodes on the main stem of each F₂ plant. One random two-seeded pod was measured from each of the top three nodes on the main stem of five plants of the 60 random F₃ lines.

Results and Discussion

The studies of inheritance of soybean seed size were conducted at the F_2 and F_3 generations. The cross of Tracy-M x PI 416808 was for large-seeded line improvement, and the reciprocal crosses of Forrest and PI 399007 were for small-seeded line improvement.

The means of the parents and F_2 populations for the characters of the cross Tracy-M x PI 416808, and reciprocal crosses of Forrest and PI 399007 are given in Tables 2 and 3. Means of seed size of the F_2 generations were near the value of the mid-parent in all three crosses. The frequency distribution of seed size of the F_2 population of Tracy-M x PI 416808 (Table 2A) showed that the seed size of the parents was recovered, but more plants equaled the smaller seed parent than the larger seed parent. The results agreed with the hypothesis that it is difficult to obtain an adequate frequency of progeny with seed size equal to the larger parent from crosses involving small-seeded cultivars⁽⁵⁾. In the frequency distribution of seed size of reciprocal crosses Forrest and PI 399007 (Table 3A), the seed size of both parents was recovered in some of the F_2 plants with six and three plants larger than the seed size of the larger parent in the reciprocal crosses, respectively. These results differ from other reports^(19,27). Which showed that the parental genotypes were not recovered, and that many genes may be involved for this trait. The reason for recovering the parent types in this study may be because the seed size difference between the parents was small. However Weber and Moorthy⁽²⁸⁾ found that the seed size of parent types was recovered by some plants of the F_2 population. They concluded that there were many different genes in the parents which controlled the seed size, and the transgressive segregation may be due to the recombination of those different genes. From the frequency distribution (Tables 2A and 3A) and the means of the F_2 populations (Tables 2 and 3), the additive variance may be the major variance contributing to seed size^(7,15).

The mean of seed yield in the F_2 was larger than the higher yielding parent for the cross Tracy-M x PI 416808 (Table 2), but this could not be found in the reciprocal crosses Forrest x PI 399007 (Table 3). It either meant that a greater number of different genes controlled yield between Tracy-M and PI 416808 than between Forrest and PI 399007 or that little confidence can be placed upon seed yields from single plants. The maturity and fruiting periods were near the parent with the shorter period in the cross Tracy-M x PI 416808, but were near the parent with the longer period in the reciprocal crosses of Forrest and PI 399007. Plant height was similar to the larger parent in the reciprocal crosses of Forrest and PI 399007, but was near the midparent in the cross Tracy-M x PI 416808.

The means of yield and seed number exceeded the higher parent, whereas the mean of the fruiting period of the F_2 population was lower than the lower parent, showing that there was transgressive segregation for these three traits in the cross Tracy-M x PI 416808. In the reciprocal crosses of Forrest and PI 399007, the means for seed number, plant height, and fruiting period for the F_2 populations were higher than the higher parent.

Table 2. Means of the parents and the F₂ population from the cross Tracy-M x PI 416808.

Characters	Tracy-M	PI 416808	Mid-parent value	Tracy-M
				X PI 416808
Seed size (g/100 seeds)	12.3 (0.28)+	22.5 (0.48)	17.4	16.2 (0.12)
Yield (g/plant)	26.6 (2.63)	23.4 (3.39)	25.0	38.2 (0.94)
Seed number (seeds/plant)	215.0 (19.29)	110.5 (22.69)	162.8	238.3 (5.90)
Plant height (cm)	84.8 (1.31)	55.3 (1.43)	70.1	67.3 (0.74)
Flowering (days)	57.8 (0.49)	49.0 (0)	53.4	52.6 (0.24)
Maturity (days)	142.3 (1.14)	128.0 (0)	135.2	128.5 (0.37)
Fruiting period (days)	84.5 (1.16)	79.0 (0)	81.8	75.9 (0.32)
Pod length (mm)	34.2 (4.54)	51.8 (7.19)	43.0	44.4 (5.89)
Pod width (mm)	9.8 (1.16)	13.8 (2.12)	11.8	11.1 (2.07)

+ Value within parentheses is the standard error of the mean.

Table 2A. Frequency distributions of 100-seed weight (g) of the parents and F₂ population of the cross of Tracy-M x PI 416808.

Mid-Point	Tracy-M	PI 416808	F ₂			
			Total	Black	Green	Yellow ^a
8			1		1	
9	1		1	1		
10	1		2			2
11	2		3		3	
12	6		16	1	11	4
13	7		26	3	15	8
14	3		38	2	28	8
15			67	12	36	19
16		1	63	16	34	13
17			71	13	43	15
18			47	13	26	8
20			20	12	6	2
21		4	4	1	1	2
22		4	5	1	3	1
23		5	2	1	1	
24		4	2	1		1
25		1				
26		1				

a. Seedcoat color groups.

Table 3. Means of the parents and F₂ population of the crosses Forrest x PI 399007 and PI 399007 x Forrest.

Characters	Forrest	PI 399007	Mid-parent value	Forrest X PI399007	PI399007 X Forrest
Seed size (g/100 seeds)	10.6 (0.12)+	7.0 (0.09)	8.8	9.5 (0.09)	8.9 (0.08)
Yield (g/plant)	28.8 (1.92)	12.1 (0.97)	20.4	26.2 (1.00)	23.4 (0.81)
Seed number (seeds/plant)	269.8 (17.72)	171.6 (13.36)	220.7	274.0 (10.01)	263.1 (9.31)
Plant height (cm)	66.1 (1.03)	55.6 (0.92)	60.9	68.9 (0.90)	69.8 (0.95)
Flowering (days)	53.7 (0.36)	64.5 (0.29)	59.1	60.5 (0.41)	59.0 (0.46)
Maturity (days)	128.0 (0)	136.0 (0)	132.0	137.3 (0.49)	135.9 (0.53)
Fruiting period (days)	74.3 (0.36)	71.5 (0.29)	72.9	76.8 (0.36)	76.9 (0.42)

+ Value within parentheses is the standard error of the mean.

Table 3A. Frequency distributions of 100-seed weight (g) of the parents and F₂ population of the reciprocal crosses of Forrest and PI 399007.

Mid-Point	Forrest	PI 399007	PI399007 X Forrest	Forrest X PI399007		
				Total	Green	Yellow ^a
4.5			1			
5.0						
5.5						
6.0		2	1	1	1	
6.5		11	5	2	2	
7.0		11	7	5	4	1
7.5		9	24	14	11	3
8.0		4	27	19	18	1
8.5	1	1	37	31	30	1
9.0	1		43	29	25	4
9.5	1		33	25	20	5
10	8		16	28	22	6
10.5	10		14	29	24	5
11	10		11	16	15	1
11.5	3		3	8	6	2
12	3		1	10	5	5
12.5			1	2	1	1
13			1	4	1	3
13.5						
14			1			

a. Seedcoat color groups.

Broad sense heritability estimates for quantitative traits in the F₂ populations of all crosses are presented in Table 4. In the cross of Tracy-M x PI 416808, the heritability estimates for pod width and seed number were the lowest (28.4% and 35.4%, respectively). The heritabilities for seed size, Yield, and pod length were 45.2%, 47.8%, and 57.4%, respectively. In the reciprocal crosses Forrest x PI 399007 and PI 399007 x Forrest, the heritability estimates were similar for the same traits. The estimates for seed size (77.8 and 72.7%) were larger than that of yield and seed number (41.8 and 62.0%), but lower than those for the traits, plant height, flowering, maturity and fruiting period.

Table 4. Broad sense heritability estimates(%) for the F₂ populations of Tracy-M x PI 416808, Forrest x PI 399007, and PI 399007 x Forrest.

Characters	Tracy-M	Forrest	PI 399007
	X PI 416808	X PI 399007	X Forrest
Seed size	45.2	77.8	72.2
Yield	47.8	62.0	41.8
Seed number	35.4	59.2	51.2
Plant height	82.3	80.3	82.4
Flowering	89.5	89.4	91.8
Maturity	76.0	100	100
Fruiting period	67.1	86.3	90.4
Pod length	57.4	-	-
Pod width	28.4	-	-

The broad sense heritability estimates for the F₃ populations of the three crosses are presented in Table 5. All heritabilities were high, ranging from 56 to 84% on a plot basis, and 71.8 to 91.3% on a family basis, for the cross Tracy-M x PI 416808. The heritabilities of yield and seed number were the lowest. The heritability of seed size was higher than those of pod length and pod width, but lower than that of maturity, the highest heritability for this cross. The heritabilities of the reciprocal crosses of Forrest x PI 399007 varied with a wide range among the traits. The heritabilities of yield and seed number were the lowest, ranging from 14.1 to 48.2%. The heritabilities of seed size, ranging from 41.7 to 77.5%, were higher than those of yield and seed number, but were lower than those of other traits, except the fruiting period of the cross PI 399007 x Forrest.

The results indicated that the heritabilities of yield and seed number were the lowest among the traits at the F₂ and F₃ generations of all three crosses. The heritability of seed size was higher than that of yield and seed number, except for the F₂ generation of the cross Tracy-M x PI 416808, and it was lower than the heritabilities of plant height, flowering, maturity and fruiting period. Similar results for these traits have been reported by many researchers^(2,3,21). For this reason, selection for seed size should be more effective than selection for yield and seed number. The heritabilities of pod length and pod width were lower than seed size, except for pod width in the F₂ for the cross Tracy-M x PI 416808. These results were different from other reports^(4,13) Mehrotra and

Chandhary⁽²⁵⁾ found that the heritability of pod length was lower than that of seed weight in two agroclimatic conditions.

Table 5. Broad sense heritability estimates(%) for the F₃ populations of the crosses Tracy-M x PI 416808, Forrest x PI 399007, and PI 399007x Forrest.

Characters	Tracy-M x PI416808		Forrest x PI399007		PI399007 x Forrest	
	Plot	Family	Plot	Family	Plot	Family
Seed size	79.9	88.8	41.7	58.9	63.3	77.5
Yield	57.8	73.3	24.7	39.6	15.6	27.0
Seed number	56.0	71.8	31.8	48.2	14.1	24.7
Plant height	68.6	81.4	70.4	82.6	66.5	79.9
Flowering	77.0	87.0	69.7	82.1	80.6	89.3
Maturity	84.0	91.3	76.2	86.5	83.2	90.8
Fruiting period	61.2	75.9	51.9	68.3	57.2	72.8
Pod length	62.8	77.2	-	-	-	-
Pod width	68.6	81.4	-	-	-	-

The realized heritabilities and genetic gains for seed size, with a 10% selection pressure are listed in Tables 6 and 7. The realized heritability for cross Tracy-M x PI 416808 was the lowest with a moderately high value of 51.1%. There was a large difference of realized heritability between reciprocal crosses (99.1% for Forrest x PI 399007 and 68.8% for PI 399007 x Forrest). The percentages of expected and observed gain were smaller for the cross Tracy-M x PI 416808 (about 10%) than in the reciprocal crosses of Forrest and PI 399007.

The cross Forrest x PI 399007 had greater observed gain (realized response) than the cross PI 399007 x Forrest. The difference in the means for seed size of the F₃ selected populations between the reciprocal crosses were not significant, so the different observed gain between them was due to the significantly smaller seed size for the unselected F₃ population for PI 399007 x Forrest than for Forrest x PI 399007 (determined by SNK-test). Even though there were differences in realized heritability and genetic gain for seed size between the reciprocal crosses, the means of seed size in the selected F₃ populations with a 10% selection pressure for seed size were similar (9.81g and 9.76 g per 100 seeds for Forrest x PI 399007 and PI 399007 x Forrest). The results indicated that selection of 10% of the smallest seeds of each population had similar effects in the reciprocal crosses. The difference between the reciprocal crosses for mean of seed size was observed in the unselected F₃ populations (Table 6). The seed size was significantly smaller (determined by SNK-test) in the cross PI 399007 x Forrest than in the reciprocal cross. At the F₂ generation (Table 3A), It was also found that the frequency of seed size inclined toward large seed in the cross Forrest x PI 399007, and it inclined toward small seed in the cross PI 399007 x Forrest. The results suggest that there is some maternal effect for seed size.

According to the results, We found that early generation selection for seed size was effective due to the high heritabilities of this trait. The same results have been reported by other scientists^(16,20,23).

Table 6. Selection differentials for F₂ populations, realized responses of F₃ populations, and realized heritabilities for seed size in three crosses.

Crosses	\bar{X}_{S, F_2}	\bar{X}_{F_2}	S	\bar{X}_{S, F_3}	\bar{X}_{F_3}	R	H _R
Tracy-M x PI 416808	20.52	16.21	4.31	20.74	18.54	2.20	51.1
Forrest x PI 399007	7.28	9.51	-2.23	9.81	11.84	-2.03	99.1
PI 399007 x Forrest	6.90	8.92	-2.02	9.76	11.15	-1.39	68.8

Table 7. The expected and observed genetic gain with 10% selection for seed size in three crosses.

Crosses	Expected gain		Observed gain		Difference
	Unit	%	Unit	%	Unit
Tracy-M x PI 416808	1.89	9.2	2.20	10.6	.31
Forrest x PI 399007	-1.91	26.2	-2.03	20.7	.12
PI 399007 x Forrest	-1.58	22.9	-1.39	12.4	-.19

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大豆種子大小之遺傳性

林維和

大豆種子之大小在大豆育種中常被忽視，不論如何在食用性大豆中對種子大小常有特殊的要求，如毛豆需大粒型大豆，而黃豆芽則要求子葉較小的大豆。目前只有少數有關大豆種子大小遺傳性之研究，有關如何改進大粒型或小粒型大豆栽培種之研究，則幾乎缺乏，因此大豆種子大小遺傳性及不同種子大小之栽培品種改進自然而成爲重要之研究課題。

本試驗爲利用雜交組合 Tracy-M × PI416808（大粒種源系）及 Forrest 和 PI399007（小粒種源系）正反交組合後代 F₂ 及 F₃ 族群做爲研究種子大小遺傳性之材料。試驗結果顯示三雜交組合的 F₂ 族群種子大小之平均，值均趨向於其親本種子大小之平均值。在大粒種改進組合（Tracy-M × PI416808）的 F₂ 族群中，只有少數單株恢復大粒種親本之種子大小，在小粒種改進組合（Forrest 和 PI399007 正反交）的 F₂ 族群中有些單株恢復小粒種親本之種子大小，但卻有更多單株之種子大小恢復或大於其較大粒種之親本。

廣義遺傳力分別由 F₂ 族群與親本遺傳變方差異比及 F₃ 族群之變方成分法估算而得。種子大小之廣義遺傳力介於 41.7% 至 88.8% 之間。在三個雜交組合中，不論 F₂ 或 F₃ 族群之種子大小遺傳力估值，均大於單株產量及種子粒數之遺傳力估值，但小於株高，始花日數，成熟日數及子實充實日數之遺傳力估值。在雜交組合 Tracy-M × PI416808 之 F₂ 及 F₃ 族群中，莢長及莢寬遺傳力估值均小於種子大小遺傳率估值。真實遺傳力（realized heritability）是由 F₃ 族群選種真實反應（realized response）與 F₂ 族群選種差異（Selection differential）之比估算而得。組合中 Tracy-M × PI416808 對大粒種子選種壓力爲 10%，Forrest × PI399007 對小粒種子選種壓力爲 10%，雜交組合 Tracy-M × PI399007 之種子大小真實遺傳力爲 51.1%，Forrest × PI399007 正反交組合之種子大小遺傳力分別爲 99.1% 及 68.8%。而 10% 小粒種選種壓力之 F₃ 族群之種子大小平均值相似，其百粒重分別爲 9.81 克及 9.76 克。綜合以上結果可知：大豆種子大小之早世代選拔比產量及種子粒數有效，而選拔大粒種品系可能比選拔小粒種品系困難。在本試驗中種子大小選拔在正反交組合中具有相似的效應。