

The Association of Seed Size With and Among the Other Traits in Soybean (*Glycine max* (L.) Merrill)

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Abstract

Large seed size was associated with high yield for all three crosses in the F₂ generation, but no correlation between seed size and yield was evident in the F₃ generation. Soybean with large seed tended to have lower seed number for all three crosses in F₃ generation. Generally, in our studies, plant height and maturity did not have much effect on the size of seed; early flowering and long fruiting period was associated with large seed. Because of the associations of seed size and other traits, and the high heritability for seed size in both the F₂ and F₃ generations, early generation selection for seed size should be successful.

Larger pod length and pod width were associated with increased seed size in the F₂ and F₃ generations of the cross Tracy-M × PI 416808, but the heritability of pod length and pod width were lower than that of seed size. The expected efficiencies of indirect selection for seed size by using selection for pod length and pod width were 0.74 and 0.42, and 0.62 and 0.58 for the F₂ and F₃ generations, respectively. The results suggested that indirect selection for seed size by using selection for pod length and width may be less effective than direct selection for seed size.

Introduction

Correlation is used to measure the association between plant characters. It is important to know how the selection of one character will cause simultaneous changes in other characters. If an undesirable character is highly correlated with a desirable character, cultivar improvement becomes increasingly challenging for the plant breeder. For improving the large-seeded and small-seeded lines of soybean, we did not only study the heritability of seed size, but also researched its association with other characters.

Woodworth⁽¹⁷⁾ studied the relationships of yield and yield components in 26 soybean cultivars. He indicated that seed weight and yield were significantly associated with large-seeded types tending to be higher yielding. But Hartwig and Edwards⁽⁸⁾ found no relation between seed size and yield.

Weber and Moorthy⁽¹⁶⁾ studied the relationships of agronomic characters in the F₂ generation of three soybean crosses. Although different associations were found in different

crosses, the most consistent association was that seed weight was positively associated with high yield and late maturity. Johnson et al.⁽⁹⁾ found heavy seed was correlated with high yield, late maturity, and long fruiting period for two crosses. No correlation between seed weight and flowering was found. There was only a low correlation between seed weight and plant height for one cross. Anand and Torrie⁽¹⁾ indicated that seed weight was negatively correlated with yield, plant height, flowering and maturity for crosses Hawkeye x Capital and Seneca x Chippewa; it was positively correlated with fruiting period for the cross Seneca x Chippewa, but no correlation for the cross Hawkeye x Capital. For the cross Hardome x Chippewa, only a negative correlation between seed weight and plant height was found. Kwon and Torrie⁽¹⁰⁾ found low seed weight was associated with tallness, susceptibility to lodging, lateness of flowering and maturity, long fruiting time, and high yield in Norchief x Clark, whereas none of these traits was correlated with seed weight in Norchief x Harosoy. Martin and Wilcox⁽¹²⁾ indicated that pod height and seed size were significantly correlated in the F₂ generation of the three crosses indicating that plants podded high tended to have large seed, but the low magnitude of the correlation coefficients between pod height and seed size indicated little association between these two characteristics in the F₃ generation.

Some studies on the heritability and relationship of pod dimensions (including length, width, thickness and volume) and seed size emphasize the use of pod dimensions as selection criteria in breeding program for large-seeded soybeans. Bravo et al.⁽³⁾ reported that the phenotypic correlations between pod width and seed weight were highly significant, and ranged from 0.55 on an individual-plant basis to 0.64 on an entry-mean basis. The genotypic correlation on an entry-mean basis was 0.72. Frank and Fehr⁽⁶⁾ indicated that the phenotypic correlations between the pod dimensions were high, except for pod thickness. Genotypic correlation on an entry-mean basis for pod dimensions with seed weight were high (from 0.71 to 0.81), except for pod thickness (0.54). Fraser et al.⁽⁷⁾ found the pod length and width were significantly correlated with final seed size ($r=0.90$ and $r=0.96$) as well as with each other ($r=0.89$).

Mehrotra and Chandhary⁽¹³⁾ studied soybean ideotypes, they found the phenotypic and genotypic correlations of pod length and seed weight were low (from 0.15 to 0.23) and non-significant. Bravo et al.⁽³⁾ found that the use of mature pod width for indirect selection of seed weight was more effective than was direct selection for seed weight on an individual plant basis. Frank and Fehr⁽⁶⁾ suggested that indirect selection for seed weight by using pod length or width was equally effective on full size green pods or mature ones, and selection for pod length or width alone was as effective as the use of pod area or volume because only a single measurement is needed for each pod.

Materials and Method

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. Three crosses of Tracy-M x PI 416808, Forrest x PI 399007 and PI 399007 x Forrest were made. The descriptive data of materials, the field design of the experiment and the data record of quantitative traits were published before⁽¹¹⁾. The phenotypic and genotypic correlation coefficients in the F₂ were calculated as follows.

$$\text{Phenotypic correlation } r_p = \frac{\text{Cov}_{xyF_2}}{(\text{V}_{xF_2} \times \text{V}_{yF_2})^{.5}}$$

$$\text{Genotypic correlation } r_g = \frac{\text{Cov}_{xyG}}{(\text{V}_{xG} \times \text{V}_{yG})^{.5}}$$

where $\text{Cov}_{xyF_2} = \text{Cov}_{xyG} + \text{Cov}_{xyE}$

Cov_{xyF_2} = total F₂ covariance between the characters X and Y;

Cov_{xyG} and Cov_{xyE} = genotypic and environmental portions, respectively, of the covariance between the characters X and Y;

Cov_{xyE} = environmental portion of the covariance calculated from parents.

The analysis of covariance and the phenotypic and genotypic correlations in the F₃ were calculated according to the formulas in Table 1.

Table 1. Form of covariance analysis, mean product expectations and correlation formulas for the F₃ generation.

Source of Variation	d.f.	Mean Product Expectation		
		XX	XY	YY
Replications	R-1			
Lines	L-1	$\sigma_x^2 + R\sigma_{1x}^2$	$\sigma_{xy} + R\sigma_{1xy}$	$\sigma_y^2 + R\sigma_{1y}^2$
Error	(R-1)(L-1)	σ_x^2	σ_{xy}	σ_y^2

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

X and Y refer to any two characters under consideration.

$$\text{Phenotypic correlation } (r_p) = \frac{\sigma_{xy} + R\sigma_{1xy}}{[(\sigma_x^2 + R\sigma_{1x}^2)(\sigma_y^2 + R\sigma_{1y}^2)]^{.5}}$$

$$\text{Genotypic correlation } (r_g) = \frac{\sigma_{1xy}}{(\sigma_{1x}^2 \times \sigma_{1y}^2)^{.5}}$$

$$\text{Environmental correlation } (r_e) = \frac{\sigma_{xy}}{(\sigma_x^2 \times \sigma_y^2)^{.5}}$$

Results and Discussion

The genotypic and phenotypic correlation coefficients among the traits for the cross Tracy-M x PI 416808 for the F₂ generation are presented in Table 2. Genotypic correlations indicated that seed size was positively associated with yield, seed number, pod length and pod width, and negatively correlated with flowering date and maturity. In the phenotypic correlations, seed size was positively associated with yield, fruiting period, pod length and pod width, and negatively correlated with seed number and flowering date. Yield was positively associated with seed number, fruiting period, pod length and pod width when measured by genotypic correlation, but only positively correlated with seed number and fruiting period by phenotypic correlation. Seed size was negatively correlated with flowering date both by genotypic and phenotypic correlation. There was a negative genotypic and phenotypic correlation between seed number and flowering date, but a positive genotypic and phenotypic correlation of seed number and fruiting period. There were positive genotypic and phenotypic correlations among plant height, flowering, maturity and fruiting period, except for the phenotypic correlation of plant height and fruiting period. Pod length and pod width were associated with seed number and fruiting period based upon genotypic correlation, and they were negatively correlated with flowering date based upon both genotypic and phenotypic correlations. There were high genotypic and phenotypic positive correlations between pod length and pod width.

Table 2. Genotypic and phenotypic correlation coefficients (right and left side of diagonal, respectively) among all traits in the F₂ generation of the cross Tracy-M x PI 416808.

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Maturity	Fruiting	pod length	Pod width
Seed size		.64	.23	.06	-.30	-.16	.06	.66	.53
Yield	.13		.92	-.08	-.41	-.03	.32	.37	.68
Seed number	-.15	.95		-.08	-.38	.04	.37	.20	.45
Plant height	-.06	.01	.03		.71	.66	.19	-.12	-.02
Flowering	-.12	-.27	-.23	.63		.59	-.15	-.26	-.27
Maturity	.01	.01	0	.49	.51		.71	.07	.03
Fruiting period	.11	.19	.16	.09	-.16	.77		.31	.27
Pod length	.27	.06	-.02	-.06	-.19	-.05	.08		.51
Pod width	.27	.03	-.06	-.04	-.16	-.03	.09	.52	

Correlation coefficients required for significance are 0.10 and 0.13 at 5% and 1% level of probability, respectively.

The genotypic and phenotypic correlations among the traits in the F₃ generation (Table 3.) showed some discrepancy with the F₂ generation. The results from table 3 indicated that the positive correlations between seed size and maturity, fruiting period, pod length, and pod width were highly significant, but correlation of seed size and seed number was negative and significant. Seed size was not correlated with yield. There were high positive genotypic and phenotypic correlations among yield, seed number, plant height, flowering date, maturity and fruiting period. Pod width was positively correlated with pod length, but was negatively correlated with seed number when calculated by genotypic and phenotypic correlation methods.

Table 3. Genotypic and phenotypic correlation coefficients (right and left side of diagonal, respectively) among all traits in the F₃ generation of the cross Tracy-M x PI 416808.

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Mat-urity	Fruiting	pod length	Pod width
Seed size		.09	-.29	.13	.14	-.30	.39	.70	.63
Yield	.05		.91	.71	-.64	-.63	.47	.11	-.10
Seed number	-.30	.92		.61	-.58	.52	.32	-.14	-.33
Plant height	.13	.53	.46		.81	.81	.62	-.07	-.25
Flowering	.11	.52	.47	.72		.88	.55	.06	-.18
Maturity	.29	.55	.44	.73	.82		.87	.16	-.03
Fruiting period	.37	.39	.26	.50	-.37	.83		.23	.12
Pod length	.62	.05	-.16	-.07	-.03	-.13	.18		.69
Pod width	.59	-.11	-.32	-.20	-.17	-.05	.09	.68	

Correlation coefficients required for significance are 0.25 and 0.32 at 5% and 1% level of probability, respectively.

Table 4 presents the environmental correlation coefficients among all traits for the F₃ generation of the cross Tracy-M x PI 416808. Seed size was correlated with pod length and pod width, but the coefficients (0.25 and 0.39, respectively) were low. There was a high environmental correlation between pod width and pod length (coefficient was 0.64). Seed size and pod width were negatively correlated with seed number. The environmental correlation between seed number and yield was very high (0.95). Maturity had positive environmental correlations with flowering and fruiting period. There was a negative environmental correlation between flowering and fruiting period.

Table 4. Environment correlation coefficients among all traits in the F₃ generation of the cross Tracy-M x PI 416808.

Characters	Seed size	Yield	Seed number	Plant height	Flow-ering	Mat-urity	Fruiting	pod length	Pod width
Yield	-.13								
Seed number	-.39	.95							
Plant height	.17	-.07	-.03						
Flowering	-.08	.04	-.07	.24					
Maturity	.24	.20	.13	.24	.34				
Fruiting period	.30	.17	.07	.07	-.38	.74			
Pod length	.25	-.15	-.21	-.08	-.14	-.06	.04		
Pod width	.39	-.17	-.26	-.01	-.16	-.17	.05	.64	

Correlation coefficients required for significance are 0.25 and 0.32 at 5% and 1% level of probability, respectively.

Selection for large seed size increased yield in the F₂ generation but seed size was independent from yield in the F₃ generation for Tracy-M x PI 416808. Early flowering was associated with larger seed size in the F₂ generation, but late maturity and long fruiting period were accompanied by large seed size in the F₃ generation. In the F₂ population, selection for large seed increased the seed number when measured by genotypic correlation, but reduced the seed number when measured by phenotypic correlation. Larger seed size resulted in lower seed numbers on the basis of genotypic, phenotypic and environmental correlations in the F₃ generation. From these viewpoints, it is not advantageous to select for both large seed size and greater seed number concurrently in early generations.

Large seed size was positively associated with pod length and pod width in all generations, but the genotypic and phenotypic correlation coefficients were not high. Selection for pod length and pod width should be less effective than selection for seed size, due to lower heritabilities for pod length and pod width than seed size. The expected efficiencies of indirect selection (calculated from $r_A \times h_x/h_y$, r_A is genotypic correlation between traits x (pod length or width) and y (seed size), and h_x and h_y is the square root of the heritability of traits x and y, respectively) for seed size by selecting for pod length and pod width were 0.74 and 0.42, and 0.62 and 0.58 for the F₂ and F₃ generations, respectively. These results conflict with the hypothesis that selection for seed weight was more effective using pod width than direct selection for seed weight^(3,5,6). Because the shape of seed varies among cultivars for almost spherical to strongly flattened and elongated⁽⁴⁾, it causes the relationships of seed size with pod length and width to become more complex. The heritability of pod length was lower than seed size, and the phenotypic and genotypic correlations of pod length and seed size were low and non-significant in two agroclimation conditions for soybean ideotypes when seed weight ranged from 3.2 to 17.5 g

per 100 seeds⁽¹³⁾ Indirect selection for seed size by using pod width or pod length may not be constant in different crosses, and may depend upon the shape of seed.

The genotypic correlation coefficients among the traits for the F₂ generations of the reciprocal crosses Forrest x PI 399007 and PI 399007 x Forrest are presented in Table 5. Seed size was positively correlated with yield and fruiting period, and negatively correlated with flowering date for both of the reciprocal crosses. A negative correlation was found between seed size and plant height for the cross Forrest x PI 399007, and between seed size and seed number for the cross PI 399007 x Forrest. Yield was positively correlated with seed number with a coefficient of 0.95, and negatively correlated with flowering date for both reciprocal crosses. Yield and seed number were positively correlated with plant height for the cross PI 399007 x Forrest. There were high positive correlations among plant height, flowering date, maturity, and fruiting period for both of the reciprocal crosses.

Table 5. Genotypic correlation coefficients among all traits in the F₂ populations of the crosses Forrest x PI 399007 and PI 399007 x Forrest (right and left side of diagonal, respectively).

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Mat-urity	Fruiting
Seed size		.37	.08	-.16	-.22	.05	.36
Yield	.18		.95	-.09	-.28	-.01	.12
Seed number	-.14	.95		-.07	-.07	.04	.02
Plant height	-.08	.18	.17		.76	.69	.0
Flowering	-.16	-.18	.06	.72		.74	-.06
Maturity	.03	-.01	-.04	.66	.67		.63
Fruiting period	.26	-.05	-.11	-.11	-.21	.58	

Correlation coefficients required for significance are 0.13 and 0.17 at 5% and 1% level of probability, respectively.

The phenotypic correlations among the traits for the F₂ generations of the reciprocal crosses of Forrest and PI 399007 are presented in Table 6. The phenotypic correlations between seed size and the other traits were similar to the genotypic correlations. Seed size was positively correlated with yield and fruiting period, and negatively correlated with flowering date. Seed number was highly correlated with yield, with a correlation coefficient of 0.96. Yield and seed number were negatively correlated with plant height and flowering, and yield was positively correlated with fruiting period for the cross Forrest x PI 399007. There were significant phenotypic correlations among plant height, flowering date, and maturity, and between fruiting period and maturity for the reciprocal crosses. A negative correlation was found between fruiting period and flowering for the cross PI 399007 x Forrest.

Table 6. Phenotypic correlation coefficients among all traits in the F₂ populations of the crosses Forrest x PI 399007 and PI 399007 x Forrest (right and left side of diagonal, respectively).

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Maturity	Fruiting
Seed size		.33	.08	-.12	-.21	.04	.30
Yield	.20		.96	-.14	-.16	-.01	.17
Seed number	-.05	.96		-.13	-.13	-.03	.01
Plant height	-.05	.02	.03		.70	.53	-.06
Flowering	-.16	-.06	-.04	.67		.70	-.17
Maturity	.03	-.01	-.03	.60	.64		.58
Fruiting period	.21	.06	.01	.01	-.28	.55	

Correlation coefficients required for significance are 0.13 and 0.17 at 5% and 1% level of probability, respectively.

Table 7 presents genotypic correlations among the traits for the F₃ generation of the reciprocal crosses Forrest x PI 399007 and PI 399007 x Forrest. Negative correlations between seed size and seed number were found for both crosses. Seed size was negatively correlated with seed number and flowering date for the cross PI 399007 x Forrest. Yield was positively associated with seed number, plant height, flowering date and maturity for the cross Forrest x PI 399007, but only with seed number and plant height for PI 399007 x Forrest. There were positive correlations among seed number, plant height, flowering date, and maturity, except the correlation of seed number with plant height for the cross Forrest x PI 399007, and the correlation of seed number with maturity for the cross PI 399007 x Forrest. A positive correlation was found between fruiting period and maturity.

Table 7. Genotypic correlation coefficients among all traits in the F₃ populations of the crosses Forrest x PI 399007 and PI 399007 x Forrest (right and left side of diagonal, respectively).

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Maturity	Fruiting
Seed size		.01	-.53	-.11	-.17	-.16	0
Yield	.45		.80	.25	.27	.37	.21
Seed number	-.56	.46		.24	.32	.40	.19
Plant height	-.24	.68	.94		.81	.64	-.17
Flowering	-.31	-.06	.26	.86		.82	-.15
Maturity	-.18	0	.22	.76	.87		.44
Fruiting period	.11	.10	.06	.24	-.24	.69	

Correlation coefficients required for significance are 0.25 and 0.32 at 5% and 1% level of probability, respectively.

The phenotypic correlations among the traits in the F₃ population (Table 8) were gen-

erally less than corresponding genotypic correlations. In the reciprocal crosses, seed number was negatively correlated with seed size, but positively correlated with yield. There were positive correlations among plant height, flowering date, and maturity, and between maturity with fruiting period. Seed size was negatively correlated with flowering date; yield and seed number were positively correlated with plant height in the cross PI 399007 x Forrest.

Table 8. Phenotypic correlation coefficients among all traits in the F₃ populations of the crosses Forrest x PI 399007 and PI 399007 x Forrest (right and left side of diagonal, respectively).

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Maturity	Fruiting
Seed size		.04	-.43	.01	-.20	-.10	.13
Yield	.24		.87	.13	.10	.19	.15
Seed number	-.32	.83		.11	.19	.24	.10
Plant height	-.10	.30	.37		.66	.57	-.07
Flowering	-.33	-.02	.18	.72		.78	-.24
Maturity	-.15	-.05	.16	.70	.83		.42
Fruiting period	.18	.11	.04	.28	.14	.66	

Correlation coefficients required for significance are 0.25 and 0.32 at 5% and 1% level of probability, respectively.

The environmental correlation coefficients among the traits for the F₃ populations from the reciprocal crosses between Forrest and PI 399007 are presented in Table 9. In both crosses, seed size was positively correlated with plant height and fruiting period. There was a high positive correlation between yield and seed number, and a negative correlation between seed size and flowering date. There was a negative correlation between seed size and seed number for the cross Forrest x PI 399007. Fruiting period was positively correlated with plant height and maturity, and negatively correlated with flowering; the correlation of flowering date and maturity was positive for both reciprocal crosses. There was a positive correlation between plant height and maturity for cross PI 399007 x Forrest.

Table 9. Environmental correlation coefficients among all traits in the F₃ populations of the crosses Forrest x PI 399007 and PI 399007 x Forrest (right and left side of diagonal, respectively).

Characters	Seed size	Yield	Seed number	Plant height	Flowering	Maturity	Fruiting
Seed size		.01	-.32	.32	-.29	.06	.37
Yield	.09		.93	-.04	-.17	-.09	.08
Seed number	-.19	.95		-.15	-.06	-.09	-.03
Plant height	.38	-.04	-.11		-.05	.21	.26
Flowering	-.43	.04	.21	-.03		.55	-.53
Maturity	-.01	.17	.19	.38	.45		.42
Fruiting period	.37	.14	.02	.42	-.38	.66	

Correlation coefficients required for significance are 0.25 and 0.32 at 5% and 1% level of probability, respectively.

Although the correlation coefficients among traits were low, small seed size was associated with low yield, late flowering and short fruiting period for both reciprocal crosses of Forrest and PI 399007 in the F₂ generation. However, small seed size was associated with greater seed number for both reciprocal crosses, and only with late flowering for cross PI 399007 x Forrest in the F₃ generation. Small seed was associated with low yield only when measured by genotypic correlation for the cross PI 399007 x Forrest.

Differences in the correlation and intensity of association among the traits were found in different generations, with higher genotypic and phenotypic coefficients, and a greater number of significant correlations between the traits being found in the F₃ generation for all crosses. Genotypic correlation coefficients in both generations for all crosses. Few estimates were high for environmental correlations. Similar results have been reported by others^(1,2,9,10)

In general, we found large seed size was associated with high yield for all three crosses at the F₂ generation, but no correlation between seed size and yield at the F₃ generation. It seems likely that the association between traits in the F₃ generation would have greater validity than those in the F₂ where traits were measured on single plants. The literature indicates that the relationship of seed size and yield was unstable, there were positive correlation in some populations, negative correlations in other populations, and no relationship in some other populations between seed size and yield^(1,9,10,14,15,17).

The soybean plants with large seed tended to have reduced seed number for all three crosses in the F₃ generation, and seed number was positively correlated with Yield. Therefore, large seed did not increase yield in F₃ population. High negative correlation between seed size and seed number has been report by Johnson et al⁽⁹⁾. Genetic changes in seed size are frequently accompanied by compensatory changes in seed number so that the final yield, which is the product of seed number and seed size, may remain constant⁽⁸⁾.

Generally, in our studies, plant height and maturity were not much affected by the size of seed. Early flowering and long fruiting period resulted in larger seed. The correlation of seed size with these traits has not been constant, as reported by different researchers^(1,9,10,17). In general, early flowering, late maturity and long fruiting period are associated with large seed.

High correlations among plant height, flowering and maturity have been found by many researchers^(1,2,9,17). Similar results were also found in our studies; there were high correlations among these traits in both the F₂ and F₃ populations for all three crosses.

High yield was associated with early flowering for all crosses in the F₂ population, but in the F₃ population, it was associated with late flowering for the cross of Tracy-M x PI 416808, and no relationship for the reciprocal crosses of Forrest and PI 399007. Plant height was essentially not important for yield in the F₂ generation, but in the F₃ generation high yield was accompanied by taller plants. In addition to the effect of the different generations and the measurement of traits on one plant vs. five, the environmental differences associated with the 1987 and 1988 growing seasons may have affected the relationship between traits.

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大豆種子大小與其他性狀之相關性

林維和

大豆種子大小品種改進研究中，除須瞭解大豆種子大小遺傳性外，亦須瞭解大豆種子大小與其他性狀之相關，以防因針對種子大小進行選種時導入其他不良性狀，或可間接利用其他性狀指標選拔以進行種子大小之選種。因此進行大豆種子大小與其他性狀相關性之研究。

在 F_2 世代中三個雜交組合均表現出大粒種子與高產有相關性。但在 F_3 世代中種子大小與產量則無相關性，而具大粒種子之植株卻表現出種子數較少的傾向。本研究中發現，株高與成熟期對種子大小無影響。而具早開花及長結實期特性者則具大粒種子之特性。種子大小之高遺傳力特性及與其他性狀相關性在 F_2 及 F_3 世代中之表現結果證實大豆種子大小在早世代選拔具有良好效果。

雜交組合 Tracy-M x PI 416808 在 F_2 及 F_3 世代均表現出較大的莢長與莢寬特性則具有增加種子大小之特性，但因莢長與莢寬之遺傳力均低於種子大小之遺傳力，使得藉由莢長及莢寬之選拔以進行種子大小選拔之間接選拔期望效率 (expected efficiency of indirect selection) 表現在 F_2 及 F_3 世代中僅分別為 0.74, 0.42, 0.62 及 0.58。由此結果得知藉由莢長及莢寬之選拔以進行種子大小之選拔比直接進行種子大小選拔較為缺乏效率。