

Analysis of Quantitative Traits and Estimation of Heritability in Early Generations of a Single Cross in Soybean (*Glycine max* (L.) Merrill)

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Abstract

Genetic variability and heritability of quantitative traits, particularly of yield contributing traits, are of great importance in understanding phenotypic variation and the heritable portion of the variation when making selection choices. In the present study, the heritability for days to 50% flowering, days to maturity, plant height at maturity, total number of pods per plant, number-filled pods per plant, 100-seed weight, and grain yield per plant were estimated by variance components from variance analysis of parents and F_2 and $F_{2:3}$ progeny families derived from a single cross. Heritability estimates were high for days to 50% flowering and 100-seed weight, moderate for the number of pods per plant and number of filled pods per plant, and low for seed weight per plant. These results suggested that in the early segregating generations, direct selection for seed size, plant height, and a number of pods per plant might be more efficient than the direct selection for seed yield.

Keywords

Soybean (*Glycine max* (L.) Merrill), quantitative traits, heritability

Introduction

High seed yield is the primary aim of most soybean breeding programs. As in many crops, the extent of genetic improvement depends upon the genetic variability of the breeding population and the efficiency of the selection schemes. Soybean breeding techniques commonly exploit the genetic variability in segregating populations developed from crosses of two or more parents followed by individual plant selection. Variability in soybeans was used to improve agronomic performance traits such as yield, seed protein and oil content, and plant height, which enabled the selection of new germplasm (Fasoula *et al.*, 2007 a, b, c). When utilized, variability can not only help improve yield and other agronomic performance traits, but also help improve plant tolerance

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to stresses and global changes in the environment. Thus, the presence and magnitude of genetic variability in a population is a prerequisite of a breeding program (St. Martin, 1985; Bhat *et al.*, 2012).

The genetic improvement of quantitative characteristics, particularly seed yield, however, is often more difficult due to their polygenic control and environmental fluctuations, resulting in low heritability (Fehr, 1987; Burton, 1987; Coryell *et al.*, 1999). As a result, selection for yield per se may not be rewarding unless other yield attributing traits are taken into consideration, especially if the individual components are highly heritable and genetically independent (Aditya *et al.*, 2011). Thus, the estimation of different variance components, particularly the heritability, would provide information about the traits' variability. Furthermore, the heritability of a quantitative trait is very important to breeders in understanding the heritable portion of the total phenotypic variation, in choosing a selection method, and in determining the response to selection because it implies the extent of transmissibility of traits to the next generation. Further, heritability estimates are helpful in knowing the performance of parents in hybrids.

Heritability can be estimated by various means, i.e. parent-offspring regression (Warner, 1952; Falconer and MacKay, 1996) and/or by generation mean analysis (Warner, 1952; Mather and Jinks, 1982). Genetic analyses in soybean indicate that genetic variances and heritability estimates vary largely depending on the source populations/crosses and traits under investigation. Studies in segregating populations revealed that the heritability of plant seed weight was low while the heritabilities of days to maturity and plant height were high (Gomes *et al.*, 2004; Hakim *et al.*, 2014; Hakim and Suyamto, 2017).

The objectives of this study were to determine the magnitude of genetic variability and heritability of quantitative traits in F_2 and $F_{2:3}$ progeny families derived from a single soybean cross.

Materials and Methods

Plant materials

Soybean plants were selected from a working collection specifically created for plant height and plant seed yield made from a cross between two soybean accessions, VI045032 and GBVN004904, during the 2014 spring season. The accession VI045032 (purple flower) was introduced from AVRDC, and the accession GBVN004904 (white flower) was obtained from the Vietnam National Plant Resources Center.

Cultural practices and trait measurements

Forty-two F_2 plants from the cross were grown in the spring of 2015. Twenty-seven F_2 plants randomly selected to establish $F_{2:3}$ progeny families were planted in the 2015 summer-autumn season in double row plots with variable numbers of plants (18-30 plants) per family depending on seed availability. The two parents, VI045032 and GBVN004904, were intercalated in duplicate. Row and intra-row spacing was 40 and 15 cm, respectively. Recommended cultural practices for growing soybean were applied. The F_2 generation and $F_{2:3}$ progeny family evaluations were conducted at the Experimental Station of the Faculty of Agronomy, Vietnam National University of Agriculture. All plants in each family were observed and measured for estimating genetic parameters. The following traits were evaluated: days to 50% flowering, days to maturity (only for the F_2 generation), plant height at maturity, a total number of pods per plant, number of filled pods per plant, 100-seed weight, and grain yield per plant.

Quantitative trait analysis and estimation of heritability

Data were analyzed using Microsoft Excel (2010). The environmental variance, V_E , was estimated as the mean-variance among plants of the two parents $(V_{P1} + V_{P2})/2$, after checking for homogeneity of variance by Barlett's test. The broad-sense heritabilities of the traits in the F_2 generation were estimated using the following formula of Acquah (2012):

$$H = \frac{V_{F_2} - V_E}{V_{F_2}}$$

where H is the broad-sense heritability, V_{F_2} is the total variance of the F_2 generation, and V_E is the environmental variance.

The trait variances for each of the $F_{2:3}$ progeny families were computed using Microsoft Excel (2010) based on the following statistical model:

$$Y_{ij} = \mu + f_i + e_{ij},$$

where Y_{ij} is an observation of the j^{th} plant of the i^{th} $F_{2:3}$ family, μ is the grand mean of the families or parents, f_i is the genetic effect attributed to the i^{th} family, and e_{ij} is the effect among plants within families or parents.

The original data of the number of pods per plant and the number of filled pods per plant were transformed using square root transformations, $\sqrt{x} + 0.5$, to adjust the data to the normal distribution curve (Costa *et al.*, 2008). The variance analysis for the $F_{2:3}$ progeny families and for each parent is presented in Table 1. Because of the different number of plants measured in each $F_{2:3}$ family and each parent, the value was adjusted as k_f , k_1 , and k_2 representing the weighted averages of the number of plants measured for the families, parent P_1 , and parent P_2 , respectively, and were calculated as described by Costa *et al.* (2008).

$$k_f = \frac{N - \left[\frac{1}{N} \sum n_i^2 \right]}{f - 1}$$

$$k_1 = \frac{N_1 - \left[\frac{1}{N_1} \sum n_i^2 \right]}{p_1 - 1}$$

$$k_2 = \frac{N_2 - \left[\frac{1}{N_2} \sum n_i^2 \right]}{p_2 - 1}$$

The variance components were estimated as follows:

The total phenotypic variance among $F_{2:3}$ progeny families

$$\sigma_{Af}^2 = \frac{MS_{Af} - MS_{Wf}}{k_f}$$

The environmental variance

$$\sigma_e^2 = \frac{1}{2} (\sigma_{e(\text{parent1})}^2 + \sigma_{e(\text{parent2})}^2) = \frac{1}{2} \left(\frac{MS_{Ap1} - MS_{Wp1}}{k_1} + \frac{MS_{Ap2} - MS_{Wp2}}{k_2} \right)$$

The genotypic variance

$$\sigma_G^2 = \sigma_{Af}^2 - \sigma_e^2$$

Broad sense heritability

$$H = \frac{\sigma_G^2}{\sigma_{Af}^2}$$

Results

Variability and heritability of the traits in the F_2 generation

The range of the F_2 family means of the cross indicates the variability that might be expected in the progeny of a cross between two accessions. Among the traits studied, plant height at maturity, number of pods per plant, number of filled pods per plant, and seed weight

Table 1. Analysis of variance for each trait measured in the $F_{2:3}$ progeny families

Source of variation	DF	Mean square	Expected mean square
For F_3 families			
Among families	f-1	MS_{Af}	$\sigma_{Wf}^2 + k_f \sigma_{Af}^2$
Within families	N-f	MS_{Wf}	σ_{Wf}^2
For parent P_1			
Among plots	p_1-1	MS_{Ap1}	$\sigma_{Wp1}^2 + k_1 \sigma_{Ap1}^2$
Within plots	N_1-p_1	MS_{Wp1}	σ_{Wp1}^2
For parent P_2			
Among plots	p_2-1	MS_{Ap2}	$\sigma_{Wp2}^2 + k_1 \sigma_{Ap2}^2$
Within plots	N_2-p_2	MS_{Wp2}	σ_{Wp2}^2

Note: f = number of $F_{2:3}$ progeny families, p_1 = number of parent 1 replications, p_2 = number of parent 2 replications, N = total number of plants in the $F_{2:3}$ progeny families observed, N_1 = total number of plants for parent 1, N_2 = total number of plants for parent 2.

Table 2. Estimates of range, mean, coefficient of variation, and of broad-sense heritability of yield contributing traits in the F₂ generation

Trait	Range	Mean	Coefficient of variation (%)	Broad-sense heritability
Plant height at maturity (cm)	12.5-53.5	26.9	42.36	0.50
Days to 50% flowering	45.0-58.0	44.8	15.40	0.86
Days to maturity	94.0-113.0	99.1	4.09	0.88
Pod number per plant	15.0-108.0	43.1	48.87	0.20
Filled pod number per plant	15.0-106.0	41.8	50.08	0.23
100-seed weight (g)	11.8-21.2	17.4	11.84	0.79
Seed weight per plant (g)	3.6-32.1	13.8	47.77	0.23

per plant showed the widest ranges and had the highest coefficients of variation (> 40%); while days to 50% flowering, 100-seed weight, and, particularly, days to maturity had lower variabilities (Table 2). These results indicated that plant height at maturity, number of pods, number of filled pods, and seed weight per plant were highly variable in the F₂ generation.

Days to 50% flowering, days to maturity, and 100-seed weight had high heritability estimates of 0.86, 0.88, and 0.79, respectively (Table 2). Plant height at maturity had moderate heritability, but the yield components (number of pods and number of filled pods per plant) and seed weight per plant had low heritability (0.20-0.23). This indicated that days to 50% flowering, maturity, and seed size were highly heritable.

Variability and heritability of the traits in the F_{2:3} progeny families

The range of the F_{2:3} progeny families demonstrated the variability within each trait to some degree, but the means for plant height at maturity, days to 50% flowering and maturity,

number of pods per plant, number-filled pods per plant, and 100-seed weight were very close to the mid-parent values, while the mean for seed weight per plant was not (Table 3). All the F_{2:3} progeny families from the present single cross had average plant seed yields exceeding both parents. Although no statistical test was conducted, one would expect that the difference is significant because of the fairly large number of observations involved in the means.

The heritability estimates were high for plant height at maturity, days to 50% flowering, a number of pods and number of filled pods per plant, and 100-seed weight (Table 4). These heritability estimates were comparable with those reported by Costa *et al.* (2008). In contrast, the seed weight per plant was of low-moderate heritability (0.42) (Table 4). Although the heritabilities in this study might be slightly overestimated due to a rather limited number of F₂ and F_{2:3} progeny families, they indicated that most of the yield contributing traits resulting from a single cross are highly heritable and can be successfully selected for in an early segregating generation.

Table 3. Range and means of measured traits for the parents and F_{2:3}-progeny families

Parent or F _{2:3} family	Plant height at maturity (cm)	Days to 50% flowering	Days to maturity	Pod number per plant	Filled pod number per plant	100-seed weight (g)	Seed weight per plant (g)
VI045032	29.3	40.9	108	28.50	25.57	27.91	7.71
G72	32.6	36.2	100	50.95	46.54	10.34	7.03
F _{2:3} family range	23.8-42.4	36.2-41.2	100-111	32.3-71.4	29.9-67.5	14.5-22.3	8.6-16.3
Mean	32.50	38.45	104.22	46.97	43.29	17.31	10.50

Table 4. Genotypic variance, environmental variance, and broad-sense heritabilities of measured traits in the F_{2:3} progeny families

Trait	V _{G(F_{2:3})}	V _E	Broad-sense heritability (H)
Plant height at maturity	33.244	6.332	0.84
Days to 50% flowering	2.242	0.859	0.73
Pod number per plant	1.224	0.199	0.86
Filled pod number per plant	1.108	0.211	0.84
100-seed weight	136.168	16.641	0.89
Seed weight per plant	1.767	2.447	0.42

Discussion

Estimates of heritability vary with each trait, population, and environment under study. Most studies have reported that seed yield was relatively low in heritability (Anand and Torrie, 1963; Toledo *et al.*, 2000; Gomes *et al.*, 2004; Costa *et al.*, 2008; Bhat *et al.*, 2012; Hakim and Suyamto, 2017; Kuswanto *et al.*, 2018), while plant height and days to maturity had moderate to high heritability (Gomes *et al.*, 2004; Hakim *et al.*, 2014; Hakim and Suyamto, 2017; Kuswanto *et al.*, 2018). For segregating populations following hybridization, heritability estimates depend on the parents used to make a cross, the handling of segregating generations during the stabilization phase, traits, and the generation per se. Anand and Torrie (1963), from studies using F₃ and F₄ generations from three soybean crosses, reported that heritability estimates for seed yield and number of pods per plant were relatively low whereas the estimates for seed weight were high. Toledo *et al.* (2000) studied F₂, F₃, F₇, F₈, F₉, and F₁₀ generations derived from six biparental crosses made from four cultivars and evaluated in 17 environments. Their results showed that the heritability for seed yield differed among cross combinations, years and, sowing dates (0.09-0.55), and the overall heritability was rather low (0.29). Gomes *et al.* (2004) also found that the heritabilities of days to maturity, plant height, and seed yield differed among crosses and generations, and, particularly, the general mean heritability estimate of all crosses for seed yield in the F₆ generation (0.58) was higher than those in the F_{6:7} (0.21) generation.

Studies with 25 soybean genotypes (Malik

et al., 2006) and with 91 soybean lines (Sulistyo *et al.*, 2017) showed that the heritabilities of 100-seed weight, days to 50% flowering, days to maturity, plant height, and grain yield per plant were high, and the authors concluded that these traits were governed by the additive type of gene action. Aditya *et al.* (2011) estimated the genetic variability of 31 soybean genotypes and found high heritability for days to 50% flowering, number of primary branches per plant, plant height, 100-seed weight, and seed yield per plant. Seed weight has also been shown to be rather high in heritability (Osekita and Olorufemi, 2014; Kuswanto *et al.*, 2018; Joshi *et al.*, 2018). In the present study, heritability estimates for the number of pods and number of filled pods per plant in the F₂ generation differed from the F_{2:3} generations, of which the heritabilities were low in F₂ but rather high in F_{2:3}. High heritabilities were estimated for days to 50% flowering, days to maturity, and 100-seed weight in both the F₂ and F_{2:3} generations, while heritability for plant height at maturity was moderate in F₂ and high in F_{2:3}. Seed yield, however, was low in heritability in both generations. This is in contrast to that reported by Osekita and Olorufemi (2014) who found that the heritability for seed yield in an F₃ population was extremely high (0.98). The high heritabilities of plant height at maturity, days to maturity, and 100-seed weight in both the F₂ and F_{2:3} generations in this study suggest that selection for these traits in early generations may be effective. In contrast, low heritability in seed yield and variable heritabilities of the yield components indicate that selection should be delayed to advanced generations among recombinant lines.

Conclusions

High heritability is an indication of the presence of higher proportions of fixable additive variance in the population. The estimates of heritability when accompanied by high genetic advances are meaningful for breeders to design selection methods to be followed. Among the quantitative traits studied in the F_2 and $F_{2:3}$ progeny families derived from a single cross of soybean in the present study, days to 50% flowering and 100-seed weight had consistently high heritability. However, the plant height showed moderate heritability, and the heritability for a number of pods per plant and number of filled pods per plant varied with generation. The heritability of seed weight per plant was of low heritability in both the F_2 and F_3 generations. This indicates that direct selection for seed yield in early generations would be less effective while selection for seed size, and probably plant height and number of pods per plant, might be more efficient. To make correct decisions for applying selections in segregating generations of soybeans derived from crosses, narrow-sense heritability estimations might be of necessity.

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