Gene Action and Heritability of Leaf and Reproductive Characteristics in Soybean

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Soybean [*Glycine max* (L.) Merr.] cultivars with smaller area and lanceolate leaves have shown better light distribution through their canopy and a higher photosynthetic rate than those with larger leaf area and oval leaf shape. However, very little information has been published about leaf characteristics in relation to yield potential and inheritance which would assist breeding effects to develop new cultivars with optimum leaf area and leaf shape. Gene action and heritability for leaf area, leaf shape, and other reproductive characteristics were studied in a diallel cross including nine parents with large, medium, and small leaf area. Most progenies from crosses among parents with different leaf areas had larger mean leaf area, longer flowering, and later maturity than the midparent and both parents, suggesting transgressive segregation for these traits. General combining ability (GCA) and specific combining ability (SCA) for leaf area and leaf shape were significant in populations. Ratios of GCA to SCA were 0.96 for leaf shape and 0.89 for leaf area, indicating that GCA effects were more important than SCA. Genetic gain for leaf area and shape may be possible through selections. Narrow sense heritability estimated on the basis of variance components was 43.4% for leaf area, 63.2% for leaf shape, and 29.1% for maturity, which were lower than days to flowering and flowering period due to large error variances (σ^2E) caused by field environmental factors. This study indicated that it is possible to optimize leaf area and leaf shape related to photosynthetic rate and subsequently yield, because of relatively large and significant GCA effects for these traits. The predominance of additive effects should improve the effectiveness of selection based on performance of individual cultivars.

Key Words: *Glycine max*, diallel analysis, genetic variance, inheritance, leaf morphology.

Introduction

Soybean [*Glycine max* (L.) Merr.] cultivars, as in many

other plant species, have various leaf shapes and areas. Studies have demonstrated a relationship between leaf morphology and the ability to intercept sunlight. The quantity and quality of solar radiation intercepted by a leaf directly affects photosynthetic rate (Lugg and Sinclair 1980, Ehleringer and Werk 1986, Sung and Chen, 1989). Lanceolate leaf genotype is characterized with narrow leaf and reduced leaf area of up to 30%. Lanceolate leaf architecture allows more light to penetrate farther into their canopy, resulting in higher CO₂ fixation than other oval leaf soybeans (Hicks *et al.* 1969). Genetic differences in soybean leaf photosynthetic rates influencing yield have been clearly associated with these leaf characteristics (Kaplan and Koller 1977, De Soyza and Kincaid 1991).

Sasahara (1984) reported that the net photosynthetic rate per unit leaf area in soybean was significantly and negatively correlated with the leaf area and CO₂ diffusion resistance. The high photosynthetic cultivars had smaller leaf area and smaller CO₂ diffusion resistance than others. CO₂ exchange rate (CER) per unit leaf area in several species, including soybean, was correlated with specific leaf weight (Kaplan and Koller 1977). CER has been shown variation and inherited quantitatively among soybean cultivars (Ojima 1972, Kaplan and Koller 1977).

Lugg and Sinclair (1980) suggested that leaf area decreased as specific leaf weight increased, while specific leaf weight increased as leaves thicken. Increased leaf thickness and specific leaf weight were due to simultaneous thickening of both palisade and spongy mesophyll layers in the leaf. The final specific leaf weight and thickness were modified with solar radiation levels during the period of leaf development. A negative relationship between specific leaf weight and leaf area was frequently observed because leaves thicken at the expense of growth in area. Genotypes with small and thick leaves had higher chloroplast numbers, soluble protein content and a higher photosynthetic rate based on unit leaf area than those with large and thin leaves (Shibles *et al.* 1987, Sung and Chen 1989).

Sung and Chen (1989) suggested that genotypes with lanceolate leaves incorporated more CO₂ per unit leaf area than the normal leaf genotype. Photosynthetic changes were very closely related to variations in the amount of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) per unit leaf area, and the specific activity of the enzyme. A narrow leaf type of the recurrent parent had a mean seed yield of 2,880 kg ha⁻¹, while the seed yield of the normal leaf type in this comparison was 2,840 kg ha⁻¹ (Hartwig and Edwards

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1970).

Seed numbers were related to the availability of assimilate to the reproductive organs during flowering and pod setting (Heitholt *et al.* 1985). The proportion of assimilate allocated to reproductive parts during flowering and seed setting periods could have a direct effect on seed numbers and yield (Shibles *et al.* 1975). Mean seed weights were less for later than earlier flowers, due to a shorter seed filling period (Egli *et al.* 1987).

It is evident that leaf area and shape in relation to leaf thickness and CO₂ assimilation affect seed yield directly, or indirectly, depending on reproductive characteristics. Elucidation of the genetic control of these complex characteristics is important to enhance genetic improvement. Limited genetic information on leaf characteristics restricts the development of high yielding cultivars with desirable leaf area and shape, as well as better reproductive characteristics. The objective of this study was to determine types of gene action and heritability for leaf area and shape relevant to CO₂ assimilation and reproductive characteristics.

Materials and Methods

Parent classification and population development

Nine soybean cultivars were used for determination of gene action types and heritability. One cultivar Camp originated from North America, two from Japan, and six from Korea. Mean values of leaf and reproductive traits for the nine parents are presented in Table 1. Mean leaf area ranging from 39.57 to 33.31 cm² was large, 30.47 to 24.15 cm² medium, and 21.08 to 9.85 cm² small. The mean leaf areas were statistically ($P < 0.05$) different among the three groups. The mean values for leaf shape were calculated by the ratio of mean leaf length to mean leaf width (leaf width/leaf length) and varied from lanceolate to oval in each parent group. Maturity ranged from 90d for Nattosan to 128d for Camp (Table 1). Based on LSD in Table 1, mean distribution of the traits including leaf area within parent groups or among parents indicated adequate genetic diversity for genetic study of gene action and heritability.

The cultivars, representing three groups of leaf area, were crossed in 1996, according to a non-reciprocal diallel pattern (Griffing 1956). Thirty six F₁ populations developed from diallel crosses were planted at the National Honam Agricultural Experiment Station in Korea, on 22 May, 1997, and examined for leaf area, leaf shape, and other reproductive characteristics, including flowering period. Four plants per replicate were randomly sampled at the beginning of flowering stage in an individual genotype and two fully expanded leaves from the upper fourth and fifth nodes on the main stem were measured for leaf area, length and width with an Area Meter AM 100 (ADC Ltd., U.K.). Reproductive growth stages were determined according to Fehr and Caviness (1977). The days for flowering were estimated from planting date to R1 stage of approximately 50% of the population in test plots. Due to the limited numbers of F₁

seeds, plots were two rows for each parent and F₁ population. Rows were 4 m in length with 60 cm row spacing and 15 cm between plants within the row. There were three replications of each treatment. During the growing season, hand weeding was done as necessary. Fertilizer was not applied at any of the test plots, which were subjected to a conventional tillage practice.

Statistical analysis

Analyses of variance were performed on the data. General and specific combining ability effects were estimated using Griffing's analysis method 4 and model 2, in which parents were assumed random, because they were completely inbred and chosen from a wide range of parents with large genetic diversity (Griffing 1956). In the random effect model used in the analysis, it was assumed that no epistasis was involved and genes were distributed independently in the parents (Sughroue and Hallauer 1997). Parents were not included in combining ability analysis in order to obtain unbiased estimates of GCA and SCA parameters (Singh *et al.* 1992). General combining ability measured performance of crosses with several plants, and usually measured additive gene action. The relative importance of general and specific combining ability were estimated using the ratio of the GCA sum of squares and GCA plus SCA sum of squares to determine the relative importance of additive and nonadditive gene effects (Auld *et al.* 1983).

Mean values of traits in three groups of the parents were compared with six groups of the F₁ populations derived from diallel crosses among the parent groups by mean separation using least significant difference (SAS Institute 1992). Additive (σ^2A), dominant (σ^2D), and error (σ^2E) variance components were estimated using the Burow and Coors' program (Burow and Coors 1994). Broad and narrow sense heritabilities were determined according to Gibrel *et al.* (1982).

Results and Discussion

Trait expression in parent and progeny

Most progenies derived from various combinations of three parent groups had larger leaf area than the midparent values and their parents (Fig. 1). For example, the crosses between parent groups with large (36 cm²) and medium (29 cm²) leaf area produced progeny with mean leaf area of 37 cm², which was significantly ($P < 0.05$) larger than the midparent (32 cm²) value and their parents (Fig. 1). Similar distributions of leaf area were generally found in most progenies from the other crosses among and within parent groups. These data indicated that since leaf areas in progenies exceeded their parents and midparents, genetic effects for leaf area was not due to complete or partial dominance. If complete dominance effects were involved in leaf area, the values of leaf area should be skewed in the direction of parent values. Leaf area was regulated by additive and/or overdominance, or interactions of different loci.

Table 1. Plant characteristics of nine soybean genotypes used to determine the types of gene action and heritability for leaf area and other growth traits

Group of leaf area	Leaf area (cm ²)		Leaf shape ¹⁾ (ratio)		Maturity (day)	
	mean	range	mean	range	mean	range
Large						
Kochang-5	39.57	36.40–42.00	0.47	0.44–0.50	126	126–127
Poongsan	34.55	33.70–35.87	0.35	0.32–0.41	127	126–127
Iksan	33.31	31.32–34.15	0.64	0.63–0.67	119	118–119
Medium						
Iri-8	30.47	29.70–32.20	0.37	0.33–0.39	119	118–119
Iri-3	30.36	29.40–31.60	0.51	0.49–0.54	125	124–126
Camp	24.15	22.25–28.65	0.29	0.28–0.29	128	127–128
Small						
Eunha	21.08	20.05–21.50	0.34	0.31–0.38	119	118–119
Nattawa	16.13	13.80–18.10	0.42	0.41–0.45	110	110–112
Nattosan	9.85	6.10–14.75	0.53	0.50–0.55	90	89–90
LSD _{0.05}	2.82	–	0.01	–	6.62	–

¹⁾ The mean values for leaf shape were calculated by mean leaf width/mean leaf length.

Mean leaf shapes of the parent groups were significantly ($P < 0.05$) different (Fig. 1). Different distributions of leaf shape were observed in progenies from the crosses among parent groups and the values for leaf shape were smaller in most progenies than their midparents and parents. As shown in Fig. 1, for instance, the value for leaf shape was 0.43 in progenies from large×medium parent group, which was close to intermediate values between two parents, but smaller than large leaf shape parent with the value of 0.49.

This indicated that leaf shape in most progenies more skewed towards lanceolate than oval leaf shape. With the skewed distribution of leaf shape toward lanceolate in progenies, which was not shown in leaf area, days to flowering, and maturity, most progenies had similar values to the midparent, but were smaller than large parent values in leaf shape as crossed between lanceolate and others.

In reproductive traits, similar distribution of the days to flowering and maturity was found in progenies as observed

Fig. 1. Mean distribution for leaf and reproductive characteristics in three parent groups based on leaf area and six groups of the progeny from diallel cross. The mean values for leaf shape were estimated by mean leaf width/mean leaf length.

Table 2. Analysis of variance and tests of significance for leaf and reproductive characteristics in soybean

Source of variation	df	Mean squares				
		Leaf area	Leaf shape	Days to flowering	Flowering period	Maturity
Replication	2	11.85	0.003	0.01	2.38**	45.56
Crosses	35	263.77**	0.013**	54.96**	90.18**	329.40**
GCA	8	652.17**	0.044**	174.62**	273.64**	725.92**
SCA	27	148.69**	0.004**	19.51**	35.82**	211.91**
Error	70	19.40	0.001	0.05	0.26	72.75

** Significant at the 0.01 probability level.

in leaf area. The days to flowering were longer in progenies from all combinations of crosses among parents, except small leaf parents, than the midparent and their parents (Fig. 1). That is, progenies from large×large parent group had 64 days for flowering and were significantly ($P<0.05$) longer than the parents with mean days of 62 for flowering. Mean maturity was about 124 days in parents with large and medium leaf area, but 106 days in parents with small leaf area. Similar to the days to flowering, the days to maturity in all progenies were longer than the midparents and most progenies had longer maturity than their parents. These studies suggest that leaf shape among examined traits could be regulated more by additive than nonadditive interaction at chromosome loci, because leaf shape values were not greater than the midparents and their parent values.

Combining ability and types of gene action

As shown in Table 2, variance analysis shows that replication effects were significant ($P<0.01$) for only flowering period. Variation for leaf area, shape, and reproductive traits, was significant ($P<0.01$) among progenies from the diallel cross. General combining ability (GCA) and specific combining ability (SCA) were significant for all traits examined in this study and suggested both additive

and nonadditive gene effects for leaf and reproductive traits. Estimated ratios between mean squares of GCA and SCA were 0.89 for leaf area, 0.87 for maturity, and 0.96 for leaf shape. The magnitude of GCA relative to SCA effects suggested that additive gene action for leaf shape was more prevalent than nonadditive gene action, but additive effects were smaller for leaf area (0.89) than those for leaf shape in soybean (Baker 1978). Genetic gain for leaf area and shape would be possible through selection, because GCA effects were most important (Simon and Cordo 1998). Prevalence of additive effects for the traits indicated that recurrent selection would be most appropriate for population development (Boe and Ross 1991).

Comparison of GCA effects of individual parents for five traits is presented in Table 3. Different GCA effects were found in parents, especially for leaf area and leaf shape. Significantly ($P<0.01$) negative GCA effects were found for leaf area in all three parents within small leaf area group, while positive and significant ($P<0.01$) GCA effects were found in four of the six parents within the large and medium leaf area groups (Table 3). These suggested that the three parents with small leaf area and with negatively significant GCA effects for leaf area relatively combined well with all other parents, but negatively and tended to small

Table 3. Estimates of general combining ability effects for leaf and reproductive characteristics among crosses of nine different soybean genotypes

Parent Class	GCA Effects				
	Leaf		Reproduction		
	Area	Shape	Days to flowering	Flowering period	Maturity
Large					
Kochang-5	6.16**	0.030**	3.10**	-0.81**	4.61*
Poongsan	4.13**	0.050**	1.25*	1.72**	4.83*
Iksan	-0.55	0.070**	2.60**	-5.74**	-5.46*
Medium					
Iri-8	3.15**	-0.042**	0.39	-4.21**	-0.67
Iri-3	8.11**	0.045**	2.39**	0.15	4.33*
Camp	-6.69**	-0.028**	0.03	1.08**	4.68*
Small					
Eunha	-6.47**	-0.028**	-1.25*	-1.71**	-10.67**
Nattawa	-3.81**	0.021*	-2.68**	5.29**	3.97
Nattosan	-4.09**	0.013	-5.83**	4.22**	-5.60*

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

Table 4. Estimated ratios for the genetic and error variances, and heritabilities for growth characteristics in nine soybean genotypes

Traits	σ^2G		σ^2E (%)	h^2	
	σ^2 (%)	σ^2D (%)		Narrow (%)	Broad (%)
Leaf					
Area	52.7 ¹⁾	47.3	17.6	43.4	82.4
Shape	80.0	20.0	16.7	63.2	80.9
Reproduction					
Days to flowering	69.5	30.5	0.2	69.3	99.8
Flowering period	65.7	34.4	0.8	65.2	99.2
Maturity	51.3	48.7	43.3	29.1	56.7

σ^2A , σ^2D , and σ^2E are the additive, dominant, and error components of variance, respectively.

¹⁾ Ratios for σ^2A were calculated by $(\sigma^2A/\sigma^2G) \times 100$, where $\sigma^2G = \sigma^2A + \sigma^2D$ and for σ^2E by $(\sigma^2E/\sigma^2G + \sigma^2E) \times 100$.

leaf area of progenies from the crosses of parents with small leaf area with others. Parents with large and medium leaf area seemed to produce progeny populations with large leaf area when crossed between large leaf area parents and other parents (Table 3).

For leaf shape, all parents, except for Nattosan, had significant GCA effects, in which four of eight parents were positively significant ($P < 0.05$) and the rest was negatively significant ($P < 0.01$). Parents within large leaf area group had either significantly negative or positive GCA effects for leaf shape. Cultivar Iksan had the largest estimated GCA effects, whereas Poongsan had the smallest GCA effects for leaf shape. This suggested that considering only the leaf shape trait, Poongsan was a potential parent for crosses with other parents to produce populations with lanceolate leaf, even though this parent had the value of 0.35 for leaf shape, which was not the smallest for leaf shape under field conditions (Table 1). When leaf area and leaf shape were considered simultaneously to develop population for efficient selection, Camp and Eunha could be better parents for crosses to produce populations with small leaf area and lanceolate leaf shape because of relatively large and negative GCA effects for both traits (Auld *et al.* 1983, Das and Griffey 1994). Thus, a preponderance of negatively and positively sufficient GCA effects for most given parents suggests that leaf traits can be modified for optimum leaf area and shape in soybean populations by crossing parents with different leaf area and shape.

It has been reported that reproductive traits were closely related to high yielding cultivar development in soybean (Shibles *et al.* 1975, Egli *et al.* 1987). All six parents within large and medium leaf area groups had positive GCA effects for the days to flowering, but four of those were statistically significant (Table 3). All three parents with small leaf area had negatively significant GCA effect to the days for flowering similar to the leaf area trait. In flowering period, two parents within both large and medium leaf area groups had positively significant GCA effects, while two of three parents with small leaf area had positive and significant

GCA effects. Nattawa with small leaf area had the largest positive GCA effects for flowering period. For estimated maturity, Eunha and Nattosan within the small leaf area group had relatively large and significantly negative GCA effects ($P < 0.05$), but Poongsan with larger leaf area than others had the largest positive GCA effects for this trait. In contrast, Eunha with the largest negative GCA effects for maturity could be a better combiner to create populations with early maturity due to significant additive effects. Only Eunha had significantly negative GCA effects for all leaf and reproductive traits evaluated in this study. Camp had negative GCA effects for leaf traits, but had significantly positive GCA effects for flowering period and maturity (Table 3). These results indicated that Eunha as a parent combined relatively well with others and could produce progenies with traits such as small leaf area and lanceolate leaf, and early maturity. But, crosses of Camp possessing negative GCA effects for leaf traits with other parents would possibly make progenies with small and lanceolate leaf, and late maturity. Generally, the magnitude of the GCA effects were in agreement with their individual performance as parents (Fig. 1). Large GCA values would indicate uniform transmission of these traits by parents to their offspring.

Variance components and heritability

Table 4 indicates the estimated ratios of genetic (σ^2G) and experimental error (σ^2E) variances, and heritability for leaf and reproductive traits. Proportions of additive (σ^2A) to genetic (σ^2G) variances were from 51.3% to 80.0% for leaf and reproductive traits. In leaf traits, proportions of additive variance to genetic variance ($\sigma^2A + \sigma^2D$) were 52.7% and 80.0% for leaf area and leaf shape, respectively. Additive genetic effects for both leaf characteristics were more predominant than nonadditive effects, but leaf shape was relatively more affected by additive effects than leaf area (Table 4). This explains that gene effects for leaf shape could be more efficiently transferred as breeding value to new populations.

Narrow sense heritabilities were 43.4% for leaf area and 63.2% for leaf shape since the dominance variance component was larger in leaf area than leaf shape (Table 4). The larger nonadditive, including dominant, effects may interfere with a line selection in a breeding program because of non-fixed effects from generation to generation (Van Ginkel and Scharen 1988). The results from the analyses of genetic variance components for leaf traits were supported by the ratios of GCA and SCA (Table 2).

In reproductive traits, the proportion of additive variances to genetic variance components ranged from 51.3 to 69.5% for examined reproductive traits, whereas those of dominant variances ranged from 30.5 to 48.7% (Table 4). Additive variance proportion for the days to flowering was 69.5% of genetic variance and was larger than dominant variance. Similarly, flowering period had 65.7% to additive variance to genetic variance and was influenced mainly by additive effects as well as partly nonadditive effects with 34.4% to genetic variance (Table 4). The results indicated that additive gene effects for both traits, days to flowering and flowering period, were more predominant than dominant gene effects and these traits were less interacted with environments than maturity and were only slightly influenced by experimental errors among plants in plots (Table 4). A similar finding was reported by Singh *et al.* (1992) who reported days to flowering in chickpea (*Cicer arietinum* L.) was predominantly under additive inheritance and was highly predictable. Thus, narrow sense heritabilities were 69.3% and 65.2% for the days to flowering and flowering period, respectively. These relatively high narrow sense heritabilities are valuable for soybean breeders to develop new populations with traits of interest. Auld *et al.* (1983) found the predominance of additive effects valuable for the selection of individual lines to improve winterhardiness in the populations in peas (*Pisum sativum* L.).

Additive variance for maturity was 51.3% to genetic variance and was slightly larger than nonadditive. Even though the proportion of additive and dominant variances to the genetic variance were very similar for maturity, error variance for maturity was 43.3% of total variance components and the largest among examined traits (Table 4). Thus, narrow sense heritability was 29.1% for maturity. The variance component analysis suggested that maturity was more dependent upon various field environments including plant individual variation within plots and plot to plot variation than any other traits. This study suggested that genetic gain is possible through breeding programs for optimizing of leaf area and leaf shape related to photosynthetic rate and subsequently yield since the predominance of additive effects was true for leaf area and shape among populations.

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