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Gene Effects for Specific Leaf Area and Harvest Index in Peanut (*Arachis hypogaea* L.)

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Abstract: Breeding for drought resistance in peanut (*Arachis hypogaea* L.) has been done primarily based on empirical selection for yield under drought stress conditions, but progress has been slow. Selection for physiological traits that can contribute to superior performance of the crop under drought stress conditions may complement conventional approach and hasten the progress. Specific leaf area (SLA) and Harvest index (HI) are physiological traits that could be used for this purpose. For the choice of an efficient breeding procedure, a good knowledge on the types of gene action controlling the expression of these two traits is needed. This study was conducted to examine the various gene effects for SLA and HI in three crosses of peanut (ICGV 86388 x IC 10, ICGV 86388 x KK 60-1 and IC 10 x KK 60-1). Seven generations of individual crosses (parents, F_1, F_2, F_3, $BC_{11}S$ and $BC_{12}S$) were grown in a group balance block experiment with six replications. Data were analyzed following a generation means analysis. The results showed that additive gene effects were predominant in determining the expression of SLA and HI in all the three crosses, accounting for 80-95% of total genetic variability for SLA and 63-73% for HI. Dominant gene effect for SLA was significant in one cross but its contribution was very small. Significant additive x dominant epistatic effects were also observed for SLA in all crosses, but additive x additive and dominant x dominant gene effects were significant in one cross each. Significant epistatic gene effects for HI were also detected in two crosses but largely being additively x additive which is fixable. The predominance of additive gene effects for SLA and HI suggested that selection for the two traits in these crosses would be effective even in early segregating generations.

Key words: *Arachis hypogaea*, gene effects, generation means analysis, Specific Leaf Area (SLA), Harvest Index (HI)

INTRODUCTION

Peanut is an important legume crop of the world. It is grown on some 26 million ha with an annual production of about 35 million tons. Developing countries account for 97% of the world peanut area and about 94% of total production[1]. In developing countries, peanut is mostly grown under rainfed conditions and drought has been identified as a major limit to its productivity[2]. In many areas, access to irrigation is either limited or too costly and breeding for drought resistance has been sought as a low-cost avenue to overcome this constraint in the long run[3].

The traditional approach to breeding peanut cultivars for drought resistance has been empirical, via selection for yield under drought stress conditions. Such an approach is both prolonged and expensive, requiring massive plant populations[4] and progress has been slow[5,6]. It is believed that more rapid progress can be aided by a prior knowledge of the physiological basis of crop performance under drought conditions[7,8]. This strategy involves breeding for superior performance under drought conditions by identifying reliable physiological traits contributing to drought resistance to complement conventional breeding programs[4].

It has been well established that water use efficiency (WUE) is a trait which could contribute to improved productivity under drought conditions[9,10]. However, accurate measurement of WUE is difficult, time-consuming and expensive. In peanut, carbon isotope discrimination (Δ) was found to be well correlated negatively with WUE in diverse peanut cultivars both in the grasshouse[11,12] and in the field[13,14]. This trait was shown to be highly heritable and has small genotype by environment interaction, raising the possibility of its use in selection for drought resistance[12]. However, its measurement is also expensive and requires mass spectrometer which is costly and normally not available in developing countries. Several studies have shown that Specific leaf area (SLA) was extremely well correlated with WUE and Δ over a wide range of cultivars and environments[13-16]. SLA is simple and inexpensive to

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measure, thus, has been suggested to be used as a rapid selection index for high WUE in peanut, particularly in developing countries where mass spectrometry facilities are not available[14].

Harvest index (HI) is also directly related to yield as it represents the proportion of total biomass partitioned into grain. Increased HI has been a major factor in the improvement of grain yield in many crops[17-19]. It is a useful trait to assess progress in improving crop yield potential[20] and is relatively easy to measure a large number of plants. In peanut, high WUE and HI can lead to improvement in crop yield[21,22]. Nigam *et al.*[6] reported that selection based on a combined index of HI, WUE and water transpired (T) was effective in improving yield of peanut under drought stress conditions. However, the selection efficiency of the physiological trait-based selection was higher than the yield-based empirical selection under late-season drought stress conditions but lower under the condition of mid-season drought stress. They suggested that the integration of physiological traits in the selection scheme would be advantageous in selecting genotypes which are more efficient water utilizers or partitioners of photosynthates into economic yields for water-limited environments.

To formulate an appropriate breeding strategy for a particular trait, a good understanding of its inheritance is required. However, very few studies on the genetic control of SLA and HI in peanut have been reported. Jayalakshmi *et al.*[23] found in their diallel study involving seven peanut lines that SLA is governed by additive gene effects. Makne[24] reported a non-additive genetic variance for HI but Dwivedi *et al.*[25] found that general combining ability effects were predominant for the expression of this trait. Nigam *et al.*[2] investigated the inheritance of SLA and HI in three peanut crosses using a generation means analysis. They reported that additive gene effects were far more important than dominance gene effects in the inheritance of SLA and HI, although non-additive gene effects were detected for both traits. More empirical evidences are still needed to firmly establish the types of gene action governing the expression these two traits in peanut. The objective of the present study was to determine gene effects for SLA and HI in three peanut crosses. Information obtained will be useful in formulating an appropriate breeding strategy for drought resistance in peanut.

MATERIALS AND METHODS

Plant materials: Three peanut genotypes varying in SLA (ICGV 86388, IC 10 and KK 60-1) were selected for used as parents to generate populations in different generations in this study. ICGV 86388 is a line from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) that has low SLA. IC 10 is a line with moderate SLA that was derived from Robut 33-1 x NC Ac 2214 and KK 60-1 is a released cultivar in Thailand with high SLA. These genotypes were crossed in all combinations excluding reciprocals, giving a total of three crosses. The F_1 seeds of each cross were divided into two parts. One half was selfed to generate F_2 and further filial generations. The second half was backcrossed to both parents and the BC_{11} and BC_{12} were selfed to produce $BC_{11}S$ and $BC_{12}S$. For each cross, seven populations (P_1, P_2, F_1, F_2, F_3, $BC_{11}S$ and $BC_{12}S$) were available.

Field experiment: All populations were evaluated in a field experiment conducted during the 2002 postrainy season at the Field Crop Research Station of Khon Kaen University in Northeast Thailand (16°28'N, 102°48'E, 200 m above mean sea level). A group balance block design with six replications was used. The three crosses formed three treatment-groups and the seven populations of each cross were treatments within each group. In a replicate, each of the non-segregating populations (parents and F_1s) was sown in one row (20 plants), while each F_2 was sown in eleven rows (220 plants) and each F_3, $BC_{11}S$ and $BC_{12}S$ was planted in four rows (80 plants). Each row was 5 m long, with 20 cm spacing between plants and 50 cm between rows. The experiment was well managed to avoid stresses from nutrients, pests, diseases, weeds and water as much as possible. Applications of soil amendments and control managements of weeds, pests and diseases were the same as described in Banterng *et al.*[26] Crop was adequately irrigated at weekly intervals, totaling 11 applications.

Measurement of SLA was done on every plant in each plot at 70 days after planting. A fully expanded leaf on the main axis of each plant at the second nodal position below the apex was collected for SLA determination following the procedure described in Nigam *et al.*[2] except a leaf area meter (Hayashi Denkoh AAC-400, Tokyo, Japan) was used in leaf area measurement. At maturity, every plant in each plot was harvested separately. Pods were detached from the plant and the two parts were oven-dried separately. HI was calculated as a ratio of pod weight to total biomass.

Genetic analysis: For each cross, means and variances for SLA and HI of each generation were calculated from individual plant data. For each character, a generation means analysis was separately conducted for each cross to determine additive, dominant and epistatic gene effects following Mather and Jinks[27] using their coefficients for

different generations based on F-infinity metric. The notation of Gamble[28] was used, i.e. m, a, d, aa, ad and dd, where m = mean, a = sum of additive gene effects, d = sum of dominance gene effects, aa = sum of additive x additive gene effects, ad = sum of additive x dominance gene effects and dd = sum of dominance x dominance gene effects. The joint scaling test[29] was also performed to provide the best estimates of the genetic parameters. As the various generation means did not have equal variances, they were weighted using the inverse of the variance[2]. The regression analysis was used to find the best-fit model as suggested by Torres *et al.* [30] including the parameters m, a, d, aa, ad and dd sequentially. Any effect that was not significant at the 5% level of probability was omitted from the model. Finally, only significant parameters were fitted using the weighted least squares method as described by Rowe and Alexander[31]. The x^2 test proposed by Mather and Jinks[27] was not done because only P_1, P_2 and F_1 generations were independent and addition of other generation mean values inflated the x^2 test[30]. The relative importance of different gene effects was estimated by partitioning the regression sum of squares of the best-fit model into individual parameters, each with one degree of freedom. Percentages of the total regression sum of squares attributable to individual gene effects were calculated to indicate their relative contribution to the variations in SLA and HI among different generations of the crosses.

RESULTS AND DISCUSSION

Significant differences among generation means for SLA were observed in all three crosses (Table 1), indicating genetic diversity in these crosses for this character. The line ICGV 86388 had the lowest SLA value, with an average over two crosses of 150.0 $cm^2\ g^{-1}$. The line IC 10 was intermediate (mean of two crosses = 182.2 $cm^2\ g^{-1}$) and the cultivar KK 60-1 had the highest SLA value (mean of two crosses = 200.55 $cm^2\ g^{-1}$). Thus, the difference between parental lines was greatest in the cross ICGV 86388 × KK 60-1 (low × high), intermediate in the cross ICGV 86388 × IC 10 (low × intermediate) and smallest in the cross IC 10 × KK 60-1 (intermediate × high). The F_1 mean was about the same as the mid-parent value in the low × high cross, but was slightly more in the low × intermediate cross and slightly less in the intermediate × high cross. The more or less average performances of the F_1 hybrids relative to their parents suggested a large contribution of additive gene effects for this character. The F_2 means were slightly higher than their corresponding F_1 means in all three crosses, but the F_3 mean was slightly lower than the corresponding F_2 mean in one cross, slightly higher in one cross and about the same in one cross. The backcross selfed means ($BC_{11}S$ and $BC_{12}S$) were higher than the F_1 means but lower than the means of their respective high parents in the crosses ICGV 86388 x KK 60-1 and IC 10 x KK 60-1 and were about the same as the F_1 mean in the cross ICGV 86388 x IC 10. These variable results suggested the present of non-additive gene effects for SLA in these crosses at varying relative importance.

Additive gene effects were significant ($p<0.01$) in all three crosses (Table 2), however, the dominant gene effect was significant ($p<0.05$) only in the low x high cross (ICGV 86388 x KK 60-1). The negative sign of the

Table 1: Means and standard errors of different generations for SLA in three crosses of peanut

Generation[a]	ICGV 86388 x KK 60-1 ($cm^2\ g^{-1}$)	ICGV 86388 x IC 10 ($cm^2\ g^{-1}$)	IC 10 x KK 60-1 ($cm^2\ g^{-1}$)
P_1	148.8±0.47[b]	151.1 ±0.18[b]	178.6±0.52[c]
P_2	200.6±0.66[d]	185.7±0.94[c]	200.5±0.69[d]
F_1	175.5±0.60	172.3±0.92	186.5±0.71
F_2	179.1±1.22	177.2±1.11	190.4±1.09
F_3	176.5±1.21	179.3±1.37	190.3±1.14
$BC_{11}S$	178.1±1.11	173.0±1.25	187.3±1.07
$BC_{12}S$	181.9±1.34	171.2±1.39	191.1±0.97
MP	174.7	168.4	189.5

[a] P_1 = Parental line 1, P_2 = Parental line 2, F_1 = First filial generation of crosses, F_2 = Second filial generation of crosses, $BC_{11}S$ = First backcross generation with parental line 1 selfed, $BC_{12}S$ = First backcross generation with parental line 2 selfed and MP = Mid-parent value
[b] ICGV 86388 with a mean over two crosses of 150.0 $cm^2\ g^{-1}$
[c] C 10 with a mean over two crosses of 182.2 $cm^2\ g^{-1}$
[d] KK 60-1 with a mean over two crosses of 200.55 $cm^2\ g^{-1}$

Table 2: Estimates of different gene effects for SLA in three crosses of peanut

Gene effect[a]	ICGV 86388 x KK 60-1[b]	ICGV 86388 x IC 10[b]	IC 10 x KK 60-1[b]
m	174.74±0.40**	174.96±0.56**	189.03±0.30**
a	25.23±0.41**	17.27±0.62**	10.81±0.42**
d	-19.76±3.46*	NS	NS
aa	NS	6.72±0.86**	NS
ad	-90.54±7.06**	-75.41±7.85**	-27.78±5.99**
dd	19.02±3.40**	NS	NS

[a] m = Mean, a = Sum of additive effects, d = Sum of dominance effects, aa = Sum of additive x additive epistatic effects, ad = Sum of additive x dominance epistatic effects, dd = Sum of dominance x dominance epistatic effects.
[b] ** significant at $p<0.01$, *significant at $p<0.05$, NS = Non significant.

Table 3: Variability (%) accounted for by different gene effects for SLA in three crosses of peanut

Gene effect [a]	ICGV 86388 x KK 60-1[b]	ICGV 86388 x IC 10[b]	IC 10 x KK 60-1[b]
a	94.90	79.84	94.29
d	0.06	NS	NS
aa	NS	7.53	NS
ad	4.20	10.02	3.18
dd	0.70	NS	NS

[a] a = Sum of additive effects, d = Sum of dominance effects, aa = Sum of additive x additive epistatic effects, ad = Sum of additive x dominance epistatic effects, dd = Sum of dominance x dominance epistatic effects.
[b] NS = Non significant.

dominance gene effect indicated that it was contributed by the genes from the high parent (KK 60-1). Significant epistatic gene effects were observed in all three crosses, but at varying degrees. The additive x dominance and dominance x dominance epistatic effects were significant in the cross ICGV 86388 x KK 60-1 (low x high), while the additive x additive and additive x dominance epistatic effects were significant in the cross ICGV 86388 x IC 10 (low x medium). For the medium x high cross (IC 10 x KK 60-1), only the additive x dominance epistatic effect was significant (Table 2). Nigam *et al*.[2] also found significant additive gene effects for SLA in all three crosses that they studied, but obtained significant dominant gene effects in both the high x low and the intermediate x low crosses. As in this study, the additive x dominant and dominant x dominant gene effects were significant in the high x low cross. However, significant epistatic gene effects in the intermediate x low and high x intermediate crosses differed somewhat from this study. In these two crosses, all epistatic gene effects were found significant except the additive x dominant gene effect in the intermediate x low cross.

Examination of the relative contributions of different gene effects for SLA revealed that additive gene effects were predominant in all three crosses, accounting for 80-95% of total genetic variability (Table 3). The contribution of the dominance gene effect in the cross ICGV 86388 x KK 60-1, though significant, was very small (0.06%). All epistatic gene effects that were significant in each cross also accounted for only a small portion of total genetic variability. The predominance of additive gene effect for SLA observed in this study was in good agreement with those of Jayalakshmi *et al*.[23] and of Nigam *et al*.[2]. Small contributions of dominance and epistatic gene effects were also in line with the study of Nigam *et al*.[2], although they observed a considerable contribution of the additive x dominant gene effect in one cross.

Significant differences among generation means were also obtained for HI in all three crosses (Table 4). For this character, ICGV 86388 also had the lowest value (mean HI = 0.315), with IC 10 being the intermediate parent (mean HI = 0.455) and KK 60-1 being the high parent (mean HI = 0.485). The F_1 means were similar to their corresponding mid-parent values in two crosses (ICGV 86388 x IC 10 and IC 10 x KK 60-1), but was greater in the cross ICGV 86388 x KK 60-1. The F_2 and F_3 means were close to the F_1 means in all three crosses, as were the backcross selfed means ($BC_{11}S$ and $BC_{12}S$). These results suggested a predominance of additive gene effect for HI in all the crosses.

Estimates of different gene effects for HI (Table 5) showed significant additive gene effects in all three crosses and significant additive x additive and additive x dominance epistatic gene effects in two crosses (ICGV 86388 x KK 60-1 and ICGV 86388 x IC 10). However, no dominance or dominance x dominance gene effect was detected in any of the crosses. It was noted that only the additive gene effect was significant in the intermediate x high cross (IC 10 x KK 60-1) presumable because of a small difference between of the two parents in their HI values (0.45 and 0.49).

Contributions accounted for by different gene effects for HI showed the largest contribution of additive gene effect in all three crosses, ranging from 63-76% (Table 6). The additive x additive gene effect accounted for 21% in the cross ICGV 86388 x KK 60-1 and 11% in the cross

Table 4: Means and standard errors of different generations for harvest index (HI) in three crosses of peanut

Generation[a]	ICGV 86388 x KK 60-1	ICGV 86388 x IC 10	IC 10 x KK 60-1
P_1	0.32±0.006[b]	0.31±0.004[b]	0.45±0.005[c]
P_2	0.48±0.005[d]	0.46±0.005[c]	0.49±0.007[d]
F_1	0.44±0.005	0.40±0.005	0.47±0.005
F_2	0.45±0.005	0.43±0.004	0.45±0.005
F_3	0.46±0.006	0.43±0.005	0.45±0.007
$BC_{11}S$	0.41±0.007	0.43±0.006	0.46±0.007
$BC_{12}S$	0.46±0.007	0.40±0.006	0.46±0.008
MP	0.40	0.39	0.47

[a] P_1 = Parental line 1, P_2 = Parental line 2, F_1 = First filial generation of crosses, F_2 = Second filial generation of crosses, $BC_{11}S$ = First backcross generation with parental line 1 selfed, $BC_{12}S$ = First backcross generation with parental line 2 selfed and MP = Mid-parent value.
[b] ICGV 86388 with a mean over two crosses of 0.315.
[c] IC 10 with a mean over two crosses of 0.455.
[d] KK 60-1 with a mean over two crosses of 0.485.

Table 5: Estimates of different gene effects for harvest index (HI) in three crosses of peanut

Gene effect[a]	ICGV 86388 x KK 60-1[b]	ICGV 86388 x IC 10[b]	IC 10 x KK 60-1[b]
m	0.449±0.003**	0.423±0.002**	0.449±0.002**
a	0.081±0.004**	0.076±0.003**	0.018±0.004**
d	NS	NS	NS
aa	0.052±0.005**	0.036±0.004*	NS
ad	-0.124±0.043**	-0.435±0.037**	NS
dd	NS	NS	NS

[a] m = Mean, a = Sum of additive effects, d = Sum of dominance effects, aa = Sum of additive x additive epistatic effects, ad = Sum of additive x dominance epistatic effects, dd = Sum of dominance x dominance epistatic effects.
[b] ** significant at $p<0.01$, *significant at $p<0.05$, NS = Non significant.

Table 6: Variability (%) accounted for by different gene effects for harvest index (HI) in three crosses of peanut

Gene effect[a]	ICGV 86388 x KK 60-1[b]	ICGV 86388 x IC 10[b]	IC 10 x KK 60-1[b]
a	76.41	67.80	62.83
d	NS	NS	NS
aa	21.04	11.12	NS
ad	1.56	17.38	NS
dd	NS	NS	NS

[a] a = Sum of additive effects, d = Sum of dominance effects, aa = Sum of additive x additive epistatic effects, ad = Sum of additive x dominance epistatic effects, dd = Sum of dominance x dominance epistatic effects.
[b] NS = Non significant.

ICGV 86388 x IC 10. Both additive and additive x additive gene effects are fixable. These two types of gene effects accounted for almost all of total genetic variance in these crosses, leaving a small portion to the additive x dominance gene effect that is non-fixable. No dominance or dominance x dominance gene effect was detected in any of the crosses. These results were in agreement with the study of Dwivedi *et al.*[25] in which general combining ability effects for the expression of HI were observed. Nigam *et al.*[2] also reported a predominance of additive gene effects for HI, though significant dominance and dominance x dominance gene effects were observed some crosses.

Results from this study, thus, indicated the predominance of additive gene effects for both SLA and HI, with non-additive gene effects playing a minor role or non-significant. These results were based on data from only one season and might be biased to some extent by genotype x environment interactions. However, our study in another set of genotypes grown in three planting dates in two years (data unpublished) showed a much smaller contribution of genotype x environment interactions to total variance compared to that of the genotypes for both SLA and HI. With the overwhelming predominance of additive gene effects obtained in this study for both characters, it was expected that the results would still be the same even when genotype x environment interactions are taken into account. It was concluded that gene effects governing the inheritance of both SLA and HI were largely additive and that selection for high SLA and HI values in these crosses would be effective even in early generations.

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