

# Inheritance of Leaflet Size in Peanut (*Arachis hypogaea* L.)<sup>1</sup>

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## ABSTRACT

Leaves are the main site of photosynthesis in plants. Leaf size and shape have been shown to be related to disease resistance. Therefore, understanding the inheritance of traits related to them is important. Conflicting results have been reported on the inheritance of leaflet size in peanut (*Arachis hypogaea* L.). Some indicate qualitative inheritance and others quantitative determination. This study was undertaken to examine the genetic factors which control leaflet size in peanut. F<sub>2</sub> populations from a modified diallel (excluding self-crosses) with three parents, *A. monticola* and two *A. hypogaea* genotypes (Argentine and T2442), were used in this experiment. In contrast with previous studies, the measurement technique used took into account the within-plant variability which occurs for this trait. Results suggest that: a) leaflet size may be quasi-quantitatively inherited; i.e., its inheritance may present distinguishable genotypes within continuous variation; b) the inheritance of leaflet size may involve two types of alleles of which one would be responsible for large leaflet size, while the other would be responsible for small leaflet size; and c) the use of progressive measurement scales and the analysis of ungrouped data are advisable on genetic studies of some morphological traits in peanut.

Key Words: Groundnut, qualitative inheritance, quasi-quantitative inheritance.

Most morphological traits are reported as qualitatively inherited in peanut (*Arachis hypogaea* L.) (Wynne and Coffelt, 1982). However, some traits have been reported to be quantitatively determined, such as branching pattern (Wynne 1975) and leaflet size (Badami 1928). Although not explicitly reported as quantitative traits, leaflet length and breadth, fruit length, main axis height, characteristics of some flower parts, and number of internodes have been treated as such (Ashri, 1968; Bhide and Desale, 1970; Emery *et al.*, 1964; Mouli *et al.*, 1984; Sandhu and Khehra, 1983).

Leaves are the main site of photosynthesis in plants. Leaf size and shape have been associated with disease resistance in peanut (Coffelt and Porter, 1982). Conflicting results have been reported on the inheritance of leaflet size in peanut. Bhide and Desale (1970) and Matlock *et al.* (1970) reported single-gene control of the trait, while Ashri (1970) found small leaflet size to be controlled by two duplicate genes. He postulated the occurrence of modifiers to explain the variation among plants. However, Sandhu and Khehra (1983), who measured leaflet length and breadth, found

significant epistatic components for both traits. Badami (1928) suggested that leaflet size may be quantitatively inherited.

Thus, some have indicated qualitative inheritance and others quantitative determination. This study was undertaken to examine the genetic factors which control this trait in peanut.

## Materials and Methods

F<sub>2</sub> populations were evaluated from a modified diallel (excluding self-crosses) with *A. hypogaea* genotypes, Argentine and T2442, and *A. monticola* Krap et. Rig. [PI 405933 (K726Y)], as parents. Argentine is a spanish-type peanut which has normal nodulation, an erect growth habit, large leaflets, and green stems with a purple shade at times. T2442 is a non-nodulating genotype with an erect growth habit, medium size leaflets, and green stems with an inconsistent purple shade. *A. monticola*, a wild tetraploid species, differs from *A. hypogaea* by its biarticulated fruits. *A. monticola* has a spreading growth habit, small leaflets, purple-colored stems, and apparently normal nodulation. PI 405933 was one parent of the cultivar Spancross (Hammons 1970).

Besides environmental factors such as shade and pests influencing leaflet size, it varies within peanut plants depending on leaf age and position on the plant. Developing leaflets located at tips of branches and early developed leaflets located at the base of stems are generally smaller than fully developed and mid-aged ones located in the middle of the canopy. The developing leaflets are generally slightly green, the fully developed dark green, and those in the middle of the canopy intermediate in color. The area covered by a peanut plant may be visually subdivided into three concentric areas when observed from the top: the central area "a" representing the main stem, the external area "c" the outer lateral branches and outer secondary branches, and area "b" falling between "a" and "c."

The rating of individual plants in our experiment was based on the size of fully developed leaflets in each of the three concentric areas. The contrasting intermediate color of fully developed leaflets, as compared to the color of younger and older leaflets, made such a grading technique feasible. Leaflets to be graded were classified into three sizes (large, medium, and small, represented by letters 'l', 'm', and 's', respectively). A three-lettered grade was assigned to each plant. Each letter represented the predominant size of fully developed leaflets in one of the concentric areas. The three letters 'l', 'm', and 's' were assigned numeric values of 0, 1, and 2, respectively. These three numbers were summed to give the final grade of the plant, which ranged from 0 for 'lll', to 6 for 'sss' (Table 1). No combination including 'l', 'm', and 's' was encountered in a single plant with this grading technique. This method of measurement took into account the within-plant variability reported above for leaflet size in peanut. *A. monticola* was classified as 'sss', Argentine as 'lll', and T2442 as 'mmm'. Sample size for the six F<sub>2</sub> populations varied from 232 to 642 plants.

Homogeneity tests were performed using chi-squares computed on contingency tables contrasting reciprocal crosses from each pair of parents. Each numerical value (0 to 6) constituted a distinctive phenotypic class in the contingency tables. Grouping of neighboring phenotypic classes was made whenever necessary to avoid class expected frequencies less than 5 in contingency tables used for chi-square tests. Skewness and kurtosis tests were performed on each F<sub>2</sub> population to check departure from normality. Sample estimates of the coefficients of skewness (g<sub>1</sub>) and kurtosis (b<sub>2</sub>) and

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Table 1. Grading scale for leaflet size in peanut.

Grade	lll†	llm	lmm	mmm†	mms	mss	sss†
Numerical value	0	1	2	3	4	5	6

† lll = classification of Argentine parent plants; mmm = classification of T2442 parent plants; and sss = classification of *A. monticola* parent plants grown in field with F<sub>2</sub> populations.

of the amount of kurtosis ( $g_2$ ), were computed as follows for each  $F_2$  population (Snedecor and Cochran 1980):

$$g_1 = m_3 / (m_2 * \sqrt{m_2})$$

$$b_2 = m_4 / m_2^2$$

$$g_2 = b_2 - 3$$

Where

$$m_2 = \text{Sum of } f_i * (X_i - m)^2$$

$$m_3 = \text{Sum of } f_i * (X_i - m)^3$$

$$m_4 = \text{Sum of } f_i * (X_i - m)^4$$

$f_i$  = Number of observations in the  $i^{\text{th}}$  class/total number of observations

$X_i$  = Numerical value of the  $i^{\text{th}}$  phenotypic class

$m$  = Sum of  $f_i * X_i$  = the numerical value mean

$i = 1, 2, 3, \dots, 7$ .

A transformation ( $X_i = x_i + 1$ , where  $x_i$  represented the numerical value for the  $i^{\text{th}}$  phenotypic class for a given population) was adopted to avoid a numerical value equal to zero for grade 'III', which would have biased population mean values. Significance levels were given for  $g_1$  and  $b_2$  only. The skewness sign was indicated by the one of  $g_1$ . Lepto-kurtosis and platy-kurtosis were respectively indicated by a positive or a negative sign of  $g_2$ .

### Results and Discussion

$F_2$  distributions for leaflet size of the six crosses were all unimodal and continuous in variation (Fig. 1). According to Allard (1960), continuous variation of a trait can be caused by low heritability or by a large number of genes. Plants of each cultivar grown in the same plot as the  $F_2$  populations were classified as 'III', 'mmm', and 'sss', for Argentine, T2442, and *A. monticola*, respectively, using our rating technique (Table 1). Since there was virtually no variation within each of the three-parent cultivars for leaflet size as measured in this experiment, which, we presumed, meant that environmental variation was negligible, the second hypothesis is more likely to be correct, i.e., leaflet size may be determined by many genes with cumulative effects.

Variable distribution shapes were observed including an i-shape for the population from the cross between T2442 and Argentine, a leptokurtic distribution for the population from the cross between T2442 and *A. monticola*, and asymmetrically bell-shaped distributions for the other populations (Fig. 1). Results of kurtosis and skewness tests (Table 2) confirmed variable distribution among the populations. Skewness tests were significant in populations of five out of the six crosses tested, while four and one tested negative and positive, respectively, for kurtosis. One of two hypotheses, or both, may explain this variability of shapes in these population distributions. First, the populations from different parental combinations might possess different allele frequencies. This might be observed when each pair of parents, as a whole, possess unequal allele frequencies.  $F_2$  populations resulting from such a pair of parents would present asymmetrical or i-shaped distributions, assuming additivity in all loci, no epistasis, and independent factors. Second, non-additive relationships (dominance and/or epistasis) may exist within and/or among some loci. Such relationships can induce asymmetry and kurtosis in  $F_2$  populations. Sandhu and Khehra (1983) found significant epistatic components for leaflet length and leaflet breadth in peanut.

Homogeneity chi-squares among reciprocal-cross populations were significant in all crosses (Table 3), suggesting that extra-nuclear factors might be involved in determining leaflet size in peanut. Extra-nuclear factors have been reported in peanut for growth habit (Ashri, 1970; Ashri,

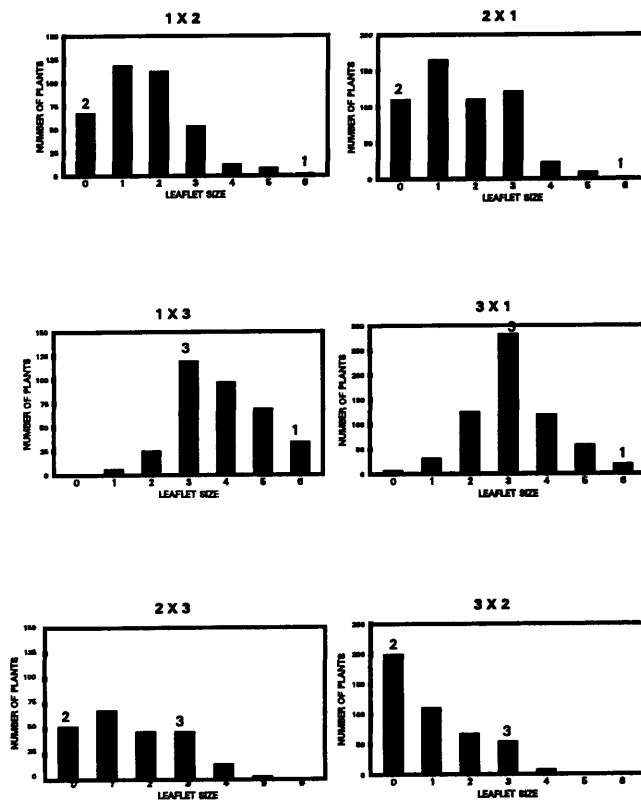


Fig. 1. Distributions of  $F_2$  reciprocal populations from crosses among *A. monticola* (1), Argentine (2), and T2442 (3) for leaflet size.

Table 2. Results of skewness and kurtosis tests on  $F_2$  population distributions from reciprocal crosses among two peanut cultivars and *A. monticola*.

Cross†	n‡	$g_1$	$b_2$	$g_2$
1 x 2	372	0.65**	3.19	0.19
2 x 1	540	0.60**	2.98**	-0.02
1 x 3	350	0.11	2.50**	-0.50
3 x 1	642	0.30**	3.35*	0.35
2 x 3	232	0.47**	2.42*	-0.58
3 x 2	438	0.81**	2.48**	-0.52

† : 1 = *A. monticola*

2 = Argentine

3 = T2442

‡ : n = sample size

\*, \*\* = significant at 0.05 and 0.01 levels, respectively.

1976; Ressler and Emery, 1978; Essomba and Coffelt, 1992), pod constriction (Coffelt and Hammons, 1974), branching pattern (Patil and Mouli, 1975), stipule shape (Mouli and Patil, 1975), stem color (Essomba *et al.*, 1991), calcium concentration (Crompton *et al.*, 1979), and resistance to leafspot disease (Coffelt and Porter, 1986; Kornegay *et al.*, 1980). Reciprocal crosses were not compared in some studies on leaflet size (Ashri, 1970; Bhide and Desale, 1970; Matlock *et al.*, 1970; Sandhu and Khehra, 1983). It is possible that extranuclear factors influenced the relationships within and/or between some nuclear genes involved in the inheritance of leaflet size in this experiment.

Transgressive individuals were observed in crosses between T2442 and the other parents (Fig. 1). Their occurrence

**Table 3. Homogeneity tests for leaflet size among  $F_2$  reciprocal-cross populations having *A. monticola*, and two *A. hypogaea* cultivars (Argentine and T2442) as parents.**

Cross	$\chi^2$	df	P-value
<i>A. monticola</i> x Argentine	30.38	5	0.001
<i>A. monticola</i> x T2442	124.18	5	0.001
Argentine x T2442	70.14	5	0.001

supports the hypothesis that the three parents differ in allele frequencies as discussed above.  $F_2$  transgressive individuals under such circumstances would have been recombinant individuals having more homozygous loci for one type of allele than one of the parents, assuming complete additivity. Recombinant individuals having a phenotype transgressing the grading scale could not have been graded. This may explain why all transgressive individuals were observed only in crosses having T2442 as a parent, the parent with the intermediate phenotype.

Two reasons may explain the diversity of results reported in the literature for the inheritance of leaflet size in peanut. The first is that leaflet size may be quasi-quantitatively inherited. Quasi-continuous variation (Gruneberg, 1952), or quasi-quantitative inheritance (Stanfield, 1983), is or involves a continuous variation with distinguishable genotypes. Quasi-quantitative inheritance may result from various situations including a) oligogenes with cumulative effects, b) polygenes having threshold effects, and c) a mixture of oligogenes and polygenes. Results obtained in this experiment could not rule out any of these three hypotheses.

However, under the first hypothesis, monogenic (Bhide and Desale, 1970; Matlock *et al.*, 1970); digenic (Ashri, 1970); and quantitative control (Badami, 1928) might have been observed in situations where pairs of parents had all identically homozygous loci except for one, two, or more loci, respectively. A case of identical homozygous loci in pairs of parental lines, which resulted in two heterozygous loci in each  $F_1$  population instead of three (i.e., less recombined genotypes in  $F_2$  than expected) as should have been expected, has been reported by Ashri (1976) for growth habit. A case of a homozygous recessive locus in two parents has been reported for stem pigmentation (Branch *et al.*, 1982).

Two facts reported by other workers favor the third hypothesis. The easy responsiveness of leaflet size to mutations in peanut (Ashri and Goldin, 1965; Bhide and Desale, 1970; Gregory, 1968) and the among-plant variation reported by Ashri (1970) both suggest that leaflet size is controlled by one or two major genes plus additional polygenes. Major genes would explain why the trait mutates so easily, while polygenes would explain the continuous variation observed in some populations. The simultaneous response of leaflet size and other traits to many mutations would mean, under such circumstances, that the major gene(s) involved may be pleiotropic.

The second reason for the diversity of reported results on the inheritance of leaflet size in peanut may be the disparity of techniques for measuring leaflet size. Ashri (1970),

Bhide and Desale (1970), and Sandhu and Khehra (1983) sampled single leaflets within the plant. The whole plant was evaluated in this experiment. Some morphological traits present a within-plant variability besides the genetic and the environmentally-related variabilities. This variability can be attributed to the physiology of the plant, such as age, growth, plant part development, etc. Despite that variability, different cultivars grown in the same environment may still present a remarkable consistency in their phenotype, allowing a clear-cut classification. Leaflet size is an example of such traits. The within-plant variability is controllable by use of measurement techniques that evaluate the whole plant and avoid within-plant subsampling. The three-lettered grade used in this experiment on individual plants is an example of such a measurement technique. Furthermore, such techniques are easily applicable to large populations, which also add reliability to the results obtained.

The case of quasi-quantitative inheritance reported on leaflet size in this experiment may not be unique. Quasi-quantitative traits are mainly recognizable by the existence of more than two stable phenotypes (Gruneberg 1952), and characteristics mixing features of both qualitative and quantitative traits resulting in conflicting results as to the type of inheritance involved. Many traits in peanut, such as growth habit, pod constriction, and pod and seed sizes, present more than two stable phenotypes. All of them have been reported to be determined by two or more genes (Wynne and Coffelt 1982).

Two reasons may explain why traits which are quantitative may have been classified as qualitative traits: a) the grouping of phenotypes in two or a few phenotypic classes, and/or b) the use of related parental lines in studies reported on these traits. A common practice in studies on morphological traits is to classify  $F_2$  populations from parental lines into as few as possible phenotypic classes to accommodate the use of chi-square tests. Such a grouping may indeed cover-up a continuous variation in some cases. The use of progressive measurement scales, a graphical analysis of ungrouped data, and the use of skewness and kurtosis statistics whenever necessary, may therefore be advisable to avoid any misinterpretation or incomplete analysis. The use of related parental lines (having one or more homozygously identical loci for the trait) may also lead to the classification of quasi-quantitative traits as qualitative traits. This last observation underlines the importance of studying morphological traits with crosses among widely divergent germplasm in *A. hypogaea* as the minimum, and intercrosses among the progenitor species when their identification is confirmed. These types of crosses are more likely to span the whole variability of these traits in their progenies; and therefore, allow the best understanding of their genetics. *A. monticola*, which is highly compatible with *A. hypogaea*, may prove to be useful for this purpose.

### Literature Cited

- Allard, R. W. 1960. Principles of plant breeding. John Wiley and Sons, Inc., New York. 485 p.
- Ashri, A. 1968. Morphology and inheritance of sterile brachytic dwarfs in peanuts, *Arachis hypogaea*. Crop Sci. 8:413-415.
- Ashri, A. 1970. Inheritance of small leaflets in a wide cross in peanuts, *Arachis hypogaea*. Oléagineux 25(3):153-154.
- Ashri, A. 1976. Plasmon divergence in peanuts (*Arachis hypogaea*): A third plasmon and locus affecting growth habit. Theor. Appl. Genet. 48:17-21.

5. Ashri, A. and E. Goldin. 1965. The mutagenic activity of diethyl sulfate in peanuts. *Radiation Bot.* 5:431-441.
6. Badami, V. K. 1928. Inheritance studies in *Arachis hypogaea* (the groundnut). Ph.D. thesis, Cambridge (England), Univ. Library.
7. Bhide, M. V. and S. C. Desale. 1970. A small leaflet mutant in groundnut. *Poona Agric. Coll. Magaz.* 59(3-4):113-114.
8. Branch, W. D., R. O. Hammons, and J. S. Kirby. 1982. Inheritance of white-stem peanut. *J. Hered.* 73:301-302.
9. Coffelt, T. A. and R. O. Hammons. 1974. Inheritance of pod constriction in peanuts. *J. Hered.* 65:94-96.
10. Coffelt, T. A. and D. M. Porter. 1982. Screening peanuts for resistance to sclerotinia blight. *Plant Dis.* 66:385-387.
11. Coffelt, T. A. and D. M. Porter. 1986. Field screening of reciprocal Chico \* Florigiant peanut populations to leafspot in Virginia. *Peanut Sci.* 13:57-60.
12. Crompton, C. E., J. C. Wynne, and T. G. Isleib. 1979. Combining ability analysis of seed calcium content and adenosine phosphates in peanuts. *Oléagineux* 34(2):71-75.
13. Emery, D. A., W. C. Gregory, and P. J. Loesch, Jr. 1964. Breeding value of the x-ray induced macro-mutant. I. Variations among normal appearing F<sub>2</sub> families segregated from crosses between macro-mutants of peanuts (*Arachis hypogaea* L.). *Crop Sci.* 4:87-90.
14. Essomba, N. B., T. A. Coffelt, W. D. Branch, and S. W. Van Scoyoc. 1991. Inheritance of stem color and non-nodulation in peanut. *Peanut Sci.* 18:126-131.
15. Gregory, W. C. 1968. A radiation breeding experiment with peanuts. *Radiation Botany* 8:81-147.
16. Gruneberg, H. 1952. Genetical studies on the skeleton of the mouse. IV Quasi-continuous variations. *J. Genet.* 51:95-114.
17. Kornegay, J. L., M. K. Beute, and J. C. Wynne. 1980. Inheritance of resistance to *Cercospora arachidicola* and *Cercosporidium personatum* in six Virginia-type peanut lines. *Peanut Sci.* 7:4-9.
18. Mather, K. and J. L. Jinks. 1978. Introduction to biometrical genetics. Cornell University Press, Ithaca, New York. 231 p.
19. Matlock, R. S., D. J. Banks, Y. P. Tai, and J. S. Kirby. 1970. Inheritance of a narrow-leaflet character in peanuts, *Arachis hypogaea* L. *Agron. Abstr., Am. Soc. Agron.* p. 15.
20. Mouli, C., D. M. Kale, and S. H. Patil. 1984. Bifurcated leaflets in groundnut. *Oléagineux* 39(7):375-377.
21. Mouli, C. and S. H. Patil. 1975. Paternal inheritance of x-ray induced foliaceous stipule in the peanut. *J. Hered.* 66:28-30.
22. Patil, S. H. and C. Mouli. 1975. Genetics of a dwarf mutant in groundnut. *Theor. Appl. Genet.* 46:395-400.
23. Pooni, H. S., J. L. Jinks, and M. A. Cornish. 1977. The causes and consequences of non-normality in predicting the properties of recombinant inbred lines. *Heredity* 38(3):329-338.
24. Ressler, P. M. and D. A. Emery. 1978. Inheritance of growth habit in peanuts: cytoplasmic or maternal modification? *J. Hered.* 69:101-106.
25. Sandhu, B. S. and A. S. Khehra. 1983. Estimates of gene effects for gynophore number, leaflet length, and leaflet breadth in groundnut. *Indian J. Agr. Sci.* 53:292-294.
26. Snedecor, G. W. and W. G. Cochran. 1980. Statistical methods. Seventh edition. The Iowa State University Press, Ames (Iowa). 507 p.
27. Stanfield, W. D. 1983. Theory and problems of genetics. Second edition. McGraw-Hill Book Co., New York. 392 p.
28. Wynne, J. C. 1975. Inheritance of branching pattern in *Arachis hypogaea* L. *Peanut Sci.* 2:1-5.
29. Wynne, J. C. and T. A. Coffelt. 1982. Genetics of *Arachis hypogaea* L. pp. 50-94. in H. E. Pattee and C. T. Young (eds.). *Peanut Science and Technology.* Amer. Peanut Res. and Educ. Soc., Inc. Yoakum, Texas.

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