Inheritance of Stem Color and Non-Nodulation in Peanut[1]

N. B. Essomba, T. A. Coffelt*, W. D. Branch, and S. W. Van Scoyoc[2]

ABSTRACT

Extra-nuclear factors have been reported in peanut (*Arachis hypogaea* L.) for many traits including growth habit, stipule shape, pod constriction, resistance to leafspot disease, and calcium concentration. However, the role of extra-nuclear factors with the inheritance of many other peanut traits remains to be ascertained. The objective of this study was to determine the inheritance of stem color and non-nodulation, and whether their inheritance is influenced by extra-nuclear factors. The study was conducted on the F_1 and F_2 progenies obtained from a modified diallel design with two *A. hypogaea* genotypes, Argentine and T2442, and one *A. monticola* Krap. et Rig. genotype, as parents. Two plant parts (main and lateral stems) were visually classified for stem color (purple, mixed, or green). Plants graded as green-green, mixed-green, or mixed-mixed were grouped as green and all others as purple for genetic analyses. Plants were classified as non-nodulating if symptons of N deficiency were observed. Distribution of data for stem color was bimodal, supporting the grouping of data into two phenotypic classes (green and purple). The F_2 generation fit ratios of 1 green: 3 purple, 6 green: 10 purple, 9 green: 7 purple, 11 green: 5 purple, or 15 green: 1 purple depending on the parents. These results indicate that a) stem color may be determined by two sets of genes of which the first one may be responsible for purple pigmentation and the second one for green pigmentation, b) these two gene sets, comprising, respectively, one and two loci for purple and green pigmentations, may have epistatic relationships, c) extra-nuclear factors may function as alleles to nuclear genes responsible for stem color, and d) extra-nuclear factors may induce or modify relationships between traits when they interfere with nuclear genes determining these traits. In the F_2 of crosses with T2442 as one parent and either *A. monticola* or Argentine as the other, ratios of 57 nodulating: 7 non-nodulating plants and 54 nodulating: 10 non-nodulating plants were observed. These results indicate that a) non-nodulation trait may be determined by three independent non-duplicate genes and b) at least two homozygous recessive loci are required in a genotype for non-nodulation. The following genotypes are proposed for the three parents:

A. monticola:	Ps1Ps1 gs1gs1 gs2gs2; N3N3 N4N4 N5N5
Argentine:	ps1ps1 Gs1Gs1 gs2gs2; N3N3 N4N4 N5N5
T2442:	ps1ps1 gs1gs1 Gs2Gs2; n3n3 n4n4 n5n5

Extra-nuclear factors have been reported in peanut (*Arachis hypogaea* L.) for many traits, including growth habit (2, 3, 32), branching pattern (30), stipule shape (24), pod constriction (10), resistance to leafspot disease (11), photosynthesis rate (8), and calcium concentration (12).

Many stem colors, including violet (4), red (20), purple and green (5, 13, 22, 28), and white (9), are reported. However, Branch *et al.* (9) stated that the observed variation in color of peanut stems and branches is generally limited to green and purple. This suggests that violet, purple, and red may represent the same color in the different studies. The same authors consider white as an aberrant color associated with albinism or lack of green or purple pigmentation.

A range of color intensity has been noted between the purple and the green stem colors (28), which probably resulted in classifications such as slight red or purple, intermediate, and dark purple (5, 20). Hayes (20) suspected that shading by the leaves was responsible for the unreliability of stem coloration. According to Branch *et al.* (9), the color of peanut stem varies in intensity due to genotype, environment, and genotype * environment interactions. Purple stem coloration has been associated with anthocyanin pigment by Patel *et al.* (28).

Many reports (5, 20, 22, 28) indicate dominance of purple pigmentation to green pigmentation. Branch *et al.* (9) observed the dominance of pigmented stem to white stem. Culp *et al.* (13) reported an incomplete dominance of purple to green stem color. Both monogenic inheritance (5, 20, 22) and digenic inheritance (28, 33) have been reported for stem coloration. Branch *et al.* (9) reported monogenic inheritance for white stem in intrasubspecific crosses between related lines and digenic inheritance between unrelated lines. Two F_2 ratios in digenic cases have been found: 15 purple: 1 green (28), and 9 purple: 7 green (29, 31, 33). These findings suggest that stem pigmentation is controlled by two genes, with possibly duplicate recessive epistasis and that cases of monogenic inheritance are the result of a common homozygous recessive locus in the two parents.

Peanut, as with other legumes, can form symbiotic associations with soil bacteria of the genus *Rhizobium*. Some peanuts do not nodulate due to a lack of effective *Rhizobium* strains, unfavorable environmental conditions for nodule formation, or a genotypic expression. In genotypic expression, non-nodulating plants are recognizable by chlorotic or yellow leaves contrasting with normally-green leaves on nodulating plants (17, 25). However, it may be assumed that such a genotypic expression is observable only under a poor nitrogen-supply of the plant from the soil, given the relationship between nitrogen-supply and leaf chlorophyll content in peanut (27).

Although other traits related to peanut-*Rhizobium* symbiosis are quantitatively determined (1, 21, 26), the non-nodulation trait may be inherited as a simple recessive trait (17). This has been reported also by Nigam *et al.* (25) in a study of F_2 and F_3 progenies from infraspecific crosses of normal nodulating culitvars. Their results indicated that non-nodulation is controlled by a pair of independent genes, $n1n1\_n2n2$, with duplicate recessive epistasis. In contrast, Dutta and Reddy (16) recently reported a model involving three genes.

The objective of this study was to determine the inheritance of stem color and non-nodulation, and whether their inheritance is influenced by extra-nuclear factors.

Materials and Methods

The study was conducted on the F1 and F2 progenies obtained from a modified diallel design (excluding self-crosses) with *A. hypogaea* gentoypes, Argentine and T2442, and *A. monticola* Krap et. Rig. as parents. Argentine is a spanish-type peanut which nodulates normally, and has an erect growth habit, large leaflets, and green stems with a purple shade at times. T2442 is a non-nodulating genotype and has 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.

The F_2 progenies and the parents were grown during 1985 on a Kenansville loamy sand at the Tidewater Agricultural Experiment Station, Suffolk, Virginia. F_2 seeds were obtained from F_1 plants grown at Tifton, Georgia. Each F_2 population was grown in two separate plots in the field. Recommended production practices were used. Since F_1 progenies had not been classified originally for the traits studied, crosses were made again in August 1986 at Suffolk, Virginia. F_1 progenies obtained were grown in pots in a greenhouse from November 1986 to May 1987.

Stem color was classified as purple ('p'), green ('g'), or a mixture of purple and green ('m'). Two plant parts were visually delimited on each measured plant: one—the main stem, and the other—the lateral branches. Each of these two parts was recorded as 'p', 'm', or 'g' depending on color. The two-digit grade ('gg', "mg', "mm', 'pg'. 'pm', or 'pp') of the whole plant (main stem plus lateral branches) allowed it to be classified on a progressive scale from the greenest to the purplest. Later, the first three classes were regrouped as green (G), and the others as purple (P) to simplify genetic analyses.

Argentine and T2442 were both classified as 'mg', and *A. monticola* as 'pp', for stem color. The sample size varied from 2 to 5 plants among F_1 progenies grown in the greenhouse and from 183 to 642 plants among F_2 progenies. Measurements were made between 5 and 13 weeks after planting. They were delayed until five months after planting with F_1 progenies due to retarded germination and growth. Only F_1 progenies from the cross Argentine *T2442 were studied.

The non-nodulation trait was scored indirectly by the presence or the absence of chlorotic leaves. Nigam *et al.* (25) found yellow leaves to be significantly correlated with non-nodulation. In this experiment, non-nodulating plants were observed only on crosses having T2442 as a parent.

Every plant was classified for the two traits. Chi-square tests were performed for homogeneity among reciprocal cross populations for each trait and for independence among the two traits. Homogeneity tests were performed using contingency tables contrasting reciprocal crosses of each pair of parents. Original data (with no grouping of phenotypic classes) were used for these two types of tests. Grouped data were used for testing genetic ratios.

Results and Discussion

Stem Color

Distribution of data for all progenies for stem color was bimodal (Table 1). This supports the grouping of data into two phenotypic classes centered around 'mg' (for green phenotype), and 'pm' (for purple phenotype) classes.

Two nonreciprocal crosses fit a 1 green: 3 purple ratio, while the four other fit the ratios - 6 green: 10 purple, 9 green: 7 purple, 11 green: 5 purple, and 15 green: 1 purple (Table 2). These results suggest segregation at two loci in all crosses. Such a situation may occur with two independent genes having three different alleles each, and each allele being carried by a different parent, or with three independent genes, each individual cross segregating only at two of them, and the third one being identically homozygous in the two parents considered. The first model is relatively uncommon and could not be tested with available data. The second hypothesis is more common and was adopted for our analysis. Such a model has been proposed by Ashri (2) for growth habit.

In matching all possible F_2 genotypes using a three-locus model as hypothesized above, and the different fitted ratios,

Table 1. Distribution of F_2 progenies for stem color in three reciprocal peanut crosses.

Cross † (♀ x ♂)	Classification ‡					
	gg	mg	mm	pg	pm	pp
1 x 2	6	48	28	55	204	31
2 x 1	19	117	57	102	218	27
1 x 3	8	55	32	46	132	77
3 x 1	42	202	95	97	186	20
2 x 3	65	73	23	22	44	5
3 x 2	199	173	31	19	16	0

† : 1 = **A. monticola**, 2 = Argentine, 3 = T2442.

‡ : g = green, m = mixed, p = purple.

it appears that genes at three loci may have been interacting to determine stem color in this experiment. Alleles at two loci, designated Gs1 gs1 and Gs2 gs2 apparently condition green pigmentation, while alleles at the third loci designated Ps1 ps1 condition purple pigmentation. The 15 green: 1 purple ratio fitted in the F_2 progeny from the cross between T2442 (female) and Argentine (male) suggests that Gs1 gs1 and Gs2 gs2 may produce duplicate effects. Tai et al. (34)

found chlorophyll-deficient peanut mutants to be determined by duplicate homozygous recessive loci with duplicate dominant epistasis for normal green pigment. Branch et al. (9) proposed a digenic model with a homozygously recessive locus for the white stem characteristic.

The following genotypes are proposed for the three parents:
A. monticola: Ps1Ps1 gs1gs1 gs2gs2 (Purple)
Argentine: ps1ps1 Gs1Gs1 gs2gs2 (Green)
T2442: ps1ps1 gs1gs1 Gs2Gs2 (Green)

The parental genotypes can be used to generate F_2 genotypes, phenotypes, and explainable frequencies for stem color in each cross (Table 3). Different three-lettered symbols have been proposed by Patil (29). The ones proposed above conform with the majority of two lettered symbols commonly found in the literature for morphological traits in peanut (35).

F_1 progenies from reciprocal crosses between Argentine and T2442 were purple when Argentine was the female parent and green when T2442 was the female parent. Chi-squares obtained for homogeneity tests of reciprocal-cross F_2 progenies were significant in all crosses (Table 4). These significant chi-squares were confirmed by differing genetic ratios fitted by reciprocal F_2 progenies in all bi-parental crosses. This variable expression of genotypes depending on the specific cross and the direction of the cross, coupled with suspected epistatic relationships between Ps1 ps1, and Gs1 gs1 and Gs2 gs2 (Table 5), suggest a) that extra-nuclear factors may have been involved, and b) that these extra-nuclear factors may have interacted with some of the allelic

Table 2. One df chi-square values computed for tested ratios of F_2 progenies from six reciprocal crosses for stem color in peanuts.

Tested Ratio	Observed ratio per cross (female * male)†					
	1 * 2 82G:290P	2 * 1 193G:347P	1 * 3 95G:255P	3 * 1 303P:339G	2 * 3 71P:161G	3 * 2 35P:403G
1:3	**1.73** ‡	33.23	**0.97**	167.16	3.88	68.29
1:15	161.32	793.52	258.48	1844.12	223.52	**2.53**
3:13	2.54	103.08	15.70	343.22	20.45	33.10
5:11	14.48	4.96	2.60	75.35	**0.07**	110.50
6:10	38.53	**0.79**	15.81	25.54	4.70	162.20
7:9	70.64	13.91	39.07	**3.06**	15.78	228.58
1:63	978.45	4342.00	1643.00	8721.00	1142.00	113.82
3:61	52.43	1184.00	408.74	2606.00	343.56	9.80
7:57	46.08	342.07	95.91	870.47	94.86	3.95
10:54	11.76	167.49	34.51	488.12	40.28	18.95

† 1 = **A. monticola**; 2 = Argentine; 3 = T2442

G = green; P = purple

‡ The lowest chi-square value in each column is printed in bold and underlined.

combinations involved to produce an allelic response for stem color in this experiment. An allelic response corresponds to a situation where extra-nuclear factors interfere with specific nuclear alleles or allele combinations, as opposed to

Table 3. Proposed F_2 genotypes, phenotypes, and frequencies for stem color classification in three reciprocal peanut crosses.

Cross †	Genotype			Freq. (1/16)	Phenotype †† (♀ × ♂)	(♂ × ♀)
1 x 2	Ps_1Ps_1	Gs_1Gs_1	gs_2gs_2	1	P	P
	Ps_1Ps_1	Gs_1Gs_1	gs_2gs_2	2	P	P
	Ps_1Ps_1	gs_1gs_1	gs_2gs_2	1	P	P
	Ps_1ps_1	Gs_1Gs_1	gs_2gs_2	2	P	G
	Ps_1ps_1	Gs_1Gs_1	gs_2gs_2	4	P	P
	Ps_1ps_1	gs_1gs_1	gs_2gs_2	2	P	P
	ps_1ps_1	Gs_1Gs_1	gs_2gs_2	1	G	G
	ps_1ps_1	Gs_1gs_1	gs_2gs_2	2	G	G
	ps_1ps_1	gs_1gs_1	gs_2gs_2	1	G	G
			Ratio:		3P : 1G	10P : 6G
1 x 3	Ps_1Ps_1	gs_1gs_1	Gs_2Gs_2	1	P	P
	Ps_1Ps_1	gs_1gs_1	Gs_2gs_2	2	P	P
	Ps_1Ps_1	gs_1gs_1	gs_2gs_2	1	P	P
	Ps_1ps_1	gs_1gs_1	Gs_2Gs_2	2	P	G
	Ps_1ps_1	gs_1gs_1	Gs_2gs_2	4	P	G
	Ps_1ps_1	gs_1gs_1	gs_2gs_2	2	P	P
	ps_1ps_1	gs_1gs_1	Gs_2Gs_2	1	G	G
	ps_1ps_1	gs_1gs_1	Gs_2gs_2	2	G	G
	ps_1ps_1	gs_1gs_1	gs_2gs_2	1	G	P
			Ratio:		3P : 1G	7P : 9G
2 x 3	ps_1ps_1	Gs_1Gs_1	Gs_2Gs_2	1	G	G
	ps_1ps_1	Gs_1Gs_1	Gs_2gs_2	2	G	G
	ps_1ps_1	Gs_1Gs_1	gs_2gs_2	1	G	G
	ps_1ps_1	Gs_1gs_1	Gs_2gs_2	2	G	G
	ps_1ps_1	Gs_1gs_1	Gs_2gs_2	4	P	G
	ps_1ps_1	gs_1gs_1	gs_2gs_2	2	G	G
	ps_1ps_1	Gs_1gs_1	Gs_2gs_2	1	G	G
	ps_1ps_1	gs_1gs_1	Gs_2gs_2	2	G	G
	ps_1ps_1	gs_1gs_1	gs_2gs_2	1	P	P
			Ratio:		5P : 11 G	1P : 15G

† : 1 = A. monticola, 2 = Argentine, 3 = T2442.

†† : P = purple, G = green.

Table 4. Homogeneity tests among F_2 reciprocal-cross progenies for stem color and non-nodulation.

Trait		CROSS † 1 x 2	1 x 3	2 x 3
STEM COLOR	x^2	30.38	124.18	70.14
	P	0.001	0.001	0.001
	df	5	5	4
Non-nodulation	x^2	-	0.10	1.39
	P	-	0.75	0.24
	df	-	1	1

† : 1 = A. monticola   2 = Argentine   3 = T2442.

Table 5. Relationships between Ps_1-ps_1 and the two other genes in three different cytoplasms of peanut.

	Cytoplasm A. monticola	Argentine	T2442
Ps_1Ps_1	Epistatic to Gs_1-gs_1 and to Gs_2-gs_2.	Same as in A. monticola.	Same as in A. monticola.
Ps_1ps_1	Epistatic to Gs_1-gs_1 and Gs_2-gs_2.	Same as in A. monticola except in presence of Gs_1Gs_1.	Same as in A. monticola except in presence of Gs_2Gs_2 or Gs_2gs_2.
ps_1ps_1	Gs_1-gs_1 and Gs_2-gs_2 epistatic to ps_1ps_1.	Epistatic to $Gs_1gs_1Gs_2gs_2$ and to $gs_1gs_1gs_2gs_2$; otherwise, same as in A. monticola.	Epistatic to gs_1gs_1 gs_2gs_2; otherwise, same as in A. monticola.

a genic response where these factors interfere with specific nuclear genes or combination of genes, independent of their alleles. Hammons (19) described epistatic relationships between two sets of genes responsible for main stem inflorescences in peanut.

Distinctive loci for purple and green pigmentations, as proposed above, confirm that green and purple stem colors are actually two different traits, and that stem color results from the alleles present rather than a mixture of the two pigmentations. The contrast between the consistency of green pigmentation and the inconsistency of purple pigmentation is in support of this hypothesis. Indeed, the occurrence of separate pigmentation loci would help explain observations concerning stem color made in this study and by others. For example, the relationships of green pigmentation with physiological phenomena such as chlorophyll-deficiency (6) and non-nodulation (25) suggest that , in itself, green stem color is a complex character. Purple pigmentation, for its part, may be related to anthocyan in pigments responsible for red flower shade, based on other unreported observations made during this study, and by other researchers (28).

The phenotype of the genotype ps1ps1 gs1 gs1 gs2gs2 may have been green in the F_2 population from the cross Argentine (female) * A. monticola (male) and purple in the one from Argentine * T2442, according to the model proposed above (Table 3). This situation, apparently contradictory given the same Argentine cytoplasm in the two populations, suggests that A. monticola, a wild species, may have different alleles than the two A. hypogaea lines at one or more loci for stem color. Expressivity and penetrance could also be involved. Further investigation is needed to confirm such a hypothesis.

Stem color is also known to be affected by factors such as light and stress. The influence of these factors was not considered to be an influence in this experiment, but do need to be investigated for complete understanding of the inheritance of stem color.

Non-nodulation

F_1 progenies were not classified for non-nodulation due to a suspected influence of nitrogen residues in the growth medium used in the greenhouse. Though both F_2 reciprocal crosses could be considered as homogenous since the chi-squares for homogeneity were not significant (Table 4), the Argentine x T 2442 progeny best fit a 54 nodulating: 10 non-nodulating ratio while the reciprocal cross progeny best fit a 57 nodulating: 7 non-nodulating ratio (Table 6). This difference in results from chi-square tests underlines the hightype II error associated with this kind of analysis and stresses the need to interpret carefully P-values in genetic studies. Reciprocal crosses between T-2442 and A. monticola fit the 57 nodulating: 7 non-nodulating ratio.

The two fitted ratios (57:7 and 54:10) suggest segregation at three loci. The following genotypes are proposed for the three parents:

A. monticola: N3N3 N4N4 N5N5   (nodulating)
Argentine   N3N3N4N4 N5N5   (nodulating)
T2442:   n3n3 n4n4 n5n5   (non-nodulating)

Subscripts adopted (3, 4, and 5) for the above genotypes follow the ones proposed by Nigam et al (25).

The good fit of observed data to a 57 nodulating: 7 non-nodulating plants and 54 nodulating: 10 non-nodulating

Table 6. One df chi-square values computed for tested ratios of F_2 progenies from four reciprocal crosses for non-nodulation trait in peanuts.

Tested Ratio	Observed ratio cross (female * male) †			
	1 * 3	3 * 1	2 * 3	3 * 2
	37NN:313N	64NN:578N	36NN:196N	21NN:162N
1:3	47.96	78.00	11.12	18.15
1:15	10.92	15.36	31.43	9.67
3:13	15.70	32.14	1.79	6.10
5:11	69.07	135.94	27.36	33.03
6:10	107.80	208.13	47.84	53.60
7:9	156.25	298.02	74.08	72.03
1:63	162.96	296.21	260.49	109.80
3:61	28.88	40.42	59.65	16.83
7:57	**0.03** ‡	**0.58**	5.42	**0.05**
10:54	6.99	15.35	**0.00**	2.63

† 1 = A. monticola; 2 = Argentine; 3 = T2442

NN = non-nodulating; N = nodulating

‡ The lowest chi-square value in each column is printed in bold and underlined.

Table 7. Proposed F2 genotypes, phenotypes, and frequencies for root nodulation in two reciprocal peanut crosses (Argentine x T2442, and A. monticola x T2442).

Genotype			Freq. (1/64)	Phenotype †	
				Population 1 ‡	Population 2
N_3N_3	N_4N_4	N_5N_5	1	nod	nod
N_3N_3	N_4N_4	N_5n_5	2	nod	nod
N_3N_3	N_4n_4	N_5N_5	2	nod	nod
N_3N_3	N_4N_4	n_5n_5	1	nod	nod
N_3N_3	N_4n_4	N_5n_5	4	nod	nod
N_3n_3	N_4N_4	N_5N_5	2	nod	nod
N_3N_3	N_4n_4	n_5n_5	2	nod	nod
N_3N_3	n_4n_4	N_5N_5	1	nod	nod
N_3N_3	N_4N_4	N_5n_5	4	nod	nod
N_3N_3	n_4n_4	N_5n_5	2	nod	nod
N_3n_3	N_4n_4	N_5N_5	4	nod	nod
N_3n_3	N_4N_4	n_5n_5	2	nod	nod
N_3N_3	n_4n_4	n_5n_5	1	nod	non-nod
N_3n_3	N_4n_4	N_5n_5	8	nod	nod
N_3n_3	N_4n_4	n_5n_5	4	nod	nod
N_3n_3	n_4n_4	N_5N_5	2	nod	nod
n_3n_3	N_4N_4	N_5N_5	1	nod	nod
N_3n_3	n_4n_4	N_5n_5	4	nod	nod
n_3n_3	N_4N_4	N_5n_5	2	nod	nod
n_3n_3	N_4n_4	N_5N_5	2	nod	nod
n_3n_3	N_4N_4	n_5n_5	1	nod	non-nod
n_3n_3	N_4n_4	N_5n_5	4	nod	nod
n_3n_3	n_4n_4	N_5N_5	1	nod	non-nod
N_3n_3	n_4n_4	n_5n_5	2	non-nod	non-nod
n_3n_3	N_4n_4	n_5n_5	2	non-nod	non-nod
n_3n_3	n_4n_4	N_5n_5	2	non-nod	non-nod
n_3n_3	n_4n_4	n_5n_5	1	non-nod	non-nod
			Ratio	57 nod:7 non-nod	54 nod:10 non-nod

† : nod = nodulating, non-nod = non-nodulating.
‡ Population 1 = Reciprocal crosses between A. monticola x T2442 and cross between T2442 x Argentine.
Population 2 = Cross between Argentine x T2442.

plants is indicative of additive effects among the three loci identified, in which at least two homozygous recessive loci are required in a genotype for non-nodulation (Table 7). This result suggests that non-nodulation may be determined by three non-duplicate genes exhibiting additive effects. It might be conjectured that these genes are involved in controlling the enzymatic pathway for nodulation.

The results in this study do not agree with results by Nigam et al. (25), who identified two duplicate genes as responsible

Table 8. Two-trait independence tests using non-grouped data in reciprocal peanut crosses.

Trait	Cross † (♀ x ♂)	Non-nodulation		
		x^2	df	P-value
Stem color	1 x 2	--	--	--
	2 x 1	--	--	--
	1 x 3	16.40	4	0.01
	3 x 1	12.90	5	0.05
	2 x 3	12.50	1	0.01
	3 x 2	02.02	1	0.17

† : 1 = A. monticola, 2= Argentine, 3 = T2442.

for non-nodulation. However, Dutta and Reddy (16) have also proposed a three-gene model in a separate study.

Relationship between stem color and non-nodulation

Chi-squares computed to test independence between stem color and non-nodulation were significant in three out of the four F_2 populations tested (Table 8). In significant F_2 progenies, non-nodulating plants were more likely to have a green than a purple stem. This is indicative of a possible existence of a relationship between stem color and non-nodulation among the three cultivars used in this experiment.

Relationships among morphological traits commonly result from situations of gene linkage, pleiotropic genes, or physiological relationships. Few cases of linkage have been reported in peanut (5, 14, 28, 29). More cases should be found with more studies on morphological traits since many traits involve genes on two or more chromosomes (35). Cases of mutations affecting many morphological traits (3, 7, 18, 23) may be an indication of the existence of pleiotropic genes in the inheritance of these traits. A case of pleitrophy has been discussed by Desale (15) for three morphological traits in peanut. An example of a physiological relationship between morphological traits is the relationship reported by Nigam et al. (25) between non-nodulation and yellow leaves in peanut.

Another noteworthy fact is that the two populations having T2442 as the female parent had greater P-values than the others (Table 8). This observation, coupled with the idea of extra-nuclear factors discussed for stem color above, suggests that extra-nuclear factors may induce or influence relationships among different traits in peanut when they interfere with nuclear genes controlling these traits. The use of reciprocal progenies in breeding programs and genetic studies is, therefore, highly advisable in peanut.

Acknowledgment

Literature Cited

1. Arrendell, S., J.C. Wynne, G. H. Elkan, and T. G. Isleib. 1985. Variation of nitrogen fixation among progenies of a virginia ° spanish peanut cross. Crop Sci. 25:865-869.

2. Ashri, A. 1976. Plasmon divergence in peanuts (Arachis hypogaea): A third plasmon and locus affecting growth habit. Theor. Appl. Genet. 48:17-21.

3. Ashir, A., and E. Goldin. 1963. Genic-cytoplasmic interactions in peanuts (Arachis hypogaea L.). Proc. XIth Int. Congr. Genetics (Netherlands) 1 Abstr. No. 12.9.

4. Badami, V. K. 1928. Inheritance studies in Arachis hypogaea (the groundnut). Ph.D. thesis, Cambridge (England), University Library.

5. Balaiah, C., P. S. Reddy, and M. V. Reddi. 1977. Genic analysis in groundnut: 1 - Inheritance studies in 18 morphological characters in crosses with Guajarat narrow leaf mutant. Proc. Indian Acad. Sci. 85 B(5): 340-350.

6. Benedict, C. R., and D. L. Ketring. 1972. Nuclear gene affecting greening in virescent peanut leaves. Plant Physiol. 49:972-976.
7. Bhide M. V., and S. C. Desale. 1970. A small leaflet mutant in groundnut. Poona Agric. Coll. Magaz. 59:113-114.
8. Branch, W. D., and J. E. Pallas, Jr. 1984. Heterosis of apparent photosynthesis rate in Arachis hypogaea L. Peanut Sci. 11:56-57.
9. Branch, W. D., R. O. Hammons, and J. S. Kirby. 1982. Inheritance of a white-stem peanut. J. Hered. 73:301-302.
10. Coffelt, T. A., and R. O. Hammons. 1974. Inheritance of pod constriction in peanuts. J. Hered. 65:94-96.
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. Oleagineux 34(2):71-75.
13. Culp, T. W., W. K. Bailey, and R. O. Hammons. 1968. Natural hybridization of peanuts, Arachis hypogaea L., in Virginia. Crop Sci. 8:109-111.
14. Dashiell, K. E., and D. W. Gorbet. 1982. Linkage between genes for non-nodulation and variegated testa color in peanuts. Proc. Amer. Peanut Res. Educ. Soc. 14:72. (Abstract).
15. Desale, S. C. 1985. A faint orange flower colored short stature mutant in groundnut. Curr. Res. Reporter 1(1):92-93.
16. Dutta, M., and L. J. Reddy. 1988. Further studies on genetics of non-nodulation in peanut. Crop Sci. 28:60-62.
17. Gorbet, D. W., and J. C. Burton. 1979. A non-nodulating peanut. Crop Sci. 19:727-728.
18. Gregory, W. C., B. W. Smith, and J. A. Yarbrough. 1968. A radiation breeding experiment with peanuts. II. Characterization of irradiated population (NC4-18.5KR).
19. Hammons, R. O. 1971. Inheritance of inflorescences in main stem leaf axils in Arachis hypogaea L. Crop Sci. 11:570-571.
20. Hayes, T. R. 1933. The classification of groundnut varieties with a preliminary note on the inheritance of some characters. Trop. Agric. (West Indies) 10:318-327.
21. Isleib, T. G., J. C. Wynne, G. H. Elkan, and T. J. Schneeweis. 1980.

Quantitative genetic aspects of nitrogen fixation in peanuts. Peanut Sci. 7:101-105.
22. Jadhav, G. D., and N. N. Shinde. 1979. Genetic studies in groundnut (Arachis hypogaea). Indian J. Agric. Res. 13:93-96.
23. Loesch, P. J., Jr., and R. O. Hammons. 1968. A radiation breeding experiment with peanuts. III. Inheritance of macro-mutants (NC4-18.5kR). Radiation Bot. 8:94-108.
24. Mouli, C., and S. H. Patil. 1975. Paternal inheritance of X-ray induced foliaceous stipule in the peanut. J. Hered. 66:28-30.
25. Nigam, S. N., V. Arunachalam, R. W. Gibbons, A. Bandyopadhyay, and P. T. C. Nambiar. 1980. Genetics of non-nodulation in groundnut (Arachis hypogaea). Oleagineux 35(10):453-455.
26. Nigam, S. N., S. L. Dwivedi, P. T. C. Nambiar, R. W. Gibbons, and P. J. Dart. 1985. Combining ability analysis of N$_2$-fixation and related traits in peanut. Peanut Sci. 12:55-57.
27. Pancholy, S. K., S. M. M. Basha, and D. W. Gorbet. 1982. Composition of seeds obtained from non-nodulating and nodulating peanut lines and cultivars. Peanut Sci. 9:50-52.
28. Patel, J. S., C. M. John, and C. R. Seshadri. 1936. The inheritance of characters in the groundnut-Arachis hypogaea. Proc. Indian Acad.. Sci. 3:214-233.
29. Patil, V. H. 1965. Genetics studies in groundnut (Arachis hypogaea L.). M. Sc. Thesis, Poona Univ., India.
30. Patil, S. H., and C. Mouli. 1975. Genetics of a dwarf mutant in groundnut. Theor. Appl. Genet. 46:395-400.
31. Prasad, S., and D. P. Srivastava. 1967. Inheritance of testa colour in groundnut (Arachis hypogaea L.) Sci. Cult. 33:489-490.
32. Resslar, P. M., and D. A. Emery. 1978. Inheritance of growth habit in peanut: cytoplasmic or maternal modification? J. Hered. 69:101-106.
33. Srivastava, A. N. 1977. Inheritance of purple pigmentation on stem and branches in groundnut. Sci. Cult. 43(1):42-43.
34. Tai, Y. P., J. S. Kirby, and R. S. Matlock. 1970. Chlorophyll mutations in peanuts, Arachis hypogaea L. II. Genetic analysis. Agron. abstr., Amer. Soc. Agron., p. 21.
35. 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.