

PEANUT SCIENCE

VOLUME 1

SPRING 1975

NUMBER 1

Inheritance of Branching Pattern in *Arachis hypogaea* L.¹

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ABSTRACT

The genetics of the branching pattern on the cotyledonary laterals of peanuts (*Arachis hypogaea* L.) was studied through scoring F_1 and F_2 generation progenies from crosses among four lines of Virginia, Valencia, and Spanish types. With one exception, these lines traced directly to gene centers in South America. When results were expressed as the ratio of reproductive branches to total branches ($R/R+V$), the F_2 from crosses of Virginia x Valencia gave a continuous distribution with the median near that of a Spanish type. Spanish x Virginia crosses gave a continuous distribution in the F_2 with the median equivalent to the Virginia parent. These results suggested that Spanish varieties may have originated from hybridization of Virginia and Valencia types. The presence, or absence, of inflorescences in the mainstem leaf axils of F_2 plants was scored for one cross. The results suggested the presence of two sets of duplicate loci with epistasis among the alleles.

Additional index words: Peanuts, Subspecies, Intraspecific, Reproductive branching, Vegetative branching, Groundnuts.

Gregory *et al.* (1) recognized the fundamental basis for subspecific differentiation of the peanut, *Arachis hypogaea* L., as differences in branching system. They divided *hypogaea* into three varietal groups—Virginia, Spanish, and Valencia—based on a description of the branching system given by Richter (7). He defined branches of peanuts as either reproductive (bearing only scale leaves in the axils which bear flowers) or vegetative (bearing leaves only). Richter designated the main axis N and the axes developing from the axils of leaves $N + 1$. He designated the next order of branches arising on the $N + 1$ branches as $N + 2$ and so on for successive higher orders of branching.

A description of the branching system of the three varietal groups is typically as follows.

Virginia (*ssp. hypogaea* var. *hypogaea*)—The $N + 1$ axes are all vegetative. The $N + 2$ axes arising on the $N + 1$ axes appear in alternating pairs of vegetative and reproductive.

Spanish (*ssp. fastigiata* var. *vulgaris*)—The $N + 1$ axes are vegetative and reproductive with the $N + 2$ axes in "runs" of vegetative and reproductive.

Valencia (*ssp. fastigiata* var. *fastigiata*)—The $N + 1$ axes are mostly reproductive. The $N + 2$ axes are all or nearly all reproductive.

Perry (6) studied X-ray-induced branching patterns (vegetative and reproductive) and two naturally occurring branching patterns (Virginia and Valencia). He concluded that (a) loci controlling the branching pattern in the Valencia type were different from those of the X-ray reproductive and (b) the alleles controlling branching pattern in the Virginia type were dominant to alleles controlling the Valencia type and both X-ray types.

Hammons (2) reported that inflorescences in the main stem axils of plants of an infraspecific cross between a Spanish and a Virginia line were governed by alleles at two sets of duplicate loci with epistasis between alleles at the loci. He states that an understanding of the genetic mechanisms modifying the frequency of reproductive events on the branches is essential for continued breeding improvement.

A change in the ratio of reproductive to vegetative branches may have important effects on the amount and maturity of fruit that a plant will produce. Whether it would be feasible to change maturity and yield through varying the branching pattern depends upon the extent to which its genetic control can be manipulated.

The purpose of this study was to assess the degree of genetic control of differences in branching pattern among three botanical varieties of peanuts.

Materials and Methods

Four lines of peanuts were used in this investigation. Three of the lines originated from three geographic areas of South America and represent different botanical varieties. The fourth line was NC 4, a Virginia-type cultivar derived from a single plant selection made in North Carolina in 1929.

A_2 , collected in Peru in 1961, is a Valencia type. B_2 , collected from Bolivia, is a Virginia type, and C_2 , collected from Paraguay, is a Spanish type. These three lines have been described previously (5).

Four characters were measured in this study. The presence or absence of inflorescences on the mainstem was recorded in some experiments, while the number of reproductive nodes per run, the number of vegetative nodes per run, and $R/R+V$ ratio were taken in all experiments.

Each plant was classified for the presence or absence of inflorescences on the mainstem as either (a) mainstems with only vegetative branches or (b) mainstems having reproductive and vegetative branches in the leaf axils. The number of reproductive nodes per run and the number of vegetative nodes per run are averages computed for the cotyledonary laterals of each plant. The $R/R+V$ ratio is a ratio of the total number of reproductive nodes on the two cotyledonary laterals divided by the total (reproductive plus vegetative) number of nodes

¹Paper Number 4396 of the Journal Series of the North Carolina Agricultural Experiment Station, Raleigh, N. C. 27607. Part of a thesis presented by the author in partial fulfillment of the requirements for the PhD degree, North Carolina State University, Raleigh, N. C. 27607.

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on the two laterals. Any branch bearing foliar leaves at its third and subsequent nodes was called a vegetative branch, while any branch producing only scale leaves and flowers was called a reproductive branch.

The study consisted of a number of experiments conducted during the 1971-73 growing seasons at the Peanut Belt Research Station at Lewiston and the Upper Coastal Plain Research Station at Rocky Mount, N. C. Plants of each experiment were planted in early May in rows 91.4 cm apart with 50.8 cm between plants. Plants were dug by hand in late September or early October. Data were recorded after harvest.

Experiment 1

Peanut lines A_2 , B_2 , and C_2 were planted in 1971 in a nursery at Rocky Mount. Each line was represented by 20 plants.

Experiment 2

A_2 , B_2 , and C_2 reciprocal F_1 hybrids among the lines, and reciprocal F_2 populations were grown at Lewiston during the 1972 season.

Parents and F_1 hybrids were represented by 20 plants each. The F_2 generation of each cross was represented by 40 plants each.

Experiment 3

Adjacent to experiment 2 at Lewiston during the 1972 season, 445 F_2 segregates from the $B_2 \times C_2$ cross were grown in a nursery. These plants represented a larger sample of the same F_2 material grown in experiment 2. Plants were grouped according to F_1 family. There were 24 F_1 families with 13 to 23 plants per family.

Experiment 4

Seeds harvested from the F_1 plants of the $A_2 \times B_2$ cross and its reciprocal described in experiment 2 plus seeds of the two parents were planted at Rocky Mount during the 1973 season in a nursery. The $A_2 \times B_2$ cross was represented by 226 plants and the $B_2 \times A_2$ cross by 354 plants. The plants were grouped by F_1 families with no more than 40 plants for each of the 35 F_1 families. Each parent was represented by 40 plants.

Experiment 5

NC 4, used as a female, was crossed with A_2 during the summer of 1971. F_2 plants were grown in a nursery at Rocky Mount during the 1973 season.

Experiment 6

Plants of six F_2 families in F_3 generation for the crosses of $B_2 \times C_2$, $C_2 \times B_2$, $B_2 \times A_2$, and $A_2 \times B_2$ were grown at Rocky Mount during the 1973 season. Each family consisted of approximately 20 plants. Twenty plants of each parent were also included. Three of the six F_2 families in F_3 for each cross were grown because the F_2 plants were selected as being extreme reproductive types and three were chosen because they were extreme vegetative types for that cross in experiment 2.

Results and Discussion

The subspecies of peanuts can be differentiated into botanical varieties by the branching system (1). Representatives of the three major varietal groups—Virginia, Spanish, and Valencia—were distinguishable by the ratio of reproductive and vegetative branches occurring on the cotyledonary laterals. All of the $N + 2$ nodes on the cotyledonary laterals ($N + 1$) of the Valencia representative (A_2) were reproductive giving a $R/R+V$ ratio of 1.00. The $N + 2$ nodes on the cotyledonary laterals of the Virginia line (B_2) alternated in an almost perfect 2 reproductive: 2 vegetative pattern with a $R/R+V$ ratio of 0.50. The Spanish line (C_2) had runs of vegetative and reproductive

nodes on the cotyledonary laterals giving a $R/R+V$ ratio of 0.65. The average run of reproductive $N + 2$ nodes was 23.5, 5.48, and 1.97 for A_2 , C_2 , and B_2 , respectively.

The Virginia type was also distinguishable from the representatives of the other two varietal groups (ssp. *fastigiata*) by the absence of inflorescences on the main stem. The alleles governing absence of mainstem inflorescences of the Virginia type were dominant to the alleles governing the presence of inflorescence on the mainstem of the Valencia and Spanish types. None of the F_1 plants from crosses of the Virginia \times Spanish or Virginia \times Valencia representative had mainstem inflorescences, while all of the F_1 plants obtained by crossing within ssp. *fastigiata* had mainstem inflorescences.

Inflorescences in the mainstem leaf axils were recorded for the F_2 segregates from the cross of NC 4 \times A_2 . Of 549 plants, 485 were devoid of inflorescences. These results agree ($P = 0.74$) with the genetic model proposed by Hammons (2) that flowering response is controlled by two sets of duplicate loci with epistasis between loci. This model results in a phenotypic ratio of 225 plants with vegetative to 31 plants with reproductive branches on the mainstem. Although the F_2 plants were grouped into only two classes in this study, the plants classified as having reproductive branches were heterogeneous. The number of inflorescences ranged from 1 to 20. This suggests that modifying genes or incomplete expressivity of genes may be contributing to this variation.

Means for the average run of reproductive and vegetative nodes and the $R/R+V$ ratio for crosses in F_1 and F_2 generations made among A_2 , B_2 , and C_2 grown in experiment 2 are given in Table 1. The Virginia-type branching pattern was dominant to the Spanish branching pattern. The average run of reproductive and vegetative nodes and the $R/R+V$ ratio for the hybrids between B_2 and C_2 were typical of those expected for a Virginia-type plant. The average reproductive run and the $R/R+V$ ratio indicates that the branching pattern of the Virginia type is not completely dominant to the Valencia type. The F_1 of the cross of A_2 (Valencia) \times B_2 (Virginia) and its reciprocal had $R/R+V$ ratios of 0.65 and 0.64, respectively. This ratio is higher than the $R/R+V$ ratio expected for the Virginia type, resembling that expected of a Spanish line. Crosses made within the ssp. *fastigiata* produced $R/R+V$ ratios intermediate between the parents. When A_2 was used as the female, the cross had a greater average run of reproductive nodes than when C_2 was used as the female. The mean values for the $R/R+V$ ratio for the crosses in F_2 generation grown in experiment 2 were not greatly different than the mean values for the crosses in the F_1 generation. However, F_2 plants of infraspecific crosses segregated widely for $R/R+V$ ratios. F_2 generation infraspecific plants contained several aberrant plants, but these plants did not appear to change the mean $R/R+V$ value for a cross. Because of the limited number of F_2 progeny, no attempt was made to separate the plants of each cross into phenotypic classes.

Table 1. Average reproductive run, average vegetative run, and R/R+V ratio for F₁ and F₂ generation crosses.

Line or cross	Average reproductive run	Average vegetative run	R/R+V*
A ₂ x B ₂ ⁺ F ₁	3.15 ± 0.2 [†]	1.80 ± 0.1	0.65 ± 0.02
B ₂ x A ₂ F ₁	2.89 ± 0.3	1.94 ± 0.1	0.59 ± 0.02
A ₂ x C ₂ F ₁	13.30 ± 1.7	1.86 ± 0.3	0.88 ± 0.03
C ₂ x A ₂ F ₁	4.24 ± 0.4	1.68 ± 0.1	0.71 ± 0.03
B ₂ x C ₂ F ₁	2.40 ± 0.1	2.17 ± 0.1	0.53 ± 0.02
C ₂ x B ₂ F ₁	2.24 ± 0.1	2.42 ± 0.2	0.49 ± 0.02
A ₂ x B ₂ F ₂	3.82 ± 0.5	1.90 ± 0.1	0.63 ± 0.03
B ₂ x A ₂ F ₂	4.20 ± 0.6	1.92 ± 0.2	0.64 ± 0.03
A ₂ x C ₂ F ₂	5.85 ± 0.8	2.15 ± 0.2	0.67 ± 0.04
C ₂ x A ₂ F ₂	7.97 ± 1.1	2.83 ± 0.5	0.70 ± 0.04
B ₂ x C ₂ F ₂	2.96 ± 0.5	2.37 ± 0.1	0.50 ± 0.02
C ₂ x B ₂ F ₂	2.77 ± 0.2	2.23 ± 0.1	0.55 ± 0.02

*R = no. of reproductive nodes and V = no. of vegetative nodes on cotyledonary laterals.

⁺A₂ = Valencia, B₂ = Virginia, and C₂ = Spanish.

[†]Standard error of mean based on within entry variance.

The segregation of factors producing branching pattern differences was observed in the F₂ generation for three intraspecific crosses grown in experiments 3-5.

F₂ generation means of the B₂ x C₂ cross for the average run of reproductive nodes, the average run of vegetative nodes, and the R/R+V ratio for 24 F₁ families representing 445 individual plants are given in Table 2. F₁ family means for the R/R+V ratio ranged from 0.43 to 0.55 with the mean for the cross being 0.48. This mean is equal to that for a Virginia type. The average run of reproductive nodes for the F₂ of the B₂ x C₂ cross is 2.2. This average also represents the expected reproductive run for a Virginia type.

The distribution of the R/R+V ratio for the 445 F₂ plants is shown in Table 3. The F₂ plant R/R+V ratios ranged from 0.04 (almost completely vegetative) to 1.00 (completely reproductive). The median for the R/R+V ratio was 0.48. The R/R+V ratio for most plants ranged from 0.41 to 0.70.

The average run of reproductive nodes, average run of vegetative nodes, and the R/R+V ratio for the parents and the F₂ plants of the cross of A₂ x

Table 2. Means of average reproductive and vegetative run and R/R+V ratio for 24 F₁ families in F₂ generation for cross of B₂ (Virginia) x C₂ (Spanish).

Cross	Average reproductive run	Average vegetative run	R/R+V*
Mean	2.2 ± 0.06 [†]	2.2 ± 0.04	0.48 ± 0.004
Range	1.8-2.8	1.9-2.7	0.43-0.55

*R = no. of reproductive nodes and V = no. of vegetative nodes on cotyledonary laterals.

[†]Standard error of mean based on within family variance.

Table 3. Frequency distribution of R/R+V ratio for F₂ plants following intraspecific hybridization.

R/R+V	Parents or cross						
	B ₂ x C ₂	A ₂	B ₂	A ₂ x B ₂	NC 4	A ₂	NC 4 x A ₂
	No. of F ₂ plants per class						
0	0						6
0.01-0.10	2						3
0.11-0.20	5						7
0.21-0.30	8						8
0.31-0.40	65						21
0.41-0.50	192		2	18	5		111
0.51-0.60	138		8	95	1		181
0.61-0.70	28	2		211			92
0.71-0.80	2	3		115		1	55
0.81-0.90	3	5		71		4	31
0.91-1.00	2	27		60		5	35
Total	445	37	10	580	6	10	550
Median*	0.48	0.94	0.54	0.68	0.47	0.91	0.54

*Median = L_e + (g)I/f where: L_e = lower limit of interval containing median, g = order statistic of median minus cumulative frequency of classes to class containing median, I = class interval and f = frequency in class containing median.

Table 4. The average reproductive and vegetative run and R/R+V ratio for A₂, B₂, and reciprocal crosses between these lines in F₂ generation.

Entry	Average reproductive run	Average vegetative run	R/R+V
A ₂	13.9 ± 1.1*	1.7 ± 0.2	0.92 ± 0.02
B ₂	2.0 ± 0.1	1.9 ± 0.1	0.54 ± 0.03
A ₂ x B ₂ F ₂	4.7 ± 0.2	2.0 ± 0.1	0.70 ± 0.01
B ₂ x A ₂ F ₂	5.0 ± 0.2	2.0 ± 0.1	0.71 ± 0.01

*Standard error of mean based on within entry variance.

B₂ are given in Table 4. A₂ had a R/R+V ratio of 0.92. The average run of reproductive nodes was 13.9. The Virginia-type parent had a R/R+V ratio of 0.54. The average run of reproductive nodes was 1.96.

The mean R/R+V ratios for the F₂ plants of the cross and its reciprocal are 0.70 and 0.71. These values are equal to the midparent value. The average run of reproductive nodes for the cross in F₂ was 4.9.

The frequency distribution of the parents and the F₂ plants is shown in Table 3. The majority of the plants representing the Valencia-type parent fall in the 0.91-1.00 R/R+V class with a median of 0.94. The R/R+V of the cotyledonary laterals of plants of the Virginia parent fall in two classes ranging from 0.41-0.60 with a median of 0.54. The median for the cross is 0.68. The reciprocal crosses do not appear to differ in the distribution of R/R+V ratios or in median values.

The average run of reproductive nodes, average run of vegetative nodes, and R/R+V ratio for NC 4, a Virginia type, and A₂ (Valencia), and the cross between these two lines represented by 21 F₁ families in F₂ generation are given in Table 5. The average reproductive run for NC 4 was 1.9, while the average reproductive run for A₂ was 17.8. Means for the F₁ families for the same trait ranged from 2.2 to 7.9 with the cross mean being 4.1. This mean is less than the expected midparent value of 9.8. The R/R+V ratio for A₂ is 0.94 and is 0.53 for NC 4. The mean for the cross in F₂ generation is 0.55.

Table 5. Average reproductive and vegetative run and R/R+V ratio for NC 4, A₂, and F₁ families in F₂ generation of the cross between the two lines.

Entry	Average reproductive run	Average vegetative run	R/R+V
NC 4 x A ₂ mean	4.1 ± 0.2*	2.1 ± 0.1	0.55 ± 0.01
NC 4 x A ₂ range	2.2-7.9	1.6-2.8	0.49-0.66
NC 4 (Virginia)	1.9 ± 0.1	1.7 ± 0.1	0.53 ± 0.01
A ₂ (Valencia)	17.8 ± 2.4	2.0 ± 0.2	0.94 ± 0.02

*Standard error of mean based on within entry variance.

The frequency distribution of the R/R+V ratio for the plants of NC 4, A₂, and the F₂ generation of NC 4 x A₂ is shown in Table 3. The F₂ segregates from the cross show transgressive segregation. Several plants have lower R/R+V ratios than the low parent, NC 4. The median R/R+V ratio for the F₂ plants occurs at 0.54.

Segregation of the R/R+V ratio for these crosses was transgressive and continuous with each population having a single mode. This segregation pattern does not allow the postulation of a simple genic model to describe differences in branching pattern between the two subspecies. Branching pattern appears to be a quantitative trait.

The segregation of branching pattern in crosses between the subspecies of peanuts is similar to the segregation pattern of partial sterility found in crosses between the subspecies of rice (*Oryza sativa* L.). The nature of the intervarietal sterility in rice is a controversy among rice workers (3, 4, 8). Some say that purely genic models account for sterility while others attribute it to structural differentiation in the chromosomes. The nature of the difference in branching pattern between the subspecies of peanuts is not known. However, it is complex and requires additional study for its elucidation.

Several F₂ plants showed depressed vigor and some sterility. These observations plus the abundance of depauperate types found in this study and by Hammons (2) resemble the results found by Stephens (9, 10) in crosses between species of *Gossypium*. He concluded that cryptic structural differentiation of the chromosomes was important in the differentiation of the materials which he studied. Since limited cytological studies have been reported for cultivated peanuts, it is impossi-

ble to determine the role of chromosomal differentiation on the segregation of branching pattern.

Selection for high and low R/R+V segregates in F₂ populations from the crosses of A₂ x B₂ and B₂ x C₂ was attempted. From the cross of A₂ x B₂ and B₂ x C₂, and their reciprocals evaluated in 1972, six F₂ plants were selected from each cross and its reciprocal. Three represented extremely high R/R+V ratios and three represented low R/R+V ratios. Means for the average run of reproductive nodes, average run of vegetative nodes, and the R/R+V ratio for each F₂ plant and for the F₂ family in F₃ are given in Table 6. For A₂ x B₂, the three families selected for high R/R+V ratio averaged 0.72 while the three families selected as low averaged 0.57 for the R/R+V ratio. One of the families selected as low had a R/R+V ratio as high as some of the families selected for a high R/R+V ratio. The mean of the R/R+V of the three families selected as high was 0.90, while the three low families averaged 0.56.

Table 6. Average reproductive and vegetative run and R/R+V ratio for six selected F₂ plants and their families in F₃ generation for two crosses and their reciprocals.*

Cross	F ₂ plant or family	F ₂ plant data			F ₂ families in F ₃ generation		
		Avg R run	Avg V run	R/R+V	Avg R run	Avg V run	R/R+V
A ₂ x B ₂	1	5.6	1.3	0.88	3.3	2.2	0.61
	2	9.7	1.0	0.94	9.3	1.2	0.80
	3	5.3	1.4	0.82	4.5	2.2	0.76
	Avg				5.7	1.9	0.72
	4	1.4	2.0	0.38	9.2	3.0	0.70
	5	1.8	2.6	0.40	2.1	3.0	0.46
B ₂ x A ₂	6	1.0	2.5	0.29	5.3	2.7	0.57
	Avg				5.3	2.7	0.57
	1	13.0	0	1.00	16.4	1.4	0.92
	2	17.0	1.0	0.98	18.3	1.0	0.90
	3	13.0	0	1.00	11.4	1.4	0.87
	Avg				15.4	1.3	0.90
B ₂ x C ₂	4	1.4	2.7	0.30	2.0	2.0	0.52
	5	1.3	1.9	0.42	4.9	1.7	0.63
	6	1.5	3.3	0.31	2.1	2.1	0.52
	Avg				3.0	1.9	0.56
	1	4.4	2.0	0.69	1.8	2.2	0.47
	2	3.3	1.9	0.64	3.1	1.8	0.57
C ₂ x B ₂	3	3.0	1.7	0.67	2.0	1.6	0.56
	Avg				2.4	1.9	0.53
	4	1.3	2.4	0.32	3.6	2.9	0.50
	5	1.6	2.9	0.36	10.4	1.5	0.75
	6	1.4	2.6	0.36	2.0	2.0	0.56
	Avg				5.4	2.1	0.60
A ₂ x C ₂	1	3.6	1.7	0.71	2.0	1.7	0.56
	2	3.8	1.5	0.79	1.6	1.7	0.45
	3	3.4	2.0	0.74	2.0	1.8	0.57
	Avg				1.8	1.7	0.53
	4	2.6	2.9	0.48	1.7	2.4	0.43
	5	1.8	2.6	0.41	1.4	1.4	0.40
B ₂ x C ₂	6	2.0	2.5	0.41	2.4	2.8	0.52
	Avg				1.9	2.2	0.45
					11.1	1.9	0.87
A ₂				2.0	1.9	0.54	
B ₂				5.1	3.9	0.69	
C ₂							

*F₂ data from 1972 experiment; F₃ data from 1973 experiment.

Selection for a high or low R/R+V ratio was not effective for the B₂ x C₂ cross. The three families selected as high had a lower average R/R+V ratio than the families selected as low. Differences between the high and low families for R/R+V ratio for the reciprocal cross (C₂ x B₂) was 0.53 for the high and 0.45 for the low.

The values for the three parents grown in this experiment agree with data from the parents from

earlier experiments. The Valencia line, A₂, had a R/R+V ratio of 0.87, while the Virginia and Spanish lines had R/R+V ratios of 0.54 and 0.69, respectively.

These results show that selection for high and low R/R+V segregates was effective for the cross of the Virginia and Valencia representatives but was ineffective for the Virginia x Spanish cross. The Valencia x Virginia cross gave greater extremes in R/R+V ratio and this might have contributed to the greater effectiveness of selection. Low heritability or selective elimination of recombinant gametes might have accounted for the ineffectiveness of selection. However, the ineffectiveness of selection for high and low R/R+V types in of selection for high and low R/R+V types in Spanish x Virginia may have resulted from the origin of the Spanish varietal group. If, as W. C. Gregory (personal communication) speculates and these branching pattern data suggest, Spanish arose from the hybridization of Valencia and Virginia types, then the cross of Spanish x Virginia would in reality be a backcross to the Virginia type. The recovery of the Virginia type in the F₂ and the ineffectiveness of selection after hybridization between the Virginia and Spanish representatives would support the hypothesis that Spanish arose from crosses of Valencia and Virginia types.

Since it has been demonstrated that R/R+V types can be selected in certain crosses, it raises the question of the effect of branching pattern on fruit productivity. Studies of the optimum branching pattern required for maximum fruit productivity are still needed in order to guide the peanut breeder in the selection of genotypes after crosses between the subspecies.

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