

Genetics of non-nodulation in groundnut (*Arachis hypogaea* L.)⁽¹⁾

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Summary. — Non-nodulating groundnut plants were identified in the crosses of a rust resistant Peruvian cultivar, PI 259747, with two Virginia cultivars, NC 17 and NC Ac 2731. Segregation in the F₂ and F₃ progeny rows of the cross PI 259747 × NC 17 indicated that a pair of independent duplicate genes controls nodulation. The genetic constitution of the non-nodulating plant could be inferred to be $n_1 n_2 n_1 n_2$.

INTRODUCTION

The host-rhizobium interaction in legumes is well documented [Voorhees, 1915; Nutman, 1954; Caldwell, 1966; Hubell and Elkan, 1967*a, b* and Vest and Caldwell, 1972]. The genetic basis of non-nodulation has been described in soybean [Williams and Lynch, 1954 and Weber, 1966], red clover [Nutman, 1949] and peas [Holl, 1975]. However, there is only one recent instance of non-nodulation occurring in the cultivated groundnut, *Arachis hypogaea* L. [Gorbet and Burton, 1979]. In this study Gorbet and Burton [1979] observed non-nodulating plants in an F₃ population in a breeding nursery and these observations were confirmed in subsequent generations. However, the authors could only conclude from their studies that non-nodulation is not conditioned by a single simple recessive gene.

In 1978 it was observed that in a rust screening nursery at the ICRISAT research farm at Patancheru, near Hyderabad in India, F₂ progenies were segregating for plant colour. Plants were either normal green or yellow in colour, indicating severe nitrogen defi-

ciency. On examination the plants with yellow foliage were found to be devoid of nodules. This first paper reports the results of the genetics of non-nodulation based on data from a number of F₂ plants, and a full study on their individual F₃ progenies.

MATERIALS AND METHODS

PI 259747 is a Valencia genotype (*A. hypogaea* subsp. *fastigiata* var. *fastigiata*) of Peruvian origin and has been found to possess a high level of resistance to rust (*Puccinia arachidis*). It has been used as a parent in many crosses in breeding programs at ICRISAT. Non-nodulating plants were observed in segregating F₂ progenies of the crosses, NC 17 × PI 259747 and NC Ac 2731 × PI 259747. NC 17 and NC Ac 2731 are Virginia cultivars (*A. hypogaea* subsp. *hypogaea* var. *hypogaea*).

F₂ progenies from individual F₁ plants in the cross NC 17 × PI 259747 were planted in rows 75 cm apart and spaced at 15 cm apart within the row during the rainy season of 1978. Seeds obtained from each F₂ plant were again progeny rowed to produce the F₃ generation during the post-rainy season, 1978-79. Each individual F₂ plant was scored during the podding phase for green or yellow foliage. At harvest, F₂ plants were individually scored as nodule-bearing or non-nodulating (Fig. 1).

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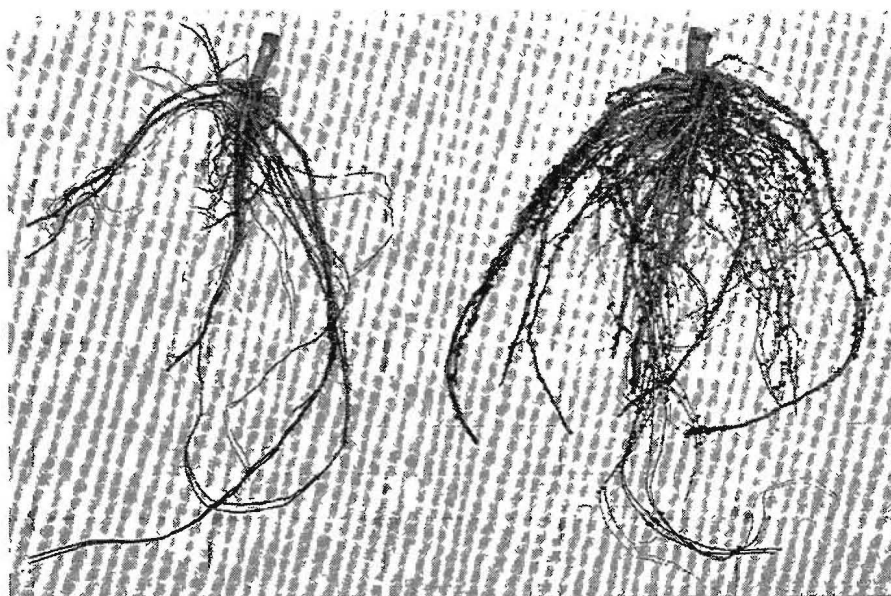


FIG. 1. — Non-nodulating (left) and nodulating (right) groundnut plants.

Data on segregation for nodulation of 19 progeny rows of the cross NC 17 × PI 259747 were examined both at F₂ and F₃ for the possible hypotheses of genetic control of nodulation using the chi-square test.

RESULTS AND DISCUSSION

When the F₂ data on the 19 progeny rows (Table I) were examined on the leaf colour-nodulation 2 × 2 contingency table, it was found that these two factors are highly associated. The data when pooled over the progeny row gave the following observed frequencies :

— Nodulating green	1 198
— Nodulating yellow	100
— Non-nodulating green	32
— Non-nodulating yellow	72
— Total	1 402

The x² test for the Null hypothesis « nodulation is independent of leaf colour » was significant (332.9) at 1 p. 100 level thus rejecting it. Hence, further analyses were based on nodulation data alone.

The F₂ data (Table I) clearly pointed to a 15 : 1 ratio for nodulating to non-nodulating plants both for most of the 19 individual progeny rows and when analysed overall. This suggests a pair of independent duplicate genes controlling nodulation. This result was based on samples of 19 to 207 plants in individual progeny rows and on 1 402 plants for the cross NC 17 × PI 259747. The genes can thus be symbolised as N₁ and N₂ with n₁ n₁ n₂ n₂ being the non-nodulating

genotype. Such an analysis was not done for the cross NC 2731 × PI 259747 in F₂.

Based on the two duplicate gene hypothesis, the F₃ data were examined for segregation with respect to nodulation in two ways. Firstly, only families which segregated for nodulation in F₃ were considered. The F₂ genotypes which would give rise to F₃ families segregating for nodulation would be

$$\frac{N_1 N_2}{n_1 n_2}, \frac{N_1 n_2}{n_1 N_2}, \frac{N_1 n_2}{n_1 n_2} \text{ and } \frac{n_1 N_2}{n_1 n_2} \text{ only.}$$

The segregation ratio for nodulating : non-nodulating would then be 27 : 5 in the F₃ generation. The test of significance of deviation from this ratio was provided by X² B. Secondly, if we consider all the F₃ families descending from all possible F₂ plants, it is apparent that we get a 1 : 1 ratio for segregating to non-segregating families in F₃, which was tested by X² C.

A remarkable fit to the expected ratios was obtained in F₃ in both cases (Table I). Since the fit to expected ratios was adequate in most of the progeny rows, as well as overall, by three tests (X² A, X² B and X² C), and as the samples are fairly large in each progeny row and adequately large over the cross, NC 17 × PI 259747, the genetic constitution of the non-nodulating plant could be inferred to be $\frac{n_1 n_2}{n_1 n_2}$.

This was well-supported by the data on the F₃ generation of the other cross, NC 2731 × PI 259747 (N = 2146 ; NN = 397 ; X² B = 0). However, the frequency of segregating to non-segregating families in F₃ did not fit to the expected ratio and this can almost certainly be attributed the loss of several F₃ families due to disease.

TABLE I
Status of nodulation in the cross NC 17 × PI 259747

Identity	Observed frequency plants in F ₂		X ² A	Observed frequency plants in segregating F ₃		X ² B	Observed frequency families in F ₃		X ² C
	N	NN		N	NN		SG	NS	
17-1	104	7	0	651	113	0.36	49	54	0.24
17-2	88	4	0.57	584	103	0.18	49	40	0.91
17-3	63	10	6.91 *	527	101	0.11	35	35	0
17-4	89	12	5.47 *	826	152	0.01	54	40	2.09
17-5	63	5	0.15	458	92	0.50	38	28	1.52
17-6	45	3	0	186	35	0	22	27	0.51
17-7	94	5	0.24	558	91	1.17	53	34	4.15
17-8	193	14	0.09	1 060	218	1.92	91	93	0.02
17-9	112	4	1.55	935	169	0.06	57	50	0.46
17-10	114	6	0.32	706	144	1.08	60	57	0.08
17-11	74	7	0.79	396	58	0.41	35	42	0.64
17-12	141	15	3.02	851	154	0.07	66	66	0
17-13	24	1	0.22	143	24	0.18	10	9	0.05
17-14	11	0	+	39	6	0.17	3	8	+
17-15	7	0	+	62	13	0.10	4	2	+
17-16	12	2	+	125	35	4.74 *	9	4	1.92
17-17	40	5	1.82	312	71	2.39	24	20	0.37
17-18	37	4	0.86	327	66	0.49	25	16	1.98
17-19	17	2	0.59	102	69	77.58 *	13	5	3.56
Total	1 298	104	3.26	8 848	1 724	3.72	697	630	3.38

N : Nodulating.
NN : Non-nodulating.

SG : Segregating.
NS : Non-segregating.

X² A : For deviation from 15 : 1 ratio.
X² B : For deviation from 27 : 5 ratio.
X² C : For deviation from 1 : 1 ratio.

* : Significant at 5 p. 100 level.

+ : Too few observations for testing a ratio.

The genetic control of non-nodulation has been well-documented in peas [Holl, 1975]. In the case of a cross, Trapper (nodulated) × Afghanistan (non-nodulated), a 3:1 F₂ segregation was obtained, indicating a single gene control for non-nodulation. However, the nitrogen fixing ability (NFA), as measured by acety-

lene reduction, was found to be controlled by two complementary genes, Trapper being the parent with high NFA. Evidence has been obtained in this study that non-nodulation is itself under the control of two duplicate genes in *Arachis hypogaea*.

REFERENCES

- [1] CALDWELL B. E. (1966). — Inheritance of a strain-specific ineffective nodulation in soybeans. *Crop Sci.*, **6**, p. 427-428.
- [2] GORBET D. W. and BURTON J. C. (1979). — A non-nodulating peanut. *Crop Sci.*, **19**, p. 727-728.
- [3] HOLL F. B. (1975). — Host plant control of the inheritance of dinitrogen fixation in the *Pisum-Rhizobium* symbiosis. *Euphytica*, **24**, p. 767-770.
- [4] HUBELL D. H. and ELKAN G. H. (1967 a). — Correlation of physiological characteristics with nodulating ability in *Rhizobium japonicum*. *Can. J. Microbiol.*, **13**, p. 235-241.
- [5] HUBELL D. H. and ELKAN G. H. (1967 b). — Host physiology as related to nodulation of soybeans by *Rhizobia*. *Phytochemistry*, **6**, p. 321-328.
- [6] NUTMAN P. S. (1949). — Nuclear and cytoplasmic inheritance of resistance to infection by nodule bacteria in red clover. *Heredity*, **3**, p. 263-291.
- [7] NUTMAN P. S. (1954). — Symbiotic effectiveness in nodulated red clover. II. A major gene for ineffectiveness in the host. *Heredity*, **8**, p. 47-60.
- [8] VEST G. and CALDWELL B. F. (1972). — R₁₄. A gene conditioning ineffective nodulation in soybean. *Crop Sci.*, **12**, p. 692-693.
- [9] VOORHEES J. H. (1915). — Variations in soybean inoculation. *J. Amer. Soc. Agron.*, **7**, p. 139-140.
- [10] WEBER C. R. (1966). — Nodulating and non-nodulating soybean isolines. I. Agronomic and chemical attributes. *Agron. J.*, **58**, p. 43-46.
- [11] WILLIAMS L. F. and LYNCH D. L. (1954). — Inheritance of a non-nodulating character in the soybean. *Agron. J.*, **46**, p. 28-29.

RÉSUMÉ

Mécanisme génétique de la non-nodulation chez l'arachide (*Arachis hypogaea* L.)
S. N. NIGAM, V. ARUNACHALAM, R. W. GIBBONS, A. BANDYOPADHYAY, et P. T. C. NAMBIAR, *Oléagineux*, 1980, **35**, N° 10, p. 453-455.

Des plants d'arachides sans nodulations ont été repérés dans des croisements entre un cultivar péruvien résistant à la rouille, le PI 259747, et deux cultivars Virginia, les NC 17 et NC Ac 2731. La disjonction dans les lignées F₂ et F₃ des descendance du croisement PI 259747 × NC 17 indique que la nodulation est contrôlée par une paire de gènes doubles indépendants. La constitution génétique de la plante sans nodulation pourrait être n₁ n₂ n₁ n₂.

RESUMEN

Mecanismo genético de la falta de nodulación en el maní (*Arachis hypogaea* L.)
S. N. NIGAM, V. ARUNACHALAM, R. W. GIBBONS, A. BANDYOPADHYAY y P. T. C. NAMBIAR, *Oléagineux*, 1980, **35**, N° 10, p. 453-455.

Plantones de maní sin nodulaciones han sido localizados en cruzamientos entre un cultivar peruano resistente a la roya, el PI 259747, y dos cultivares Virginia, los NC 17 y NC Ac 2731. La disyunción en las líneas F₂ y F₃ de las descendencias del cruzamiento PI 259747 × NC 17 muestra que la nodulación queda controlada por un par de genes duplicados independientes. La constitución genética de la planta sin nodulación podría ser n₁ n₂ n₁ n₂.

