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Absence of Root Hairs in Non-Nodulating Groundnut, *Arachis hypogaea* L.

P. T. C. NAMBIAR[1], S. N. NIGAM, P. J. DART AND R. W. GIBBONS

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru P.O., Andhra Pradesh, India 502 324

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ABSTRACT
Root hairs observed at the site of lateral root emergence in nodulating groundnut cultivars were found to be absent in non-nodulating groundnut lines. In a segregating F_2-population of the cross NC 17 × PI 259747 a strong association was observed between the presence of root hairs and nodulation, and the absence of root hairs and non-nodulation.

Keywords: Root hairs; *Arachis hypogaea*; Non-nodulation.

INTRODUCTION
The outer layers of the primary root of the groundnut seedling slough off as the growth of the root proceeds, destroying the structural base for root hairs (Petit, 1895; Richter, 1899 and Yarbrough, 1949—cited by Gregory, Gregory, Krapovickas, Smith, and Yarbrough, 1973). Hence it was suggested that groundnut seedlings lacked root hairs. Allen and Allen (1940) later observed that instead of the hairs being uniformly common and abundant in the regions of elongation of the central and lateral roots, they were extremely rare. When lateral or root tip hairs were observed they were few in number and arose at random from widely separated epidermal cells (Allen and Allen, 1940). However, tufted clusters or rosettes of hairs, were frequently found in the junction of the root axils (Waldron, 1919 and Reed, 1924—cited by Gregory *et al.*, 1973). These hairs were less fragile than those commonly found on the lateral surfaces of other leguminous roots, they had moderately thick cell walls, and averaged 2–4 mm in length (Allen and Allen, 1940). Chandler (1978) reported that some of these hairs were septate. Although these structures are often referred to as root hairs, in the strict botanical sense this may be a misnomer (Allen and Allen, 1940; Chandler, 1978).

In *Arachis hypogaea* nodules also occur at the junction of lateral root emergence (Allen and Allen, 1940; Inouye and Maeda, 1954). Rhizobia enter the root at the junction of the root hair and the epidermal and cortical cells (Chandler, 1978).

Non-nodulating lines have recently been reported in *Arachis hypogaea* (Gorbet and Burton, 1979; Nigam, Arunachalam, Gibbons, Bandyopadhyay, and Nambiar, 1980). At ICRISAT F_2-progenies of 13 crosses in the groundnut rust screening nursery were also found to be segregating for non-nodulation (Nambiar and Dart, 1980; Nambiar, Dart, Nigam, and Gibbons, 1981). Non-nodulation in groundnut is controlled by a pair of independent duplicate

[1] To whom correspondence should be addressed.

recessive genes (Nigam *et al.*, 1980). Grafting studies indicated that translocated compounds from the shoot do not influence the ability of the root to nodulate (Nambiar, 1982).

In the present study we examined the association between root hairs and nodulation in groundnut.

MATERIALS AND METHODS

Nodulating cultivars/lines

Twenty-one randomly selected, normally nodulating, groundnut cultivars/lines were tested for nodulation and they are listed in Table 1. Ten seeds each from the above were tested.

Non-nodulating lines

F_4–F_9 generation true breeding non-nodulating lines derived from 5 crosses were used in this study. The identity and the pedigree of the lines are given in Table 2. Ten plants from each from the above lines were tested.

TABLE 1. *Nodulating cultivars/lines tested for root hair formation*

1. Florunner	8. ICGS 105	15. ICG 4753
2. Florigiant	9. NC Ac 2821	16. M 13
3. TMV 2	10. MH 2	17. PI 259747
4. J 11	11. NC Ac 18089	18. NC 17
5. Gangapuri	12. Ah 7691	19. Shantung Ku No. 203
6. Kadiri 71-1	13. C 1025	20. NC Ac 2654
7. ICGS 15	14. NC Ac 10	21. NC Ac 1740

TABLE 2. *Non-nodulating lines tested for root hair formation*

Sl. No.	Cross	Generation
1	NC-Fla-14 × NC Ac 17090	F_4
2	NC-Fla-14 × NC Ac 17090	F_4
3	NC 17 × EC 76446(292)	F_4
4	NC Ac 2731 × PI 259747	F_7
5	NC 17 × PI 259747	F_8
6	NC Ac 2731 × PI 259747	F_6
7	NC Ac 2731 × PI 259747	F_6
8	NC Ac 2731 × PI 259747	F_6
9	NC 17 × PI 259747	F_9
10	NC 17 × PI 259747	F_9
11	NC 17 × PI 259747	F_9
12	NC 17 × PI 259747	F_9
13	NC 17 × PI 259747	F_9
14	NC 17 × PI 259747	F_9
15	NC 17 × PI 259747	F_9
16	NC 17 × PI 259747	F_9
17	NC 17 × PI 259747	F_9
18	NC Ac 2731 × PI 259747	F_6
19	NC 17 × PI 259747	F_9
20	NC 17 × PI 259747	F_9
21	NC Ac 2731 × PI 259747	F_6
22	Shantung Ku 203 × PI 259747	F_9
23	Shantung Ku 203 × PI 259747	F_6
24	Shantung Ku 203 × PI 259747	F_6

F_2-population

An F_2-population of the cross NC 17 × PI 259747, that produces nodulating and non-nodulating plants even though the parents are normally nodulating, and the reciprocal cross was tested for root hair production and ability to nodulate.

Scoring for root hair production

A nutrient culture techniques was used to grow plants for scoring for root hair formation. The composition of the nutrient solution used was similar to the one described by Broughton and Dilworth (1971). The seeds were germinated on wet blotting paper in trays. When the radicle was 2–4 cm in length the seedlings were transferred to a water culture system. The radicle was inserted through a 1–2 cm hole in the lid of a 22 cm diameter plastic pot that served as a suspending system for the seedling. Initially the complete root system was submerged in the nutrient solution. At the quadrifoliate stage the nutrient solution level was lowered to expose 3–4 cm of the root system to the water-saturated atmosphere in the pots. Two days later the roots axils were examined for the presence or absence of root hairs. These observations were continued for a period of five to six days.

Scoring for nodulation

After scoring for root hair formation the F_2 plants were transplanted to pots containing a mixture of sand and vermiculite (2:1, v/v) inoculated with a mixture of three *Rhizobium* strains (5a/70, NC 92 and IC 6006). The plants were supplied with nutrient solution on alternate days, and were watered to 60% water holding capacity. Thirty days after transplanting the plants were scored for nodulation.

RESULTS AND DISCUSSION

Abundant and uniform root hair production was observed in the root axils of all nodulating cultivars including those of the parents of the non-nodulating lines. The root hairs were observed only above the nutrient solution level. Other plant culture techniques failed to produce uniform root hair formation. None of the 24 stabilized non-nodulating lines produced any root hairs (Fig. 1).

The F_2 data of the cross NC 17 × PI 259747, and the reciprocal, were examined on the root hair-nodulation 2 × 2 contingency table (Table 3). It was observed that the two characters are highly associated. The x^2 test for the Null hypothesis 'nodulation is independent of root hairs' was significant for all three cases, i.e. NC 17 × PI 259747 ($x^2 = 72{\cdot}13$), PI 259747 × NC 17 ($x^2 = 22{\cdot}01$), and overall basis ($x^2 = 105{\cdot}56$), at the 0·01 probability level, thus rejecting the Null hypothesis.

However, one plant on which no root hairs were recorded at the time of observation, did bear two nodules when scored for nodulation. We have earlier reported that in the F_2 population in which non-nodulating segregants were recorded some plants had a few nodules larger than the normal ones (Nambiar *et al.*, 1981). It is possible that these plants had limited infection sites, and produce root hairs at these limited sites, and they were not observed when they were scored for root hair formation.

The F_2 data pointed to a 15:1 ratio for root hair presence to root hair absence in all three cases, i.e. NC 17 × PI 259747 ($x^2 = 0{\cdot}33$), PI 259747 × NC 17 ($x^2 = 0{\cdot}10$) and on an overall basis ($x^2 = 0{\cdot}70$). Similar ratios were obtained earlier for nodulation versus non-nodulation in much larger populations (Nigam *et al.* 1980; Nigam, Nambiar, Dwivedi, Gibbons, and Dart, 1982).

Root hairs and nodules in *Arachis hypogaea* occur only where lateral roots emerge (Allen and Allen, 1940; Inouye and Maeda, 1954; Chandler, 1978). Rhizobia cause curling and deformation of the root hair, but only enter the root at the junction of the root hair and the epidermal and cortical cells where they associate with cells at the base of the hair (Inouye and Maeda, 1954; Chandler, 1978; Dart 1977). Bhuvaneswari, Bhagwat, and Bauer, (1981) reported that nodule formation in groundnut is associated with a particular developmental stage of the root hairs. Nodules failed to develop at the bases of the laterals that possessed well developed root hairs at the time of inoculation, and are formed only when *Rhizobium* is inoculated before the emergence of the root hairs. These observations indicate either that the root hairs themselves are important in *Rhizobium* infection or that they indicate a susceptible

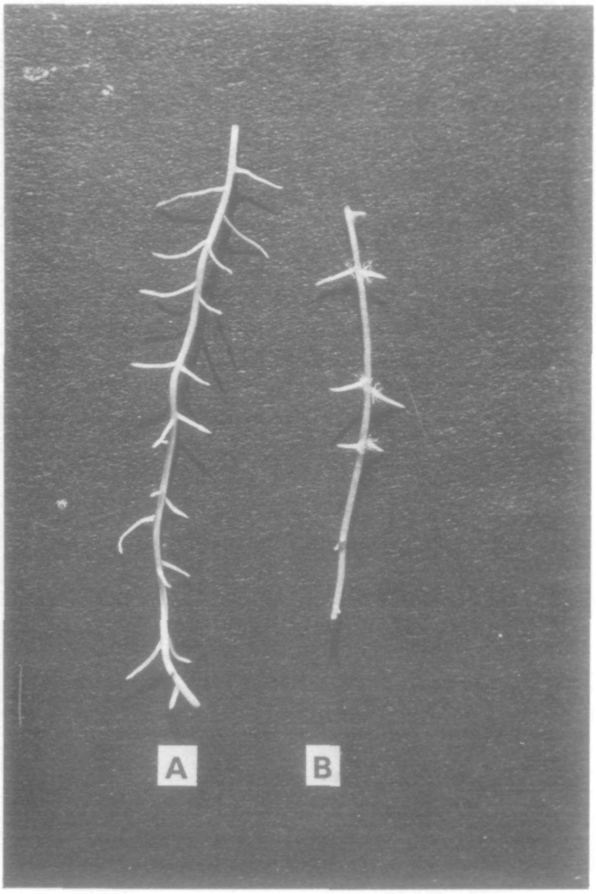

FIG. 1. (A) Root hairs are absent on the root axils of a non-nodulating line. (B) Root axils of a nodulating line with root hairs.

TABLE 3. x^2 *analysis for fitness of ratio (15 : 1) and independence of characters*

Identity		Nodulating	Non-nodulating	x^2A	x^2B
PI 259747 × NC 17	Root hair +ve	30	0	0·10	22·01**
	Root hair −ve	0	3		
NC 17 × PI 259747	Root hair +ve	90	0	0·33	72·13**
	Root hair −ve	1	7		
Total	Root hair +ve	120	0	0·70	105·56**
	Root hair −ve	1	10		

x^2A: For deviation from 15 : 1 ratio.
x^2B: For deviation from independence.
**: Significant at 1% level.

stage of lateral root emergence. However, taken together with the information of Chandler (1978) on the root hair basal cells and the correlations reported here it is difficult to avoid the conclusion that nodulation failure is associated with absence of root hairs.

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