

Inheritance of Late Leafspot Resistance and Agronomic Traits in Peanut¹

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ABSTRACT

Twenty peanut (*Arachis hypogaea* L.) populations in F₂ generation from an M x N mating design involving five late leafspot (*Cercosporidium personatum*)-resistant female parents and four adapted male parents were evaluated for late leafspot resistance with a detached leaf culture technique. Agronomic traits were evaluated in the field. Objectives were 1) to identify the best parent for agronomic traits and the best source of resistance to late leafspot, 2) determine the correlations among components of resistance, 3) determine the correlations of resistance and agronomic traits, and 4) estimate heritability of late leafspot resistance. General combining ability was highly significant for agronomic traits and for most measurements of late leafspot resistance. Specific combining ability was significant for pod length and seed size. Of the male parents, NC 6 and NC 7 produced the best progenies for both agronomic traits and late leafspot resistance. Components of resistance to late leafspot among resistant female parents were not significantly different. NC 17090 produced the best progenies for pod yield and seed yield. NC 17135 produced progenies with good agronomic traits. Correlations among components of resistance to late leafspot indicated that lines with increased latent period, decreased lesion number, lesion size and defoliation, and reduced spore production can be selected. However, high yielding plants tended to be susceptible to late leafspot. Broad-sense heritability for components of resistance was low to moderate (0.13-0.68). Narrow-sense heritability for parameters of

resistance was consistently low (0.0-0.128). Selection for late leafspot resistance in the F₂ populations was not effective.

Key Words: Groundnut, late leafspot, *Cercosporidium personatum*, combining ability, correlation, heritability.

Leafspots [*Cercospora arachidicola* Hori (early leafspot) and *Cercosporidium personatum* (Berk. & Curt.) Deighton (late leafspot)] are the most serious diseases of peanut (*Arachis hypogaea* L.) in the world (5). Yield losses from these diseases range from 15 to 50% in many production areas (5). Yield losses of 10% have been reported when fungicides were applied to control these diseases (5, 10). Differences between the two peanut leafspots have been described (4, 8). The two diseases may occur in the same geographical area or on the same leaf of a plant. Late leafspot has a greater potential to decrease yield because it produces more spores, progresses more rapidly, and causes more rapid defoliation (5) than early leafspot. Management of late leafspot with fungicides is more difficult than management of early leafspot (4). Subrahmanyam *et al.* (15) reported that PI 350680, PI 259747, EC 76446, NC 17132, NC 17133RF, NC 17135, and NC 17090 were useful sources of resistance to late leafspot. Walls and Wynne (16) crossed five of these lines (PI 259747, NC 17090, NC 17132, NC 17133RF, and NC 17135) as females with four male parents (NC 6 and NC 7 from North Carolina; Tainan 9 from Thailand; and CES 103 from Philippines) in an M x N mating design (13). All

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female parents are valencia botanical types (*A. hypogaea* L. spp. *fastigiata* var. *fastigiata*) with resistance to late leafspot and rust. They have two to four small seeds per pod. NC 6 and NC 7 are Virginia runner types (*A. hypogaea* L. spp. *hypogaea* var. *hypogaea*). NC 7 has a low level of resistance to early leafspot while NC 6 has a high degree of resistance to southern corn rootworm. NC 6 and NC 7 have large seed and pods with two seeds per pod. Tainan 9 and CES 103 are spanish types (*A. hypogaea* L. spp. *fastigiata* var. *vulgaris*) lines with small seed and pods and are both very susceptible to early and late leafspots. Walls and Wynne (16) reported that NC 7 was the best parent of the four males when evaluating disease resistance by using the detached leaf technique, but they found no significant difference among the five resistant lines for disease resistance in terms of general combining ability estimated using F_1 generation progenies.

Additional information on the performance of the resistant lines is needed to identify the best parents for use in a cultivar development program. This study was conducted to determine the combining ability for late leafspot resistance as well as agronomic traits for the parents used by Walls and Wynne (16) with F_2 generation progenies. This study also provides correlation estimates among components of partial resistance and between components of partial resistance and agronomic traits. In addition, a separate study was conducted to determine both broad- and narrow-sense heritability estimates for components of late leafspot resistance for two of the populations.

Materials and Methods

Study 1

The 20 breeding populations in the F_2 generation from the $M \times N$ mating of Walls and Wynne (16), the nine parents (NC 17090, NC 17132, NC 17133RF, NC 17135, PI 259747, NC 7, NC 6, Tainan 9, and CES 103), and a susceptible check (NC 3033) were planted at the Peanut Belt Research Station, Lewiston, NC in May 1985 using a randomized complete block design with 10 replications. Seeds were treated with fungicide and planted in five-seed, single-row plots with 25 cm between plants within a row and 91 cm between rows. Normal cultural practices were followed during the growing season except that no fungicide was used to control leafspots. A detached leaf culture technique (9) was used to evaluate resistance to late leafspot. Eight weeks after planting, a fully expanded leaf was detached from each plant at the third node from the terminal bud of the main stem. Leaves were detached from approximately 40-50 plants per cross for evaluation. Individual leaves were placed separately into plastic bags which were placed in chests containing ice and transported to Raleigh, NC. Petioles of the detached leaves were inserted into moist sand in a plastic tray with the same design as the field planting. Trays were placed in a mist bed where they were sprayed with water for 10 seconds every 3 minutes. After 15 days the trays were removed from the greenhouse, and leaves were allowed to dry in preparation for inoculation. Conidia of *C. personatum* from susceptible infected leaves of greenhouse-grown NC 3033 were collected into small test tubes using a Cyclone spore collector (Eri Machine Shop, Iowa State Univ., Ames). Conidia were suspended in water with a few drops of Tween 80 (polyoxyethylene sorbitan monooleate). Spore concentration was determined with a hemacytometer and adjusted to 35,000 spores/mL. Leaves were inoculated with a mist of the spore suspension using an atomizer (approximately 20 mL of suspension per 50 leaves). Trays of inoculated leaves were placed in a mist bed and covered with chambers made of wooden frames enclosed with plastic. Temperatures of 26-30 C and humidity of approximately 80-90% were maintained throughout the test.

The following components of resistance were evaluated on detached

leaves:

1. Total number of lesions/leaf on day 22 after inoculation;
2. Lesion area in mm^2 , taken as an average of four representative lesions/leaf on day 27;
3. Latent period, determined as the number of days from inoculation until 50% of leaf lesions were sporulating;
4. Spore production based on a visual rating at day 26 using a scale of 1-5 with 1 indicating very little sporulation and 5 indicating heavy sporulation;
5. Defoliation as the number of defoliated leaflets at day 30; and
6. Lesion number/100 cm^2 of leaf area (total lesion number \times 100/leaf area). Leaf area in cm^2 was measured on a Li-Cor Leaf Area Meter (Li-Cor, Ltd., Lincoln, NB).

After leaves were detached, plants in the field were treated with fungicides to control diseases and allowed to reach maturity. Individual plants were harvested and the following agronomic traits were determined: (a) pod yield (g/plant), (b) pod length (cm/10 pods), (c) seed yield (g/plant), (d) seed size (g/100 seeds), and (e) shelling percentage (seed yield \times 100/pod yield).

Univariate analysis was performed on the data. A natural log transformation was required to normalize distributions for pod yield, pod length, seed yield, lesion number per 100 cm^2 of leaf area, and defoliation. A sine⁻¹ transformation was required for shelling percentage. Multivariate analysis was performed for all components of resistance except defoliation. Principal components were created with the following formula:

$$\text{Principal components} = \text{ESSQ} * \text{TSSQ}$$

where: ESSQ = errors sums of squares and the cross product inverse matrix, and

TSSQ = treatment sums of squares and cross product matrix.

Coefficients from the first principal component, which explained most of the variation for disease resistance, were used to weight each resistant component (12). A disease index was created by summing the weighted products. Analysis of variance on parents in the hybrid combinations from an $M \times N$ mating design was performed to estimate general and specific combining ability (GCA, SCA). GCA and SCA effects were calculated using the methods of Simmonds (13). Simple correlations among components of resistance, agronomic traits, and components of resistance with agronomic traits were computed.

Study 2

F_2 Generation. In November 1984, two crosses (NC 17090 \times NC 7 and NC 17090 \times Tainan 9) in F_1 and F_2 generations, the parents, and a susceptible check (NC 3033) were planted in the greenhouse at North Carolina State University in 22-cm plastic pots with a 3:2:3 mixture of soil, peat moss, and sand in a randomized complete block design with eight replications. Seeds were treated with fungicide and planted one seed in a pot with five seeds for segregating material and one seed for nonsegregating material per replication. Plants were maintained for 10 weeks and were not sprayed with fungicide. A leaf at the third node from the terminal bud of the main stem from each of 40 plants per cross was removed and resistance to late leafspot was determined using the previously described detached leaf culture technique. Inoculated leaves were incubated at 23-26 C and 80-90% relative humidity.

F_3 Generation. Individual F_2 plants were harvested to obtain F_3 seeds. The F_3 progenies, parents, and a susceptible and resistant check were planted at the Peanut Belt Research Station, Lewiston, NC in May 1985 in a randomized complete block design. Ten seeds from each F_2 plant, parental cultivars, and susceptible checks (NC 3033) were separately planted in two replications of single row plots with five plants each. Eight weeks after planting, a leaf was removed from each of approximately 10 plants per family and the detached leaf culture technique was used to evaluate resistance to late leafspot. Components of resistance were evaluated as previously described.

A natural log transformation was required to normalize the distribution for lesion number and defoliation. A disease resistance index was computed as previously described. Broad-sense heritability was estimated using the method suggested by Allard (1). Narrow-sense heritability was estimated by regression of a trait for the F_3 progeny mean on the same trait measured on individual F_2 plants (14).

Results and Discussion

Combining Ability Analysis (Study 1)

Mean squares for general combining ability (GCA) were highly significant for all agronomic traits. Specific

combining ability (SCA) was significant for pod length and seed size. Results indicate that agronomic traits are conditioned by genes acting in an additive manner. Nonadditive gene effects, however, were important for pod length and seed size. Similar results were reported by Hamid *et al.* (6) and Wynne (17). The GCA effects for agronomic traits (Table 1) indicate that NC 7 and NC 6 were consistently the best male parents for all agronomic traits except shelling percentage. CES 103 and Tainan 9 had the lowest GCA for agronomic traits, indicating that these cultivars produced agronomically unacceptable progenies when evaluated in North Carolina. Among female parents, NC 17090 was best for GCA effects for pod and seed yield. NC 17135 was one of the best parents for GCA effects for pod and seed yield. Lesion size, lesion number, spore production, and disease index had significant GCA effects; but SCA effects were nonsignificant for all parameters of resistance to *C. personatum*. These results indicate that resistance to late leafspot was controlled by additive genes in these populations. Similar results had been reported earlier (2, 6, 16). NC 7 and NC 6 had the best GCA effects of the four male parents for all components of resistance except defoliation and latent period (Table 2). A large negative value for both GCA and SCA effects is desirable for all components of resistance except latent period. CES 103 and Tainan 9 produced progenies that had the lowest GCA effects for almost all resistance parameters. Resistant parents were not significantly different for GCA effects. These results indicated that resistance to late leafspot was controlled by a similar genetic system in each of the resistant parents.

Table 1. Estimates of general combining ability effects for agronomic traits for nine peanut genotypes.

Parent	Pod yield (g/plant)	Pod length (cm/10 pods)	Seed yield (g/plant)	Seed size (g/100 seed)	Shelling percentage
Females					
NC 17090	0.19	-0.06	0.20	-5.16	0.01
NC 17132	-0.06	0.06	-0.04	2.38	0.02
NC 17133RF	-0.09	0.07	-0.06	4.21	0.03
NC 17135	0.04	0.06	0.01	2.36	-0.02
PI 259747	-0.07	-0.12	-0.13	-3.78	-0.03
LSD 0.05	0.16	0.04	0.18	2.81	0.04
Males					
NC 6	0.08	0.08	-0.01	2.78	-0.04
NC 7	0.19	0.11	0.14	9.51	-0.02
CES 103	-0.15	-0.07	-0.09	-7.05	0.04
Tainan 9	-0.12	-0.10	-0.05	-5.24	0.05
LSD 0.05	0.14	0.04	0.17	2.51	0.03

Table 2. Estimates of general combining ability effects for components of resistance to late leafspot for nine peanut genotypes.

Parent	Lesion size (mm ²)	Lesion no. (/100 cm ² leaf area)	Latent period (days)	Defoliation (%)	Sporulation (1-5)	Index
Females						
NC 17090	0.10	-0.08	-0.15	-0.05	0.15	0.02
NC 17132	-0.07	0.10	-0.10	0.01	0.02	0.00
NC 17133RF	0.08	0.00	0.02	-0.04	0.03	0.01
NC 17135	-0.04	-0.02	0.31	0.02	-0.15	-0.01
PI 252747	-0.08	0.02	-0.07	0.06	-0.03	0.00
LSD 0.05	NS	NS	NS	NS	NS	NS
Male						
NC 6	-0.21	-0.11	0.10	0.05	-0.21	-0.03
NC 7	-0.33	-0.09	0.13	0.01	-0.31	-0.04
CES 103	0.25	0.15	-0.08	0.01	0.23	0.04
Tainan 9	0.30	0.07	-0.14	-0.07	0.31	0.05
LSD 0.05	0.27	0.01	NS	NS	0.19	0.04

Walls and Wynne (16) found that NC 7 was the best parent when selecting for resistance to late leafspot. There was no significant difference among the resistant parents when combining ability was determined in the F₁ generation. NC 7 was selected from a breeding line of NC 5 x Fla 393 involving a parent with partial resistance to late leafspot. Kornegay *et al.* (8) reported that NC 5 was the best parent for resistance to both early and late leafspots. NC 7, selected from the progeny of NC 5, also may have some resistance genes. Hamid *et al.* (6), Kornegay *et al.* (8) and Anderson (2) also reported that GP-NC 343 was the best cultivar for incorporation of resistance to early and late leafspots into a single genotype. Since GP-NC 343 was a parental line of NC 6, this cultivar is expected to have leafspot resistance genes. Based on our results, both NC 6 and NC 7 as parents contributed to resistance of progenies, especially in terms of reduced lesion size and decreased sporulation. Estimates of GCA effects among source of resistant parents were nonsignificant, *i. e.*, all resistant parents produced progeny with similar resistance to late leafspot.

Heritability (Study 2)

Broad-sense heritability for all parameters of resistance to late leafspot in F₂ generation of the cross of NC 17090 x Tainan 9 was low, especially for latent period and sporulation. Broad-sense heritability estimates for the cross of NC 17090 x NC 7 were intermediate for lesion size and sporulation, but low for latent period and lesion number (Table 3).

Table 3. Broad-sense (H) and narrow-sense heritability (h²) for components of resistance to *C. personatum* of two selected peanut breeding populations.^a

Components	H = σ_G^2/σ_P^2	h ² = 2/3 b
NC 17090 x Tainan 9		
Lesion size (mm ²)	0.49	0.009
Latent period (days)	0.13	0.006
Lesion no. (/100 cm ² leaf area)	0.20	0.036
Sporulation (1-5)	0.13	0.014
NC 17090 x NC 7		
Lesion size	0.68	0.000
Latent period	0.33	0.019
Lesion no.	0.30	0.128
Sporulation	0.55	0.023

^a σ_G^2 = genotypic variance, σ_P^2 = phenotypic variance, b = parent-offspring regression coefficient.

Narrow-sense heritability estimated from parent-offspring regression was consistently low for all parameters of both breeding populations (Table 3). These results suggested that selection for superior plants would be ineffective in the F₂ generation, and selection for resistance to *C. personatum* should be done in an advanced generation.

In contrast, Anderson (2), in a crossing study with four *C. personatum* and four *C. arachidicola*-resistant parents, reported that high heritability was found for all components of resistance to both early and late leafspots in F₂ generation. He concluded that individual plant selection would be effective for assessment of resistance in the greenhouse during early generations. His heritability estimates, however, were broad-sense. Nevill (11)

reported that the magnitudes of correlation between resistant characters recorded on F₂ plants in the laboratory and F₃ in the field were generally low. He indicated that this was probably caused by environmental difference and by large nonadditive components of gene action.

Estimated heritability by parent-offspring regression can be confounded either by environment or interaction of genotype and environment. In practice, progeny-parent regression involves regressing the data obtained from the progeny in one environment upon the parental data obtained in another environment. In this study, the F₂ plants were in the greenhouse while the F₃s were in the field. Predisposition probably alters susceptibility of plants (18). Hassan and Beute (7) indicated that plants maintained continuously in the greenhouse tended to develop more lesions than those maintained outside. Cook (3) found that detached leaves from field plants were less susceptible to *C. personatum* than those from greenhouse plants.

The low narrow-sense heritability estimates in this study may have been attributable to the number of leaves evaluated. Only one leaf from each plant was used to evaluate resistance to disease in both the F₂ and F₃ generations. Multiple samples may have given better estimates of individual plant resistance.

Correlations (Study 1)

All components of resistance were significantly correlated. Latent period was negatively correlated with the other components which were positively correlated with one another (Table 4). Correlations between the components of resistance found in this study are in agreement with results obtained by Anderson (2), Nevill (11), and Walls and Wynne (16). Nevill (11) reported a high correlation among components of resistance and proposed that a similar polygenic system acted to control the expression of all these characters. The results of this study support previous observations that peanut breeding lines can be selected that have increased latent period, decreased lesion number, decreased lesion size and defoliation, and reduced spore production.

Table 4. Correlation coefficients for factors associated with resistance to *C. personatum* of F₂ peanut genotypes (study II).

Components	Lesion no. (/100 cm ² leaf area)	Lesion size (mm ²)	Defoliation (%)	Sporulation (1-5)
Latent period (days)	-0.29**	-0.44**	-0.32**	-0.57**
Lesion no. (/100 cm ² leaf area)	--	0.59**	0.50**	0.61**
Lesion size (mm ²)		--	0.21**	0.81**
Defoliation (%)			--	0.22**

**Indicates significance at 1% level.

Pod yield was significantly correlated with seed yield and size but was not correlated with pod length and shelling percentage (Table 5). Pod length was not correlated with seed yield or seed size with shelling percentage. Pod length was correlated with seed size but negatively correlated with shelling percentage. Seed yield was positively correlated with both seed size and shelling percentage.

Correlation of components of resistance and the disease resistance index to agronomic parameters (Table 6)

Table 5. Correlation coefficients for agronomic traits of F₂ peanut genotypes (study I).

Traits	Pod length (cm/10 pods)	Seed yield (g/plant)	Seed size (g/100 seed)	Shelling percentage
Pod yield (g/plant)	0.03	0.94**	0.36**	0.01
Pod length (cm/10 pods)	--	-0.06	0.55**	-0.35**
Seed yield (g/plant)		--	0.30**	0.31**
Seed size (g/100 seed)				-0.09

**Indicates significance at 1% level.

indicated that pod yield, seed yield, and shelling percentage were positively correlated with plant susceptibility to disease. In contrast, pod length and seed size were negatively correlated with plant susceptibility. These results indicated that pod length, seed size, and disease-resistance genes were associated.

Table 6. Correlation coefficients of components of resistance and agronomic traits of F₂ peanut genotypes (study I).

Traits	Lesion size (mm ²)	Lesion no. (/100 cm ² leaf area)	Latent period (days)	Defoliation (%)	Sporulation (1-5)	Index ^a
Pod yield (g/plant)	0.05	0.05	-0.13*	0.02	0.12*	0.12*
Pod length (cm/10 pods)	-0.34**	-0.18**	0.32**	-0.08	-0.47**	-0.49**
Seed yield (g/plant)	0.09	0.08	-0.12*	0.03	0.16**	0.16**
Seed size (g/100 seed)	-0.12*	-0.01	0.03	0.01	-0.13*	-0.12*
Shelling percentage	0.13*	0.11*	-0.04	0.03	0.16**	0.16**

^aCreated by using the first principle component from multivariate analysis of lesion size, lesion number, spore production, and latent period.

*,**Significant at the 5 and 1% levels, respectively.

Although selection of individual plants for disease resistance with these peanuts would not be effective in the F₂ generation of these breeding populations because of low heritability, selection was possible for highly heritable traits such as increased pod length and seed size. Wynne (17) found high correlations of early and advanced generation selection for pod length and seed size. In this study of these breeding populations, we observed a high correlation between pod length and seed size with disease resistance, *i.e.*, plants having longer fruit and larger seeds were more resistant to leafspot. These results suggest that selection for desired pod length and seed size could be practiced in early generation while selection for disease resistance would be more effective in later generation.

Literature Cited

- Allard, R. W. 1960. Principles of Plant Breeding. John Wiley & Sons, Inc., New York. p. 103-107.
- Anderson, W. F., J. C. Wynne, and C. C. Green. 1986. Potential for incorporation of early and late leafspot resistance in peanut. Plant Breeding 97:163-170.
- Cook, M. 1981. Susceptibility of peanut leaves to *Cercosporidium personatum*. Phytopathology 71:787-791.

4. Feakin, S. D. 1973. Pest Control in Groundnut. PANS Manual No. 2. 138 pp.
5. Garren, K. H., and C. R. Jackson. 1973. Peanut diseases, pp. 429-433. Peanut Culture and Uses. Amer. Peanut Res. Educ. Assoc., Yoakum, TX.
6. Hamid, M. A., T. G. Isleib, J. C. Wynne, and C. C. Green. 1981. Combining ability analysis of *Cercospora* leafspot resistance and agronomic traits in *Arachis hypogaea*. *Oleagineux* 36:605-612.
7. Hassan, H. N., and M. K. Beute. 1977. Evaluation of *Cercospora* leafspot in peanut germplasm potentially useful in a breeding program. *Peanut Sci.* 4:78-83.
8. 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.
9. Melouk, H. A., and D. J. Banks. 1978. A method of screening peanut genotypes for resistance to *Cercospora* leafspot. *Peanut Sci.* 5:112-114.
10. Mixon, A. C., R. O. Hammons, and W. D. Branch. 1983. Germplasm for use in genetic enhancement of peanut genotypes. *Amer. Peanut Res. Educ. Soc.* 15:15-38.
11. Nevill, D. J. 1982. Inheritance of resistance to *Cercosporidium personatum* in groundnut: A genetic model and its implications for solution. *Oleagineux* 37:355-366.
12. SAS. 1985. User's Guide: Statistic. Version 5 Ed. Cary, NC. p. 445-504.
13. Simmonds, N. W. 1979. Combining ability, pp. 110-111. in N. W. Simmonds (ed.), *Principles of Crop Management*. Longman Group, Ltd., London.
14. Smith, J. D., and M. L. Kinman. 1965. The use of parent-offspring regression as a parameter of heritability. *Crop Sci.* 5:595-596.
15. Subrahmanyam, P., D. McDonald, R. W. Gibbons, S. N. Nigam, and D. J. Nevill. 1982. Resistance to rust and late leafspot diseases in some genotypes of *Arachis hypogaea*. *Peanut Sci.* 9:6-10.
16. Walls, S. B., and J. C. Wynne. 1985. Combining ability for resistance to *Cercosporidium personatum* for late leafspot-resistance peanut germplasm lines. *Oleagineux* 40:389-395.
17. Wynne, J. C. 1976. Evaluation of early generation testing in peanut. *Peanut Sci.* 3:62-66.
18. Yarwood, C. D. 1976. Modification of host response predisposition, pp. 703-718. in R. Heitefuss and P. H. Williams (eds.), *Physiological Plant Pathology*. Springer-Verlag, New York.

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