

Components of Resistance in Peanut to *Cercospora arachidicola*

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ABSTRACT

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Twenty genotypes of peanut (*Arachis hypogaea*) were tested in the greenhouse and ranked in increasing order of resistance to early leaf spot (*Cercospora arachidicola*) for each of the following components of rate-reducing resistance: number of lesions per leaf, lesion diameter, latent period, time until leaflet defoliation, and sporulation. With the exception of lesion diameter, differences among genotypes were found for all components. Number of lesions was influenced greatly by environment and therefore was an unreliable means to evaluate these genotypes in the greenhouse. Ranking of genotypes for latent period was consistent with two methods of measuring latent period: time until at least two lesions sporulated and time until 50% of the lesions sporulated. Genotypes with longer latent periods and fewer sporulating lesions generally had a longer period until leaflet defoliation. Genotype NC 3033 showed the greatest overall resistance to early leaf spot.

Early and late leaf spot, caused by *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton, respectively, are serious diseases of peanut (*Arachis hypogaea* L.) wherever the crop is grown (3-5). Significant losses occur in the absence of control measures (2,10,15). Cultural practices offer only partial control, fungicide spray programs are generally expensive, and all cultivated varieties of peanuts are susceptible to the pathogens (18). Therefore, the development of peanut cultivars resistant to leaf spot is essential.

Parlevliet (17) discussed the value of evaluating rate-reducing resistance through its components and suggested that the components are often interrelated. Several investigators have used this approach for leaf spot of peanut (7,8,14,16). Nevill (16) found that leaves of cultivars resistant to *Cercosporidium personatum* had longer latent periods, reduced capacity for sporulation, and less defoliation than leaves of susceptible cultivars; however, such interrelationships among the components were not so

clearly present for *Cercospora arachidicola* and the same cultivars.

In a recent study, little or no sporulation was observed on attached leaflets of *Arachis batizocoi* Krep. et Greg. (7), a species resistant to *C. arachidicola*. Abscinded leaflets of *A. batizocoi* supported abundant sporulation of *C. arachidicola*. This may indicate the presence of additional differences in resistance. It is not known if the increase in sporulation after defoliation is an occurrence common to most peanut genotypes.

The objectives of this investigation were to evaluate 20 peanut genotypes for components of rate-reducing resistance to early leaf spot, to test for possible interrelationships among the components, and to determine the effect of leaflet detachment on fungal sporulation.

MATERIALS AND METHODS

Isolates of *C. arachidicola* were collected from infected Florigiant plants in a field at Lewiston, NC, on 7 October 1982 and maintained on peanut leaf extract agar (1) supplemented with 0.5 g of yeast extract per liter. After the initial test in this study, *C. arachidicola* was maintained on plants in the greenhouse. After incubation for 3 days, spores were collected from lesions on the stock plants with a cyclone spore collector (ERI Machine Shop, Iowa State University, Ames). These dry spores were viable after 3 mo of refrigerated storage. Inoculum could be collected more easily, in larger amounts, and presumably with less loss of pathogenicity than from the peanut extract medium described by Abdou and Cooper (1). Spores were suspended in deionized water with one drop of Tween 80 per 100 ml, and concentrations were determined with a hemacytometer. Inoculum was applied to the upper surface of each peanut leaflet with an

artist's airbrush at about 0.6 kg/cm² air pressure so that the leaves were wetted without droplet runoff.

Seventeen peanut breeding lines and the commercial cultivars Florigiant, NC 2, and NC 5 were obtained from J. C. Wynne, North Carolina State University. These genotypes, representing a range of resistance to early leaf spot, were chosen after evaluation in small field plots at North Carolina State University. Plants of each genotype were grown either from seed or from shoot cuttings taken from peanut plants in field plots. Plants were grown in a soil-sand mixture (2:1, v/v) containing *Rhizobium* inoculant (Nitragin Co., Inc., Milwaukee, WI). The detached leaf inoculation technique of Melouk and Banks (13) was used. The third fully expanded leaf from the shoot terminus was excised at the base of the petiole. A maximum of two leaves were collected from each. Petioles were inserted in test tubes (1 × 10 cm) containing modified Hoagland's solution (Sequestrene 330 was used as the source of chelated iron) (6). Tubes were placed in holes drilled into boards and put inside moist chambers equipped with either automatic misters or electrical cool-vapor humidifiers. Detached leaves were hand-misted three times per day.

Genotypes were evaluated in the greenhouse for the following components of rate-reducing resistance: number of lesions per leaf, lesion diameter, latent period, maximum percentage of lesions sporulating (MPLS), sporulation per lesion, and time until leaflet defoliation. Shoot cuttings for each genotype were taken from peanut plants in a field at Lewiston, NC. Twenty cuttings per genotype (about 12 cm from the short terminus) were prepared. Rootone F was applied to the freshly cut surface of each cutting before it was placed in a flat of sterile sand under a misting system. Ten cuttings per genotype were transferred first to 10-cm-diameter plastic pots and then to 30-cm-diameter plastic pots 1 mo later. Twelve leaves per genotype were inoculated with an aqueous suspension of spores of *C. arachidicola* (9×10^3 spores per milliliter) and returned to bench-top moisture chambers (19-39°C) with a cool-vapor humidifier running continuously in each chamber. Number of lesions per leaf was recorded 21 days after inoculation (day 21). On day 27, one large and one medium-sized lesion from each leaf were excised (within a small circle of leaf tissue), grouped by genotype and

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chamber, and placed on moist filter paper in sterile petri plates. Three days later, each lesion was placed in a 1-ml aliquot of water plus Tween 80 (one drop per 100 ml). Number of spores was estimated with four subsamples per each 1-ml volume aliquot with a hemacytometer. Lesion diameter was then measured in two perpendicular directions. Sporulation was expressed as spores per lesion.

Sixteen leaf cuttings per genotype were inoculated with an aqueous suspension containing 1×10^4 , 2.5×10^4 , 5.5×10^4 , or 1×10^5 spores per milliliter, placed in chambers (14–28 C) under a greenhouse bench, and misted every 2 min for 30-sec intervals. Lesions were counted on day 19. Beginning on day 18, the percentage of lesions sporulating was determined three times per week with a hand-held magnifying lens. Leaflet defoliation was recorded concurrently.

Two additional tests were conducted with detached leaves obtained from the 20 genotypes grown from seed in the greenhouse. In one test, 16 cuttings from each genotype were inoculated with 2×10^4 spores per milliliter. Leaves were maintained for 2 wk and misted every 2 min for 2-sec intervals. Leaves were then moved to chambers with humidifiers, and total number of lesions was recorded on day 21. Percentage of lesions sporulating was determined on days 15, 17, 19, 21, 24, 27, and 30. A second test was conducted with cuttings from the same plants. All procedures were identical to the previous test, except 20 cuttings were collected from each genotype.

Two tests were conducted to quantify sporulation on attached and detached leaflets. In the first test, leaves containing lesions from genotypes Florigiant (entry

81), NC 5 (entry 3), NC-GP 343 (entry 336), NC 5 × Florigiant (entry 65), and Florigiant × NC-GP 343 (entry 44) were collected from a field in Lewiston, NC. Ten pairs of lesions were matched by size for each genotype. One lesion from each pair (on an intact leaflet excised from a leaf) was placed on an open counter top overnight. The second lesion was on a single leaflet attached to the peanut stem held in a tube of Hoagland's solution. Conidia were removed from the lesions the following morning with a nylon brush and a stream of water. Detached leaflets were placed on plates of moistened field soil to simulate conditions after defoliation. Tubes and plates were left in a tabletop moisture chamber in the greenhouse for 2 days. Lesions were then excised from the leaflets and one lesion was placed in each tube containing 0.5 ml of water plus Tween 80. Spores per lesion were counted with a hemacytometer.

In the second test, leaflets of genotypes NC 3033 (entry 12), NC 2 × NC 5 (entry 21), NC-GP 343 × NC 2 (entry 58), NC-TP 343 × NC 5 (entry 88), and NC 3033 × NC-GP 343 (entry 104) were inoculated in the greenhouse and treated as in the previous test, but tubes and plates were incubated in plastic boxes containing water and left in the laboratory under continuous fluorescent light. Leaflets were hand-misted with deionized water four times per day. Two days later, two lesions per genotype treatment were excised and assayed as in the previous test.

In all tests, genotypic subsamples were blocked within each of three to five chambers because of observed differences in light incidence. For each test, genotypes were ranked in increasing

order of resistance for the given component under evaluation. These rankings were used to evaluate genotypic performance, to compare results between tests, and to identify possible inter-relationships among the components of resistance. Rankings were compared with Spearman's nonparametric test of rank correlation (20).

RESULTS

Number of lesions. When ranked by number of lesions per leaf, genotypes varied from test to test (Table 1). Genotype NC-Ac 3139 × NC-GP 343 (entry 75), for instance, had the greatest number of lesions in test 1, the fewest in test 2, and an intermediate number in test 3. Within a single test, however, order of genotypes was relatively consistent among the four inoculum densities (Table 2). Because variance of number of lesions increased with increasing inoculum density, weighted regression analyses were performed using the reciprocals of the variances as weights (20). Inoculum density as the independent variable in linear regression analysis accounted for 71–99% of the variation in the average number of lesions per genotype. From the linear model, it was determined that the inoculation methods were quantitatively acceptable, and the proportion of variance explained by the model for variability in number of lesions within a single test was acceptable. Leaf area was not measured in any of the tests, since Foster et al (8) found that conversion to number of lesions per square centimeter of leaf is not necessary if all the peanut germ plasm are either wild or cultivated lines.

Table 1. Rankings of 20 peanut genotypes for average number of lesions of *Cercospora arachidicola* per leaf

| Test 1 | | | Test 2 | | | Test 3 | | |
|------------------------|-------|------------------|------------------------|-------|-------------------|------------------------|-------|------------------|
| Genotype | Entry | Lesions per leaf | Genotype | Entry | Lesions per leaf | Genotype | Entry | Lesions per leaf |
| NC-Ac 3139 × NC-GP 343 | 75 | 24.6 | NC 3033 | 12 | 71.6 | NC 3033 × NC 2 | 64 | 55.2 |
| Florigiant × NC-GP 343 | 50 | 22.9 | Florigiant × NC-GP 343 | 50 | 65.3 | NC 3033 × NC-GP 343 | 104 | 54.2 |
| NC-GP 343 × NC 2 | 57 | 22.9 | NC-Ac 3139 × NC-GP 343 | 75 | 59.5 | NC 2 × NC 5 | 21 | 51.1 |
| NC-GP 343 × NC 5 | 88 | 17.7 | NC-GP 343 × NC 5 | 86 | 58.6 | NC-GP 343 × NC 2 | 57 | 50.3 |
| NC 5 × Florigiant | 66 | 16.2 | NC 3033 × NC-GP 343 | 102 | 57.9 | NC-Ac 3139 × NC-GP 343 | 75 | 49.5 |
| NC 3033 × NC-GP 343 | 104 | 15.5 | NC 5 | 3 | 55.8 | NC 5 × Florigiant | 66 | 47.6 |
| NC-GP 343 × NC 2 | 58 | 15.1 | NC-GP 343 × NC 2 | 57 | 55.3 | Florigiant × NC-GP 343 | 50 | 46.4 |
| NC 3033 | 12 | 14.9 | NC 5 × Florigiant | 66 | 53.5 | NC 5 | 3 | 46.1 |
| Florigiant × NC-GP 343 | 44 | 14.1 | NC 3033 × NC 2 | 64 | 52.2 | NC 5 × Florigiant | 65 | 43.2 |
| NC-Ac 3139 × NC-GP 343 | 79 | 13.5 | NC 2 × NC 5 | 8 | 49.4 | NC-GP 343 | 336 | 40.8 |
| NC 5 | 3 | 13.5 | NC-GP 343 × NC 2 | 58 | 48.1 | NC-GP 343 × NC 5 | 86 | 38.9 |
| Florigiant | 81 | 12.5 | NC-Ac 3139 × NC-GP 343 | 79 | 46.8 | NC 2 × NC 5 | 8 | 38.2 |
| NC-GP 343 | 336 | 9.6 | NC-GP 343 × NC 5 | 88 | 45.1 | Florigiant | 81 | 36.6 |
| NC 2 × NC 5 | 21 | 8.7 | Florigiant × NC-GP 343 | 44 | 44.8 | NC 3033 × NC-GP 343 | 102 | 35.6 |
| NC 5 × Florigiant | 65 | 8.7 | NC 5 × Florigiant | 65 | 43.9 | NC 3033 | 12 | 34.8 |
| NC 3033 × NC 2 | 64 | 8.5 | NC 3033 × NC-GP 343 | 104 | 43.3 | NC 2 | 1 | 33.4 |
| NC 2 | 1 | 8.2 | Florigiant | 81 | 42.1 | NC-Ac 3139 × NC-GP 343 | 79 | 33.1 |
| NC-GP 343 × NC 5 | 86 | 8.0 | NC 2 | 1 | 40.9 | NC-GP 343 × NC 2 | 58 | 31.9 |
| NC 3033 × NC-GP 343 | 102 | 6.1 | NC-GP 343 | 336 | 40.3 | Florigiant × NC-GP 343 | 44 | 28.8 |
| NC 2 × NC 5 | 8 | 5.3 | NC 2 × NC 5 | 21 | 38.8 | NC-GP 343 × NC 5 | 88 | 26.5 |
| SE ^a | | 3.7 | | | 6.2 | | | 6.1 |
| df | | 49 | | | 57 | | | 57 |
| ID | | 9×10^3 | | | 2.5×10^4 | | | 2×10^4 |

^aSE = standard error of lesions-per-leaf means, df = error degrees of freedom, and ID = inoculum density applied to leaves (spores per milliliter).

Lesion diameter and sporulation. Differences in sporulation among genotypes were apparent when estimated on a per-lesion basis (Table 3). Significant differences in lesion diameter were not found among genotypes; means ranged from 1.25 mm for NC-GP 343 (entry 336) to 1.92 mm for NC-GP 343 × NC-2 (entry 57).

Lesion size varied among the inoculum densities; most of the lesions at 1×10^5 spores per milliliter never developed beyond small necrotic flecks (0.4 mm in diameter) with chlorotic halos. Lesions resulting from lower inoculum densities were larger in all tests.

Latent period. Latent period was quantified in two ways. For the first two tests, it was defined as the first day after inoculation when sporulation was observed on at least two lesions per leaf (T_2). This method was quick but might have been a function of the number of lesions (Fig. 1); i.e., the more lesions present on a leaf the more likely that at least two might be sporulating on any given day. In other tests, T_{50} (the number of days until 50% of the sporulating lesions sporulated) was calculated with Shaner's (19) probit regression method. Day 30 was chosen as the cutoff date for T_{50} estimation so that sporulation counts included few or no secondary lesions. This method was unsatisfactory when high inoculum densities were used, because leaflets with many lesions defoliated too rapidly to be evaluated. Shaner's method proved, however, to be adaptable to peanut leaves with low to moderate levels of infection; leaves that lost a leaflet were excluded from further counts when the lesions were no longer recognizable on the abscinded leaflet. Number of days after inoculation accounted for 87–99% of the variation for percentage of lesions sporulating. Mean T_{50} values ranged from 21 to 26 days after inoculation (Table 4). NC 3033 (entry 12) had the longest latent period. Genotypes NC-GP 343 (entry 336) and NC-Ac 3139 × NC-GP 343 (entry 75) also had long latent periods.

Slopes of regressed probit lines (probit percentage of lesions sporulating vs. day) were also analyzed. The slopes were variable and not correlated with T_{50} , but the slope (0.13) of NC 3033 × NC-GP 343 (entry 102) was less than the average of all others (0.21) (Table 4). The latent period (T_{50}) of this genotype was only average in the group of 20. Entry 102 ranked low for MPLS (Table 3); however, the number of lesions that sporulated occurred over an extended period of time.

Genotypic order for latent period determined by T_2 was similar to that for T_{50} (Table 5). NC 3033 (entry 12) had a significantly longer latent period in both tests than any other genotype tested (Tables 3 and 4). A latent period × peanut genotype interaction was not observed.

MPLS. During these tests, sporulation

often never occurred on some leaf spot lesions; therefore, a technique was devised to determine if genotypes differed in the percentage of sporulating lesions. This concept is not addressed by Shaner's (19) method of quantifying latent period, since T_{50} is based on 100% of all final lesions sporulating. The MPLS value was determined as the number of lesions that sporulated by day 30, divided by the number of lesions counted on day 21, multiplied by 100. Day 21 was judged to be about the last day on which lesions could be counted without including lesions from secondary infections. Day 30 was chosen as the final day to count sporulating lesions so as to include as many lesions originating from day 0 as

possible; counts made soon after this day apparently included secondary lesions. Genotypic order for MPLS was similar to that of latent period; i.e., genotypes that had a lower MPLS generally had longer latent periods (Tables 3 and 5). Genotypes varied from 34 to 77% for this component. NC-GP 343 (entry 336) and NC 3033 (entry 12) had the lowest means.

Defoliation. Time until leaflet defoliation decreased with increasing number of lesions (Fig. 2). Inoculum density and number of lesions as independent variables accounted for 91 and 98%, respectively, of the variation of the dependent variable mean defoliation. When the concentration of spores per milliliter was increased from 1×10^4 to $1 \times$

Table 2. Rankings of 20 peanut genotypes for average number of early leaf spot lesions at four inoculum densities

| Genotype | Entry | Lesions | | Genotype | Entry | Lesions | |
|------------------------|-------|-------------------|----------|------------------------|-------|-------------------|----------|
| | | per leaf | per leaf | | | per leaf | per leaf |
| | | 1×10^4 | | | | 2.5×10^4 | |
| NC 3033 × NC 2 | 64 | 65.3 | | NC 3033 × NC-GP 343 | 102 | 103.3 | |
| Florigiant | 81 | 53.8 | | NC 2 × NC 5 | 21 | 95.5 | |
| NC 5 × Florigiant | 66 | 41.8 | | NC 2 | 1 | 90.0 | |
| NC-Ac 3139 × NC-GP 343 | 75 | 35.0 | | NC-GP 343 × NC 5 | 88 | 85.0 | |
| NC 5 | 3 | 33.5 | | NC-Ac 3139 × NC-GP 343 | 79 | 82.8 | |
| Florigiant × NC-GP 343 | 44 | 33.5 | | Florigiant | 81 | 79.5 | |
| NC 2 | 1 | 30.5 | | NC 3033 × NC 2 | 64 | 77.8 | |
| NC-Ac 3139 × NC-GP 343 | 79 | 29.5 | | NC 3033 × NC-GP 343 | 104 | 76.3 | |
| NC 5 × Florigiant | 65 | 28.0 | | NC-GP 343 × NC 2 | 57 | 72.8 | |
| NC 3033 × NC-GP 343 | 102 | 25.8 | | NC 5 × Florigiant | 65 | 67.3 | |
| Florigiant × NC-GP 343 | 50 | 24.5 | | NC 5 × Florigiant | 66 | 65.8 | |
| NC 2 × NC 5 | 21 | 22.8 | | NC-Ac 3139 × NC-GP 343 | 75 | 58.5 | |
| NC-GP 343 × NC 5 | 88 | 22.0 | | NC 3033 | 12 | 58.3 | |
| NC 3033 | 12 | 17.8 | | NC 2 × NC 5 | 8 | 54.5 | |
| NC-GP 343 × NC 2 | 58 | 16.5 | | Florigiant × NC-GP 343 | 50 | 52.5 | |
| NC-GP 343 | 336 | 15.8 | | NC-GP 343 | 336 | 49.3 | |
| NC-GP 343 × NC 2 | 57 | 15.5 | | Florigiant × NC-GP 343 | 44 | 46.3 | |
| NC-GP 343 × NC 5 | 86 | 15.3 | | NC 5 | 3 | 44.8 | |
| NC 3033 × NC-GP 343 | 104 | 14.8 | | NC-GP 343 × NC 2 | 58 | 32.8 | |
| NC 2 × NC 5 | 8 | 14.3 | | NC-GP 343 × NC 5 | 86 | 32.3 | |
| Av. ^b | | 27.7 | | | | 66.2 | |
| SE | | 12.4 | | | | 18.8 | |
| df | | 57 | | | | 57 | |
| | | 5.5×10^4 | | | | 1×10^5 | |
| NC 5 × Florigiant | 66 | 178.3 | | NC 3033 × NC-GP 343 | 102 | 302.5 | |
| NC 3033 × NC-GP 343 | 102 | 151.0 | | NC 5 × Florigiant | 65 | 254.3 | |
| NC-Ac 3139 × NC-GP 343 | 79 | 149.8 | | NC 5 × Florigiant | 66 | 253.0 | |
| Florigiant | 81 | 142.3 | | Florigiant | 81 | 250.0 | |
| NC 3133 × NC 2 | 64 | 123.3 | | NC 3033 | 12 | 234.5 | |
| NC 5 × Florigiant | 65 | 123.0 | | NC-GP 343 | 336 | 234.3 | |
| NC-GP 343 × NC 5 | 86 | 104.8 | | Florigiant × NC-GP 343 | 44 | 228.0 | |
| NC 2 | 1 | 102.0 | | NC 2 | 1 | 222.8 | |
| NC 5 | 3 | 97.3 | | NC 3033 × NC 2 | 64 | 222.0 | |
| Florigiant × NC-GP 343 | 44 | 93.8 | | NC 3033 × NC-GP 343 | 104 | 215.0 | |
| NC-GP 343 × NC 2 | 57 | 83.0 | | NC-GP 343 × NC 2 | 58 | 201.8 | |
| NC-GP 343 × NC 2 | 58 | 82.8 | | NC 5 | 3 | 183.5 | |
| NC 3033 × NC-GP 343 | 104 | 81.3 | | NC-Ac 3139 × NC-GP 343 | 79 | 179.3 | |
| Florigiant × NC-GP 343 | 50 | 81.0 | | NC-GP 343 × NC 2 | 57 | 168.0 | |
| NC 2 × NC 5 | 21 | 78.0 | | Florigiant × NC-GP 343 | 50 | 149.5 | |
| NC-GP 343 | 336 | 76.3 | | NC-GP 343 × NC 5 | 86 | 139.5 | |
| NC 3033 | 12 | 75.8 | | NC 2 × NC 5 | 21 | 131.8 | |
| NC-GP 343 × NC 5 | 88 | 74.0 | | NC 2 × NC 5 | 8 | 119.5 | |
| NC 2 × NC 5 | 8 | 65.8 | | NC-GP 343 × NC 5 | 88 | 110.3 | |
| NC-Ac 3139 × NC-GP 343 | 75 | 60.3 | | NC-Ac 3139 × NC-GP 343 | 75 | 89.3 | |
| Av. ^b | | 101.2 | | | | 194.4 | |
| SE | | 28.7 | | | | 40.3 | |
| df | | 57 | | | | 57 | |

^aInoculum density (spores per milliliter).

^bAv. = average number of early leaf spot lesions, SE = standard error of genotypic mean, and df = error degrees of freedom.

Table 3. Rankings of 20 peanut genotypes for average sporulation per lesion (SPL), number of days until two *Cercospora arachidicola* lesions sporulated (T_2), maximum percentage of lesions sporulating (MPLS), and number of days until leaflet defoliation (DEF)

| Genotype | Entry | SPL | Genotype | Entry | T_2 |
|------------------------|-------|-------------|------------------------|-------|------------------------|
| Florigiant | 81 | 2,639 | NC 5 × Florigiant | 65 | 17.8 |
| NC-GP 343 × NC 2 | 57 | 1,412 | NC 5 × Florigiant | 66 | 17.9 |
| NC 5 × Florigiant | 65 | 1,319 | NC 2 | 1 | 18.1 |
| NC 2 × NC 5 | 21 | 1,204 | NC 2 × NC 5 | 21 | 18.4 |
| NC 2 | 1 | 1,111 | NC 3033 × NC-GP 343 | 104 | 18.7 |
| NC 3033 × NC-GP 343 | 104 | 1,042 | NC-GP 343 × NC 2 | 57 | 19.3 |
| NC 3033 × NC 2 | 64 | 1,019 | Florigiant | 81 | 19.4 |
| NC-GP 343 × NC 2 | 58 | 972 | Florigiant × NC-GP 343 | 44 | 19.7 |
| NC-GP 343 × NC 5 | 86 | 972 | NC 5 | 3 | 19.8 |
| NC-Ac 3139 × NC-GP 343 | 79 | 926 | NC 3033 × NC-GP 343 | 102 | 20.0 |
| NC 2 × NC 5 | 8 | 903 | NC-Ac 3139 × NC-GP 343 | 79 | 20.1 |
| Florigiant × NC-GP 343 | 50 | 880 | NC-GP 343 × NC 5 | 86 | 20.3 |
| NC 3033 | 12 | 857 | NC 2 × NC 5 | 8 | 20.4 |
| Florigiant × NC-GP 343 | 44 | 810 | NC 3033 × NC 2 | 64 | 20.6 |
| NC 3033 × NC-GP 343 | 102 | 787 | NC-GP 343 × NC 2 | 58 | 20.8 |
| NC 5 × Florigiant | 66 | 787 | NC-GP 343 × NC 5 | 88 | 20.8 |
| NC-Ac 3139 × NC-GP 343 | 75 | 764 | NC-GP 343 | 336 | 21.4 |
| NC-GP 343 | 336 | 579 | Florigiant × NC-GP 343 | 50 | 21.5 |
| NC-GP 343 × NC 5 | 88 | 486 | NC-Ac 3139 × NC-GP 343 | 75 | 21.9 |
| NC 5 | 3 | 370 | NC 3033 | 12 | 24.4 |
| SE ^a | | 277.4 | | | 0.8 |
| df | | 38 | | | 57 |
| | | MPLS | | | DEF^b |
| NC 2 | 1 | 77.0 | NC 2 × NC 5 | 21 | 38.8 |
| NC 5 × Florigiant | 66 | 68.9 | NC-GP 343 | 336 | 40.3 |
| Florigiant | 81 | 68.5 | NC 2 | 1 | 40.9 |
| NC 2 × NC 5 | 21 | 62.4 | Florigiant | 81 | 42.1 |
| NC-GP 343 × NC 2 | 57 | 60.3 | NC 3033 × NC-GP 343 | 104 | 43.3 |
| NC × GP 343 × NC 5 | 88 | 58.1 | NC 5 × Florigiant | 65 | 43.9 |
| NC 5 × Florigiant | 65 | 57.1 | Florigiant × NC-GP 343 | 44 | 44.8 |
| NC 2 × NC 5 | 8 | 56.6 | NC-GP 343 × NC 5 | 88 | 45.1 |
| NC-GP 343 × NC 2 | 58 | 56.1 | NC-Ac 3139 × NC-GP 343 | 79 | 46.8 |
| Florigiant × NC-GP 343 | 44 | 55.6 | NC-GP 343 × NC 2 | 58 | 48.1 |
| NC 3033 × NC-GP 343 | 104 | 53.3 | NC 2 × NC 5 | 8 | 49.4 |
| NC-Ac 3139 × NC-GP 343 | 79 | 52.1 | NC 3033 × NC 2 | 64 | 52.2 |
| NC 3033 × NC 2 | 64 | 49.6 | NC 5 × Florigiant | 66 | 54.5 |
| Florigiant × NC-GP 343 | 50 | 43.1 | NC-GP × NC 2 | 57 | 55.3 |
| NC 5 | 3 | 38.9 | NC 5 | 3 | 55.8 |
| NC 3033 × NC-GP 343 | 102 | 38.5 | NC 3033 × NC-GP 343 | 102 | 57.9 |
| NC-Ac 3139 × NC-GP 343 | 75 | 36.9 | NC-GP 343 × NC 5 | 86 | 58.6 |
| NC-GP 343 × NC 5 | 86 | 36.8 | NC-Ac 3139 × NC-GP 343 | 75 | 59.5 |
| NC 3033 | 12 | 35.5 | Florigiant × NC-GP 343 | 50 | 65.3 |
| NC-GP 343 | 336 | 33.6 | NC 3033 | 12 | 71.6 |
| SE ^a | | 5.4 | | | 6.2 |
| df | | 57 | | | 57 |

^aSE = standard error of genotypic means, df = error degrees of freedom.

^bGenotype averages are from 2.5×10^4 spores per milliliter.

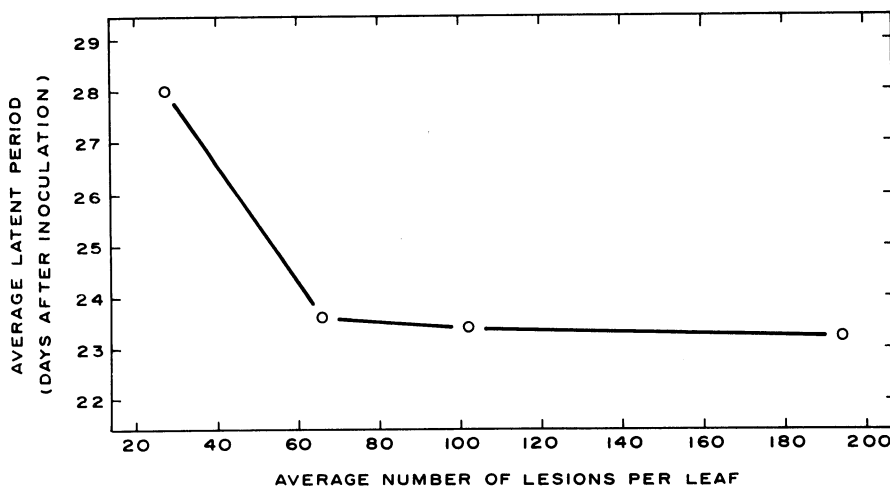


Fig. 1. Relationship of number of lesions of *Cercospora arachidicola* per leaf to latent period averaged over all peanut genotypes.

10^5 , time until defoliation was decreased by nearly 50%. Genotypic orders for the four inoculum densities were similar, yet their orders at 1×10^4 and 2.5×10^5 spores per milliliter correlated best (Table 6). NC 3033 (entry 12) consistently ranked lowest for defoliation, ranging from 51 to 85 days after inoculation for 1×10^4 and 1×10^5 spores per milliliter, respectively. Genotypic order for time until leaflet defoliation was similar to that of latent period and MPLS (Tables 3 and 4).

Sporulation on detached vs. attached leaflets. We observed that when a lesion sporulated, it continued to sporulate until the leaf abscinded. Whether lesion sporulation increased, decreased, or stopped entirely after defoliation had not been determined. In the first test, with lesions collected from five genotypes from field plots, no difference in sporulation was observed between lesions of attached and detached leaflets. In the second test, with lesions collected from five genotypes growing in the greenhouse, detached leaflets supported almost two and one-half times as much sporulation as attached leaflets (Table 7). In both tests, there was no overall genotype × treatment interaction, although sporulation of NC 3033 (entry 12) increased more than the other four genotypes. Genotypes that supported greater sporulation on attached leaflets generally supported greater sporulation on detached leaflets.

DISCUSSION

The numbers of lesions produced on detached leaves in greenhouse inocu-

Table 4. Rankings of 20 peanut genotypes for time until 50% of lesions sporulate (T_{50}) and slope of the probit line for the population of the latent periods of lines infected with *Cercospora arachidicola*

| Genotype | Entry | T_{50} ^a | Slope |
|------------------------|-------|-----------------------|-------|
| NC 5 × Florigiant | 66 | 21.7 | 0.20 |
| | 65 | 21.8 | 0.17 |
| Florigiant | 81 | 22.0 | 0.27 |
| NC 5 | 3 | 22.2 | 0.21 |
| NC 2 | 1 | 22.4 | 0.22 |
| NC-GP 343 × NC 5 | 88 | 22.4 | 0.22 |
| NC 2 × NC 5 | 21 | 22.6 | 0.19 |
| NC 3033 × NC-GP 343 | 104 | 22.6 | 0.24 |
| | 102 | 22.7 | 0.13 |
| Florigiant × NC-GP 343 | 44 | 22.8 | 0.16 |
| NC 2 × NC 5 | 8 | 22.9 | 0.20 |
| NC-Ac 3139 × NC-GP 343 | 79 | 23.0 | 0.18 |
| NC-GP 343 × NC 5 | 86 | 23.2 | 0.19 |
| Florigiant × NC-GP 343 | 50 | 23.3 | 0.22 |
| NC-GP 343 × NC 2 | 57 | 23.5 | 0.22 |
| | 58 | 23.7 | 0.20 |
| NC 3033 × NC 2 | 64 | 24.0 | 0.25 |
| NC-Ac 3139 × NC-GP 343 | 75 | 24.3 | 0.18 |
| NC-GP 343 | 336 | 24.4 | 0.17 |
| NC 3033 | 12 | 26.3 | 0.21 |
| SE ^b | | 0.5 | 0.02 |
| df | | 57 | 57 |

^aDays after inoculation when 50% of the lesions that will sporulate will do so.

^bSE = standard error of genotypic means, df = error degrees of freedom.

lations were unreliable to evaluate resistance to *C. arachidicola* for the 20 peanut genotypes in this study. Tests were conducted during each month of two consecutive years. Changes in environmental conditions apparently influenced the peanut leaf surface or the processes of fungal infection, resulting in an interaction of number of lesions, genotype, and time. Light intensity or quality, in addition to temperature, were probably involved in this interaction. Metabolic processes within the leaf were probably not affected, because latent period and sporulation did not interact with genotype and time. These results, however, do not preclude the possibility that some peanut genotypes will give consistent results over time.

Ranking of genotypes on the basis of leaflet defoliation may be obtained within a shorter period of time with greater inoculum densities, since genotypic order was similar at each inoculum density. Unfortunately, because of the close relationship between number of lesions

and leaflet defoliation (Fig. 2), variability in numbers of lesions may confound evaluation of defoliation data. Latent period also decreased with increasing inoculum density (Fig. 1), but genotypic order remained relatively constant regardless of number of lesions. Latent period should, therefore, be useful in selection of peanut lines for resistance to early leaf spot, as first suggested by Foster et al (7). Genotypic rankings were similar for the four components of resistance evaluated in these studies (Table 5). MPLS and the two means of measuring latent period, T_2 and T_{50} , were highly correlated. All three were moderately correlated with spores per lesion and time until leaflet defoliation, which in turn were weakly correlated with each other. A previously undescribed component of resistance, MPLS, is suggested to select for resistance in peanuts. Genotypes differed twofold for this parameter; however, for late leaf spot (*Cercosporidium personatum*), genotypes were not separated by this component

(J. C. Wynne, *personal communication*).

Genotype NC 3033 (entry 12) was the most resistant entry in greenhouse tests. It had the longest latent period and time until leaflet defoliation and the second lowest MPLS. Genotypes NC-GP 343 (entry 336), NC-Ac 3139 × NC-GP 343 (entry 75), and Florigiant × NC-GP 343 (entry 50) also performed well. Although NC 3033 outperformed NC-GP 343, the latter appears better able to pass on early leaf spot resistance to its offspring (12). Surprisingly, NC 3033 × NC-GP 343 (entries 102 and 104) did not perform as well as either parent.

Sporulation of *C. arachidicola* was observed on detached peanut foliage, as noted by Foster et al (7). Although genotype did not interact with detachment, the number of spores produced was in part due to peanut genotype. For example, sporulation of *C. arachidicola* on detached leaves of NC 3033 (entry 12) increased more than on the other four genotypes studied. If field conditions are conducive, abscinded leaflets may significantly contribute to epidemics of early leaf spot, perhaps more than lesions of attached leaflets. The longevity of sporulation on abscinded leaflets may depend on the rate of leaflet decay.

Field screening of large numbers of peanut genotypes for leaf spot resistance is time-consuming. Advanced lines must

Table 5. Spearman's test of rank correlation for five components^a of peanut resistance to *Cercospora arachidicola*

| | MPLS | T_2 | T_{50} | SPL | DEF |
|----------|--------------------------------------|--------------|--------------|--------------|-----|
| MPLS | ... ^b ... ^c | | | | |
| T_2 | 0.70 0.01 | ... | | | |
| T_{50} | 0.68 0.01 | 0.79 0.01 | ... | | |
| SPL | 0.51 0.02 | 0.51 0.02 | 0.16 0.50 | ... | |
| DEF | 0.52 0.02 | 0.67 0.01 | 0.50 0.03 | 0.40 0.08 | ... |

^aMPLS = maximum percentage of lesions sporulating, T_2 = time until two lesions begin to sporulate, T_{50} = time until 50% of the sporulating lesions sporulate, SPL = spores per lesion, and DEF = time until leaflet defoliation (correlations with DEF used the average ranking of genotype for four inoculum densities).

^bSpearman's nonparametric coefficient of rank correlation.

^cProbability of exceeding coefficient assuming no correlation.

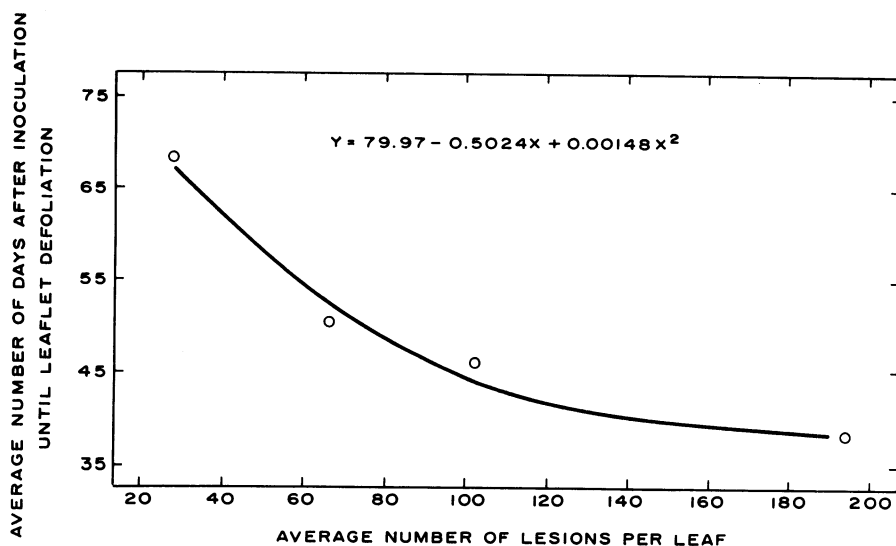


Fig. 2. Relationship of number of lesions of *Cercospora arachidicola* per leaf to time until leaflet defoliation averaged over all peanut genotypes.

Table 6. Spearman's test of rank correlation for leaflet defoliation of 20 peanut genotypes

| | Inoculum density (spores/ml) | | | |
|-------------------|--------------------------------------|-------------------|-------------------|-----------------|
| | 1×10^4 | 2.5×10^4 | 5.5×10^4 | 1×10^5 |
| 1×10^4 | ... ^a ... ^b | | | |
| 2.5×10^4 | 0.72 0.01 | ... | | |
| 5.5×10^4 | 0.42 0.46 | 0.22 0.35 | ... | |
| 1×10^5 | 0.54 0.01 | 0.35 0.13 | 0.41 0.08 | ... |

^aSpearman's nonparametric coefficient of rank correlation.

^bProbability of exceeding coefficient assuming no correlation.

Table 7. Average number of spores of *Cercospora arachidicola* per lesion produced on attached and detached leaflets of five peanut genotypes

| Genotype | Leaflets | | |
|---------------------|----------|----------|----------|
| | Entry | Attached | Detached |
| NC-GP 343 × NC 2 | 58 | 196.8 | 231.5 |
| NC 3033 × NC-GP 343 | 104 | 185.2 | 335.6 |
| NC 3033 | 12 | 46.3 | 393.5 |
| NC 2 × NC 5 | 21 | 46.3 | 219.9 |
| NC-GP 343 × NC 5 | 8 | 34.7 | 46.3 |
| SE ^a | | | 76.7 |
| df | | | 45 |

^aSE = standard error of genotypic means, df = error degrees of freedom.

be field-tested for percent disease and yield loss, but initial screenings could be accelerated with greenhouse testing. It is necessary, however, to determine which components of the resistant genotypes differ quantitatively from those of susceptible genotypes and if components are the same for all resistant genotypes. Few studies to date have included both greenhouse and field tests with the same genotypes. Hassan and Beute (11) reported that certain genotypes reacted differently in two environments. Foster et al (9), however, found a correlation between numbers of lesions in field and greenhouse tests when they compared 16 botanically diverse peanut genotypes. Both investigations considered only numbers of lesions and did not include disease progress curves from the field. Others have studied multiple components of resistance in peanut (8,14,16) but did not include both field and greenhouse data with components of resistance. Disease progress rates have been determined for our 20 genotypes in field tests for three consecutive years. The ranking of genotypes by disease progress rates will be compared with their ranking for resistance components in this study.

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