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Inheritance of Resistance to *Cercospora arachidicola* and *Cercosporidium personatum* in Six Virginia-type Peanut Lines[1,3]

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ABSTRACT

The inheritance of resistance to two cercospora leafspots, *Cercospora arachidicola* (early leafspot) and *Cercosporidium personatum* (late leafspot) in Virginia-type peanuts (*Arachis hypogaea* L.), was determined using F_1 and F_2 generations and parental lines from a six parent diallel cross under natural field conditions. Two techniques for rating disease severity were employed. General combining ability, determined from both rating techniques, was significant for both F_1 and F_2 generations, indicating that resistance to both fungi and tolerance to infection i. e., minimal leaf defoliation, was primarily due to additive genetic effects.

The six parents produced offspring with different levels of resistance to both fungi. From the estimates of general combining ability effects, only NC-GP 343 and NC 5 produced progeny resistant to both early and late leafspot. NC 3033 was resistant to early leafspot, but susceptible to late leafspot. NC-Ac 3139, Florigiant and NC 2 were resistant to late leafspot, but susceptible to early leafspot. Disease indices ranked NC 3033 and NC-GP 343 as, overall, the most resistant of the six lines and the most useful to include in a cercospora leafspots resistance breeding program.

Key Words: Disease resistance, diallel cross, general combining ability, *Arachis hypogaea*, groundnut.

Cercospora leafspots of peanut (*Arachis hypogaea* L.) are caused by *Cercospora arachidicola* Hori (early leafspot) and *Cercosporidium personatum* (Berk. & Curt.) Deighton (late leafspot). The perfect stages of these fungi, *Mycosphaerella arachidicola* and *M. berkeleyii*, respectively, were described by Jenkins (9) in 1938 and may be involved in the initial dissemination of the fungus. Although symptoms caused by the fungi vary with environment and cultivar, lesions caused by *C. arachidicola* generally are light to rust brown in color, are usually encircled by a yellow, chlorotic halo and the conicial sporulation is mainly on the upper leaf surface (9.14). The lesions caused by *C. personatum* generally are darker in color, especially on the lower surface of the leaf, where sporulation predominately occurs. The conidia of *C. personatum* may be produced in concentric rings during periods of heavy sporulation. Yellow halos are usually absent in late leafspot.

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The infected leaflets or leaves amy abscise as a response to infection by both of these fungi (14). The abscission rate varies with the number of lesions present on the leaflet and relative tolerance of the peanut lines to infection. When defoliation occurs, the net photosynthetic capacity of the plant is reduced, causing the plant to lose vigor (2). The increased leaf litter may also stimulate growth of facultative peanut pathogens, such as *Sclerotium rolfsii* by providing a food base (3).

Economically, cercospora leafspots are the most important disease problems of peanuts in the world, with yield losses ranging from 10 to 50 percent in many areas (9, 12). The two leafspots have been reported only on members of the genus *Arachis* and may occur together anywhere peanuts are grown (14). In North Carolina, early leafspot usually becomes visible in mid-July and increases in incidence through the remainder of the growing season. Late leafspot usually does not appear in North Carolina until late August.

These two leafspots can be effectively controlled and peanut yield increased through the use of fungicide sprays and dusts (4). In many areas of the world, fungicides are either unavailable or are uneconomical for use by the peanut farmer. Also, strains of *C. arachidicola* tolerant to benomyl and other related fungicides have developed in many areas, including North Carolina (10). In response to these situations, screening for disease resistance to cercospora leafspots is being conducted in peanut growing countries around the world (1, 6, 12). The purpose of this study was to evaluate resistance in six Virginia-type peanut lines to both cercospora leafspot diseases and to determine the inheritance of resistance and tolerance to infection (i.e., minimal leaf defoliation) of these lines to *C. arachidicola* (early leafspot) and *C. personatum* (late leafspot).

Materials and Methods

Six Virginia-type peanut lines were ranked for their level of resistance to early leafspot in field plots at the Peanut Belt Research Station, Lewiston, North Carolina in 1977. In previous tests, five of these lines (NC 3033, NC 5, NC 2, NC-Ac 3139 and Florigiant) were rated resistant to early leafspot (6). The sixth line, NC-GP 343, was included because of its resistance to the twospotted spider mite (*Tetramychus urticae*) and the southern corn root worm (*Diabrotica undecimpunctata howardi*), two major insect pests in North Carolina.

Each parent line (P_1) to be evaluated for resistance to early leafspot was planted in a randomized complete block design with four replications. Each plot consisted of two rows of a single P_1 line with 35 plants per row.

Disease severity in 1977 was evaluated by counting lesions and defoliation. Number of lesions on two leaves (located midway on the main stem) and percent defoliation of infected leaves on two branches originating from the base of the plant was calculated:
Percent defoliation ratio=

$$\frac{\text{number of nodes per branch without leaves}}{\text{total number of nodes on that branch}} \times 100.$$

Two separate ratings were made (September 17th and 29th) to determine the disease reaction of the six parental lines to early leafspot. For each parental line, each character was rated on 10 plants in each plot and the mean values of number of lesions and percent defoliation were determined. A disease index (DI-1), developed by Hassan *et al.* (6), was used to combine the effects of number of lesions and the defoliation ratio of a line into a single value. DI-1 = average number of *C. arachidicola* lesions X average defoliation ratio. Mean DI-1 values were calculated for each P_1 line.

F_1 full-sib familes were produced by crossing all of the six P_1 in a complete diallel, including reciprocals (5) in the greenhouse. Fifteen seeds from each cross were planted in a winter nursery in Puerto Rico to produce F_2 seeds and 15 seeds were saved for planting in 1978. The F_2 seeds were harvested in April, 1978 and returned to North Carolina for field evaluation under local seasonal conditions.

In 1978, the P1 lines, and the F1 and F^2 generations were evaluated for resistance to both early and late leafspot at the Peanut Belt Research Staion. To ensure germination and growth of the limited number of F_1 progeny, the seeds were planted and grown in a greenhouse, for three weeks prior to being transferred to the field. The P_1 line, F_1's and F_2's were planted in a randomized complete block design with four replicates. Each plot of the P_1 lines and F_2's consisted of one row of 15 plants, and each plot of the F_2's consisted of one row of 3 plants. A border row of NC 5 was planted between each plot. No fungicides were applied to any plots in 1977 or 1978.

Disease ratings similar to those used in 1977 were used on September 25, 1978 to rate the disease reaction for the P_1 lines and F_1 and F_2 combinations. Both *C. arachidicola and C. personatum* were identified as causing lesions on peanut plants during the 1978 growing season. The number of *C. arachidicola and C. personatum* lesions were counted on two leaves on each of 5 plants (selected at random) per plot of the P_1 lines and F_2's, and on 3 plants per plot of the F_1's. Percent defoliation was measured on one branch originating from the base of the parent on each of the 5 (3 with the F_1 progeny) plants per plot.

DI-1 values were determined from the number of *C. arachidicola* lesions and percent defoliation ratio. However, due to the presence of late leafspot, a second disease index (DI-2) was devised to include its effects, where DI-2 = (average number of *C. arachidicola* lesions + average number of *C. personatum* lesions) X average defoliation ratio. Mean disease index values (1 and 2) were determined for each P_1 line and F_1 cross.

To determine whether visual estimates of disease could accurately reflect the disease reaction to cercospora leafspots (as determined by counting lesions per leaf and leaf defoliation), a qualitative disease rating technique (11) was also used during the 1978 growing season in the same test plots. This second rating technique consisted of assigning a value to each plant on each evaluation date based on the incidence of lesions and leaf defoliation being less than (L) or equal to (S) a reference cultivar (standard) growing adjacent to the test plants. The standard represented the amount of disease during each rating period on the adjacent NC 5 border rows. NC 5 had been shown in the previous summer (1977) to have an intermediate disease reaction to early leafspot among the six P_1 lines by the end of the growing season. Any plant which had less disease (including lesions and defoliation) than NC 5 was considered resistant and received a rating of L. Any plant with equal or more disease than NC 5 was considered susceptible and received a rating of S. Each plant in a plot was rated S or L individually. The rating was repeated six times during the disease epidemic starting July 31 and ending October 2. The percentage of plants rated S was computed for each P_1 line and F_1 cross. The mean percentage of S ratings represented a disease index (DI-3) value for each line or cross, where DI-3 =

$$\frac{\text{number of plants rate S}}{\text{total number of plants rated}} \times 100.$$

Thus, the greater the DI-3 value that a parental line or cross received, the more susceptible it was, and conversely, the lower the DI-3 value, the more resistant.

Analysis of variance of early leafspot and percent defoliation was used to determine the variation among the six parental lines in both 1977 and 1978. During 1978, the variation in resistance to late leafspot was also detemined.

The data from the two rating techniques for the diallel cross and P_1 lines were analyzed as follows. Means of P_1 lines and progeny, for each replication, were used as data entries in a computer program (DIALL) developed by Schaffer and Usanis for the general least squares analysis of diallel designs (13). Sources of variation in the model chosen are: general combining ability (g. c. a.), specific combining ability (s. c. a.), reciprocal effects, maternal effects and replications. The parental lines were regarded as a fixed sample; therefore, inferences made from the data can only be applied to the parental populations (5).

To determine whether performances of a P_1 line can predict the future performance of that line used in F_1 and F_2 combinations, correlation coefficients - which determined the degree of association between disease reactions of the P_1 line and the F_1 and F_2's - were computed.

Correlations among early leafspot, late leafspot, percent defoliation and disease indices 1, 2, and 3, averaged over F_1 crosses, were calculated to determine the relationship of one disease character to another disease character. Among the F_2 progeny, the correlation coefficients were determined only for early and late leafspot, and percent defoliation.

Results and Discussion

Evaluation of P_1 lines for number of lesions per leaf on September 17, 1977 indicated that NC 5 had fewer *C. arachidicola* lesions than NC-Ac 3139, Florigiant and NC2 but did not differ from NC-GP 343 or NC 3033 (Table 1). NC 3033 had less defoliation (P = .05) than all other lines, except NC 5, and NC-GP 343 had the most defoliation (P = .05). On September 29 (just prior to harvest), no differences could be detected among the six lines for number of *C. arachidicola* lesions. However, NC 3033 and Ac 3139 had significantly less (P = .05) defoliation than the other parental lines. The DI-1 values (number of *C. arachidicola* lesions X defoliation), determined for the ratings taken September 17, indicated that NC 5 was, overall, the least diseased of the six lines while NC-GP 343 was the most severely diseased line. By September 29, no differences among the disease index values for the six parental lines were detected. However, in ranking the parental lines for their overall disease reactions, NC 3033 was ranked as the least diseased line and NC 2 was the most severely diseased line.

In 1978, both early and late leafspot occurred in

Table 1. 1977 Early leafspot ratings on peanut lines used as parents in a diallel cross.

Parental lines	Number of lesions/leaf[w] 9/17	9/29	Percent defoliation[x] 9/17	9/29	Disease index 1[y] 9/17	9/29
NC 5	9 a	30 a	5.2 ab	48.9 b	0.4 a	14.2 a
NC-GP 343	15 ab	37 a	16.8 c	57.0 b	2.34 b	22.2 a
NC 3033	17 ab	39 a	0.6 a	28.0 a	1.16 ab	10.9 a
NC-Ac 3139	24 b	40 a	9.3 b	30.0 a	2.22 ab	12.2 a
Florigiant	26 b	40 a	8.4 b	56.0 b	2.04 ab	22.0 a
NC 2	28 b	51 a	7.2 b	46.0 b	1.61 ab	22.6 a

[w] Average number of lesions per leaf determined from 40 plants (2 leaves/plant) of each parental line.

[x] Average percent defoliation per plant determined from 40 plants (2 branches/plant) of each parental line.

[y] Disease index 1 is expressed as the mean product of average number of lesions per leaf X average defoliation ratio, over 4 replications.

[z] Means in each column followed by the same letter do not differ (p=.05) according to Duncan's new multiple range test.

the test plots. Evaluation of disease on September 25 indicated that NC 3033 had fewer (P = .05) *C. arachidicola* lesions per leaf than Florigiant, but did not differ from NC 2, NC 5, NC-GP 343 or NC-Ac 3139 (Table 2). NC 3033, however, had more (P= .05) *C. personatum* lesions per leaf than NC-Ac 3139, NC-GP 343 or Florigiant, but did not differ from NC 2 or NC 5. Although NC 3033 was the most resistant line to early leafspot and the least resistant line to late leafspot, it was still the most tolerant of the six lines to defoliation (P = .05). When DI-1 values were compared (Table 2), NC 3033 had a lower rating (P = .05) than NC-Ac 3139, but did not differ from the other four P_1 lines. No differences were found among the six lines when DI-2 values (incidence of *C. arachidicola plus C. personatum* lesions X defoliation) were compared. With DI-3 (the progressive visual estimate), NC 3033 was the most resistant (P = .05) of all the P_1 lines. NC-GP 343 was ranked second with significantly (P = .05) less disease than NC 5, but did not differ from NC 2, NC-Ac 3139 or Florigiant. The visual rating technique (DI-3) underestimated expected disease on NC 5 parental lines (DI-3 = 74), indicating that accuracy in visual discernment of disease incidence decreases when number of lesions per leaf or leaf area diseased is great (8).

The overall means of the F_1 and F_2 generations, averaged over the number of observations within each replicate, were compared in diallel tables (Tables 3, 4, and 5). In the F_1's and F_2's, the parental lines which produced the most progeny resistant to early leafspot were NC 5 and NC-GP 343. The parental lines which produced the most resistant progeny to late leafspot were NC-Ac 3139,

Table 2. 1978 *Cercospora arachidicola* (early leafspot) and *Cercosporidium personatum* (late leafspot) ratings on peanut lines used as parents in a diallel cross.

Parental lines	Number of[w] C. arachidicola lesions/leaf	Number of[x] C. personatum lesions/leaf	Percent[y] defoliation	Disease indices[z] 1	2	3
NC 3033	5 a[v]	9 b	28.3 a	1.5 a	5.8 a	39 a
NC-GP 343	8 ab	2 a	47.1 b	4.0 a	5.0 a	53 b
NC 5	11 ab	5 ab	52.1 b	6.7 ab	9.4 a	74 c
NC-Ac 3139	13 ab	3 a	48.7 b	8.3 b	8.3 a	67 bc
NC 2	14 ab	4 ab	41.4 b	5.7 ab	7.5 a	64 bc
Florigiant	15 b	3 a	47.5 b	6.9 ab	8.6 a	60 bc

[w] Average number of C. arachidicola lesions per leaf determined from 20 plants (2 leaves/plant) of each parental line.

[x] Average number of C. personatum lesions per leaf determined from 20 plants (2 leaves/plant) on each parental line.

[y] Average percent defoliation per plant from 20 plants (1 branch/plant) of each parental line.

[z] Disease index 1 is expressed as the mean of the product (average number of C. arachidicola lesions per leaf X average defoliation ratio) over 4 replications.

Disease index 2 is expressed as the means of the product (average number of C. arachidicola lesions + average number of C. personatum lesions per leaf) X average defoliation ratio, over 4 replications.

Disease index 3 is expressed as the percentage of plants rated (S), average over 6 ratings.

[v] Means in each column followed by the same letter do not differ (P=.05) according to Duncan's new multiple range test.

Table 3. Diallel table of F_1 progeny means and selfs for disease response to number of early leafspot lesions (E. L.), late leafspot (L. L.) lesions, and the resulting percent defoliation (%D).

FEMALE PARENT		MALE PARENT NC-GP 343	NC 5	NC 3033	Florigiant	NC 2	NC-Ac 3139	Mean over crosses
NC-GP 343	E.L.	8.3	6.0	9.1	6.8	9.2	6.6	7.5
	L.L.	2.2	2.0	5.0	2.5	5.3	2.6	3.5
	% D.	47.1	41.1	39.1	54.0	42.2	44.0	45.7
NC 5	E.L.	5.1	11.1	2.8	10.1	6.1	9.9	6.8
	L.L.	3.0	5.1	7.4	3.8	3.1	5.9	5.1
	% D.	56.1	52.1	43.8	54.8	35.0	19.8	23.9
NC 3033	E.L.	7.5	7.1	5.5	10.3	13.5	14.1	10.5
	L.L.	8.5	7.9	9.2	2.7	5.3	5.1	5.9
	% D.	16.5	27.5	28.3	21.0	35.0	19.8	23.9
Florigiant	E.L.	8.2	8.9	8.5	15.1	15.1	10.7	10.3
	L.L.	3.5	3.9	8.9	3.4	1.8	2.3	4.0
	% D.	41.7	59.4	38.6	27.5	52.5	50.3	48.5
NC 2	E.L.	6.7	5.5	11.1	7.3	14.0	13.3	8.7
	L.L.	3.3	7.0	6.5	4.1	4.3	2.5	4.7
	% D.	38.9	51.6	31.1	48.5	41.1	56.6	45.3
NC-Ac 3139	E.L.	12.0	10.9	13.4	14.2	14.4	13.0	13.0
	L.L.	3.0	4.4	4.3	3.2	3.3	3.3	3.6
	% D.	42.2	43.1	30.1	47.9	58.2	48.7	44.7
Mean over crosses	E.L.	7.8	7.7	9.0	9.8	11.7	10.9	
	L.L.	4.2	5.0	6.4	3.3	3.8	3.7	
	% D.	39.1	44.5	36.5	45.2	44.6	41.2	

L.S.D. (P=.05) for means: E.L. = 6.59 L.L. = 4.36 % D. = 16.0

Table 4. Diallel table of F_2 progeny means and selfs for disease response to number of early leafspot (E.L.) lesions late leafspot (L.L.) lesions, and the resulting percent defoliation (%D).

FEMALE PARENT		MALE PARENT NC-GP 343	NC 5	NC 3033	Florigiant	NC 2	NC-Ac 3139	Mean over crosses
NC-GP 343	E.L.	8.3	6.9	10.2	11.5	8.7	9.6	9.4
	L.L.	2.1	2.5	9.9	6.9	6.1	6.7	6.2
	% D.	47.1	50.5	39.8	38.8	45.8	47.7	44.4
NC 5	E.L.	5.5	11.1	12.1	7.9	12.5	11.7	9.9
	L.L.	3.7	5.1	7.8	6.2	4.8	5.5	5.6
	% D.	50.5	52.2	50.1	59.9	45.9	51.5	51.6
NC 3033	E.L.	6.4	10.1	5.5	14.0	8.3	14.3	10.6
	L.L.	12.1	9.5	9.2	11.1	6.9	9.9	9.9
	% D.	33.3	43.1	28.3	36.0	35.0	46.3	38.4
Florigiant	E.L.	7.0	10.5	16.3	15.1	12.5	16.0	12.5
	L.L.	4.5	3.7	8.9	3.4	4.1	3.6	4.9
	% D.	42.2	52.3	27.5	27.5	53.7	43.2	43.8
NC 2	E.L.	8.7	10.7	13.0	15.2	14.0	13.6	12.2
	L.L.	4.3	3.5	14.6	2.3	4.3	1.9	5.3
	% D.	36.5	51.4	37.3	49,2	41.1	53.4	45.6
NC-Ac 3139	E.L.	8.8	11.6	16.1	15.8	17.7	13.0	14.0
	L.L.	3.4	5.1	4.9	3.1	3.7	3.3	4.0
	% D.	37.9	33.8	44.9	53.5	53.1	48.7	44.6
Mean over crosses	E.L.	7.3	10.0	13.5	12.8	11.9	13.0	
	L.L.	5.6	4.9	9.2	5.7	5.1	5.5	
	% D.	40.1	45.8	39.9	47.3	46.7	48.4	

L.S.D. (P=.05) for means: E.L. = 6.59 L.L. = 5.60 % D. = 17.0

Table 5. Diallel table of disease indices 1, 2, and 3 for F_1 progeny means and selfs.

FEMALE PARENT		MALE PARENT: NC 3033	NC-GP 343	NC 5	NC 2	Florigiant	NC-Ac3139	Mean over crosses
NC 3033	1	2.1	1.1	2.0	4.8	3.4	3.6	3.0
	2	5.8	3.4	4.2	6.7	4.4	4.5	4.6
	3	39.0	32.0	44.0	50.0	38.0	42.0	41.2
NC-GP 343	1	4.0	4.0	2.6	4.1	3.6	2.6	3.4
	2	6.0	5.0	3.5	6.5	4.7	4.0	4.0
	3	32.0	53.0	46.0	57.0	61.0	59.0	51.0
NC 5	1	0.9	2.9	6.7	2.2	5.5	4.1	3.1
	2	4.9	4.6	9.4	5.9	7.3	6.1	5.8
	3	42.0	52.0	74.0	39.0	54.0	50.0	50.0
NC 2	1	3.7	2.5	3.1	5.7	3.6	7.9	4.3
	2	5.9	4.0	6.9	7.5	5.6	9.2	6.3
	3	46.0	53.0	56.0	64.0	53.0	65.0	54.6
Florigiant	1	3.0	3.8	5.8	7.8	6.9	6.5	5.4
	2	6.7	5.3	8.2	8.7	8.6	7.7	7.3
	3	56.0	50.0	45.0	71.0	60.0	61.0	56.6
NC-Ac 3139	1	4.6	5.6	4.8	8.5	7.5	8.3	6.2
	2	5.6	6.7	6.7	10.4	8.9	8.3	7.7
	3	65.0	47.0	57.0	51.0	60.0	67.0	
Mean over crosses	1	3.2	3.2	3.7	5.5	4.7	4.9	
	2	5.9	4.8	5.9	7.6	6.2	6.3	
	3	48.2	46.8	49.6	53.6	53.2	55.4	

L.S.D. (P=.05) for means: 1 = 3.91 2 = 4.69 3 = 18.3

Florigiant, NC-GP 343 and NC 2. Among the F_2's, all of the parental lines, except NC 3033, produced progeny with some resistance to late leafspot. Only NC 3033, in the F_1 generation, and NC 3033 and NC-GP 343, in the F_2 generation, produced progeny having low amounts of leaf defoliation. In a comparison of the disease indices values for F_1's, NC 3033, NC-GP 343 and NC 5 produced, overall, the progenies most resistant to early and late leafspot, and the lowest in leaf defoliation.

Results from the F_1 and F_2 generations and parental lines were used to estimate the genetic variance of the six parental lines (5). In all analyses, the variance due to general combining ability (g. c. a.) was highly significant (Table 6). Specific combining ability (s. c. a.) and maternal effects were also significant (P = .05) for percent defoliation among the F_1 progeny, but not among the F_2 progeny.

The g. c. a. effects for each of the six parental lines were calculated from the ratings of F_1 and F_2 means for each disease character according to the methods described by Griffing's model I (5). The importance of a parent in hybrid combination is reflected by the relative magnitude of the estimated g. c. a. effects for each disease character. The

Table 6. Analysis of F_1 and F_2 progeny means and selfs for disease response to early leafspot, late leafspot, and the resulting percent defoliation.

		F_1 Mean Squares			F_2 Mean Squares		
Source of variation	d.f.	Early Leafspot	Late Leafspot	Percent Defoliation	Early Leafspot	Late Leafspot	Percent Defoliation
Mean	1	13,668.1	2790.39	2575.3	15,659.11	4273.44	2403.34
Replicates	3	411.74	62.60	71.29	740.41	179.36	51.19
General Combining ability	5	153.51**	67.46**	18.95**	185.03**	152.41**	5.83**
Selfs	6	53.98*	1.34	1.94			
General Combining ability	9	18.48	7.02	2.85*	14.14	12.49	2.63
Maternal	5	28.01	4.87	3.43*	23.3	7.23	1.39
Reciprocal	10	16.0	14.37	2.22	9.5	23.27	1.17
Error	105	21.94	9.83	1.29	20.12	17.23	1.45

*, ** indicate significance at P=.05 and P=.01 level, respectively.

more negative the estimate, the greater the value of the parent for resistance and the more advantageous for use in a breeding program. From the estimates of g. c. a. effects of the F_1 combinations, NC-GP 343, NC 5 and NC 3033 contributed genes for early leafspot resistance to their progeny (Table 7). The other parental lines had positive estimates of g. c. a. effects, thereby contributing to early leafspot susceptibility. Similar results were found for estimates of g. c. a. effects based on F_2 data.

The parental lines with general combining ability for late leafspot resistance were NC-GP 343, NC-Ac 3139, Florigiant and NC 2. NC 3033 had a high positive value indicating that its progeny were highly susceptible to late leafspot. NC 5 also had a positive estimate for its g. c. a. effect for late leafspot based on the F_1 data, but the g. c. a. effect was negative in the F_2. The g. c. a. effects of the other parental lines for early or late leafspot resistance were consistently either positive or negative in both generations.

The estimate of g. c. a. effects for defoliation from the F_1 data showed only NC 3033 to be negative, however, in the F_2 estimates, NC-GP 343 was also negative. Estimates of g. c. a. effects were also determined for DI-3 values of the F_1 hybrids. NC 3033 and NC-GP 343 had negative estimates, with NC 3033 the more resistant of the two.

Nonadditive genetic variation was important for percent defoliation in the F_1 generation as indicated by significant s. c. a. (Table 6). Estimates of s. c. a. reflect dominance and nonallelic interaction genetic variances. It is measured as the deviation of a cross from an expected value based on the average performance of the parents involved (7). In the F_2 generation, however, the s. c. a. effects were smaller and nonsignificant. This nonsignificant s. c. a. effects probably occurred because inbreeding reduced the nonadditive genetic effects in the F_2 generation (7).

Maternal effects also significantly influenced defoliation in the F_1 generation. A significant maternal effect indicates that some parental lines performed consistently better over corses as females than as males. In the F_2, however, the maternal effects had dissipated. This change indicated the

Table 7. Estimates of general combining abilty effects for parents based on F_2 progeny means of disease ratings for early leafspot, late leafspot and percent defoliation.

	General combining ability effects		
Parental lines	Early leafspot	Late leafspot	Percent defoliation
NC-GP 343	-3.06	-0.48	-1.6
NC 5	-1.25	-0.57	+4.7
NC 3033	-0.42	+3.73	-7.3
NC 2	+1.00	-0.71	+0.7
Florigiant	-1.67	-0.76	+1.3
NC-Ac 3139	+2.05	-1.22	+2.3
Std. deviation	0.591	0.547	1.58

possibility that the F_1 maternal effects were caused by a phenotypic characteristic of the maternal parent that influenced disease development rather than a cytoplasmic genetic effect of the maternal parent which would still be present in the F_2 generation.

The relationship between the disease reaction of the parents to the disease reaction of the F_1 and F_2 progeny of the parents were determined by computing the correlation coefficients (Table 8). For all characters, except late leafspot, the correlations were nonsignificant. Using these rating techniques, the performance of the parental lines themselves will not predict the average performance of the same lines used in crosses. The incidence of late leafspot on the parents, however, was correlated ($P = .05$) with the incidence of late leafspot on the F_1 progeny. For this character, the parental lines per se will predict the average performance of a line in hybrid combination.

The correlations between F_1 and F_2 ratings were positive as expected, but only the correlation between early leafspot incidence in the F_1 and F_2 progeny ($r = .92$) was significant ($P = .05$). The correlation coefficients for late leafspot ($r = .84$) and percent defoliation ($r = .85$) were nonsignficant, but were of a high positive value and therefore suggests a possible relationship.

Correlations were also used to determine the relationship among the six disease ratings (number of *C. arachidicola* and *C. personatum* lesions, percent defoliation and disease indices 1, 2, and 3) for the F_1 hybrids (Table 9). Disease indices 1, 2, and 3 were positively correlated ($P = .05$). Therefore, each disease index reflected the disease reaction of the other indices. The visual estimate of rating general resistance (DI-3) appears to be an effective means of determining leafspot resistance.

Late leafspot was negatively correlated with the other five ratings, i. e. when the incidence of early leafspot was high, the incidence of late leafspot was low. A world of caution should be mentioned in regards to the interpretation of the results involving late leafspot susceptibility or resistance among the six parental lines. Since there were no test plots in which late leafspot alone was present, it is now known whether there may be an inhibitory or stimulatory effect on *C. personatum* germination and infection due to the presence of *C. arachidicola* lesions on the peanut leaves.

In summary, resistance to early and late leafspot appears to act in an additive manner as indicated by significant general combining ability in both F_1 and F_2 generations. Only two lines, however, NC-GP 343 and NC 5 showed resistance to both fungi. NC 3033 was resistant to early leafspot, but susceptible to late leafspot. NC-Ac 3139, Florigiant and NC 2 were the lines most resistant to late leafspot, but were susceptible to early leafspot. Defoliation response appears to act mainly in an additive manner in this study though specific combining ability and maternal effects were present in the F_1 hybrids. NC 3033 and NC-GP 343 were the only two lines tested that are potentially useful in breeding for a low defoliation response. If resistance is specifically aimed for reduced number of *C. arachidicola* lesions, then NC 3033, NC-GP 343 and NC 5 would be the best lines to use. If resistance is specifically aimed for reduced number of *C. personatum* lesions then NC-GP 343, NC-Ac 3139, Florigiant and NC 2 could all be used. In a comparison of all six parental lines, over all crosses, NC 3033 and NC-GP 343 appear to be the most useful lines to include in a leafspot resistance breeding program. In North Carolina, since both early and late leafspot occur, the use of both NC 3033 and NC-GP 343 is recommended for a cercospora leafspots breeding program.

Table 8. Correlations between the mean of the parents and the mean of the progeny from each parent used over all cross combinations.

Disease ratings	r-values	
	F_1	F_2
Early leafspot	0.39	0.45
Late leafspot	0.95**	0.84
Percent defoliation	0.86	0.82

**Indicates significance at P = .01 level.

Table 9. Correlations among disease rating characters based on means of F_1 crosses.

Character	Early leafspot	Late leafspot	Percent defoliation	Indices	
				I	II
Index 3	0.73	-0.83	0.71	0.97**	0.88*
Early leafspot		-0.27	-0.40	0.79	0.70
Late leafspot			-0.80	-0.72	-0.50
Percent defoliation				0.60	0.58
Index 1					0.93**

*,**Indicates significance at P = .05 and P = .01 levels, respectively.

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