Combining Ability and Heritability of Resistance to Early and Late Leafspot of Peanut[1]

W. F. Anderson, J. C. Wynne,* C. C. Green and M. K. Beute[2]

Abstract

Four parental lines with resistance to early leafspot caused by *Cercospora arachidicola* Hori and four parental lines with resistance to late leafspot caused by *Cercosporidium personatum* (Berk. & Curt.) Deighton and the F_1 hybrid progeny from crosses between the two groups of parents were evaluated for resistance to both leafspot diseases in the greenhouse using a detached leaf technique. The subsequent F_2 plants of all crosses were evaluated in the field for resistance to early leafspot in order to estimate combining ability effects for components of partial resistance and to identify parents useful in developing lines resistant to both diseases. General combining ability, attributed largely to additive genetic variance, accounted for the largest portion of the variability among the F_1 and F_2 generations for most parameters of resistance to both early and late leafspots. Reciprocal effects and heterosis toward the susceptible parents were also significant for parameters of resistance to the two pathogens. GP-NC 343 and FESR 5-P2-B1 were the best parents for incorporating genes for resistance to both early and late leafspots. Progenies of NC 17090 had a high level of resistance to late leafspot in detached leaf tests and progeny of PI 350680 had reduced defoliation from early leafspot in the field. Broad-sense heritabilities ranged from 0.2 to 0.4 for parameters of resistance to early leafspot estimated from the pooled variances of F_2 plants of all crosses planted in the field. Parameters of resistance evaluated in the greenhouse for F_1 hybrids were compared to parameters evaluated in the field for the F_2 population by rank correlation of entry means. Latent period and sporulation of the fungus on detached leaves of F_1 generation plants correlated ($r = -0.46$ and 0.54, respectively) with defoliation of F_2 plants in the field.

Key Words: M x N mating, disease resistance, components of resistance, general combining ability.

The leafspot diseases are among the important constraints to peanut (*Arachis hypogaea* L.) production. *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. and Curt.) Deighton, the causal agents of early and late leafspot, respectively, are distributed throughout peanut-growing areas of the world and may occur in the same or different areas (20). Farmers in many countries cannot afford fungicides to control these diseases, which magnifies the importance of finding resistant peanut germplasm and incorporating resistance into adapted peanut cultivars.

Complete resistance to either disease has not been found in the cultivated peanut and, although high resistance is present in wild species of *Arachis*, the incorporation of these genes for resistance into improved cultivars is difficult (1, 2, 4). Partial resistance of the cultivated peanut to early leafspot (6, 8, 10, 12) and late leafspot (5, 13, 18) is of more immediate use. Investigation of the genetics of the components of resistance may help in developing effective methods for selection of resistant germplasm. Sharief *et al.* (16) and Nevill (15) reported that resistance to leafspots results from multiple recessive genes. Combining ability analysis conducted for resistance to both early and late leafspot has indicated that additive genetic variance is two to four times greater than nonadditive variance (7, 10, 19).

The major objective of this research was to estimate combining ability effects for the components of resistance to early and late leafspot measured in the field and greenhouse. The information can be useful in identification of the best sources of resistance for inclusion in a breeding program for developing lines with resistance

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[2]Graduate Research Assistant, Professor, and former Graduate Research Assistant, respectively, Department of Crop Science; and Professor, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695-7629.

to both leafspots. Heritabilities were also determined for the components of resistance measured in the field to provide an indication of the effectiveness of phenotypic selection in early generation.

Materials and Methods

Preparation of Host Material - Four parents resistant to *C. arachidicola* and four parents resistant to *C. personatum* were crossed in an M x N mating design with reciprocals. The late leafspot-resistant lines, all valencia types, were identified at the International Crops Research Institute for the Semi-Arid Tropics (5, 14, 15, 18). NC 17133 (RF), PI 350680 and FESR-5-P2-B1 have shown moderate to high levels of resistance, while NC 17090 was included because of its moderate resistance to *C. personatum* and high levels of resistance to peanut rust (*Puccinia arachidis* Speg.). Parents PI 109839, GP-NC 343, PI 269685, and NC 270806 have partial resistance to *C. arachidicola* (2, 3, 7, 8). PI 109839 is a small-seeded virginia type while the others are larger seeded virginia types. Eight F_1 plants of each cross, the parents, and two checks were grown in 22-cm plastic pots. The checks included Florigiant, a cultivar susceptible to early leafspot, and the breeding line NC 3033, which is susceptible to late leafspot. The pots were arranged on a greenhouse bench in a randomized complete block design. This same randomization was maintained during the F_1 detached leaf test. Plants were allowed to self-pollinate to produce F_2 seed. Normal pesticide treatment was curtailed 3 weeks prior to inoculation with the pathogens to ensure minimum chemical residue that may interfere with disease reaction.

Preparation of Inoculum - Cultures of *C. arachidicola* and *C. personatum* originating from infected peanut at the Peanut Belt Research Station, Lewiston, NC were maintained on the cultivars Florigiant and NC 3033, respectively, in separate humidity chambers in the greenhouse. Approximately 4 days prior to the inoculation in greenhouse tests, infected leaves of the host plants were detached and placed on moist towels in plastic trays. The trays were enclosed in plastic bags. Approximately 24 h later, conidia were collected from the leaves into small test tubes with the use of a cyclone spore collector (Eri Machine Shop, Iowa State Univ., Ames) attached to a vacuum pump run at 6.9×10^4 Pa pressure. Just prior to their use the conidia were suspended in distilled water with Tween 80 (1 drop/100 mL H_2O). The concentration of the conidial suspension was measured using a hemacytometer and diluted to concentrations of 20,000 conidia/mL for *C. arachidicola* and 40,000 conidia/mL for *C. personatum*. These were judged to be the most useful concentrations for disease resistance evaluations by previous investigators (8, 14).

F_1 Detached Leaf Test - The F_1 and parental genotypes were evaluated in the greenhouse by a detached leaf technique (11, 14). The third fully expanded leaves from the terminal end of the lateral branches of 10-week-old greenhouse-grown plants were detached, and the petioles were placed in sand-filled plastic trays. Eight replications (one leaf/replication/tray) were tested for each of the peanut pathogens. The trays were placed in a mist bed for 1 week prior to inoculation to allow callus and root formation. One day before inoculation the trays were covered by a chamber made with a wood frame and clear plastic sides to prepare a dry leaf surface.

Leaves were inoculated by misting the conidial suspension onto the leaves with a Paasche-H air brush (Paasche Airbrush Co., Chicago, IL). All leaves within a replication were misted evenly, allowed to air dry and misted again. The light misting was repeated three times. For each replication of 42 leaves, approximately 15 mL of conidial suspension was used. The trays were then covered with plastic humidity chambers and placed in a mist bed which was timed for four 10-second mists of warm water every 3 minutes. A temperature of 23-25C and a relative humidity of 85-90% was maintained for the duration of the test. Leaves were misted lightly with water once a day for the first 4 days of incubation. Approximately 10 days of incubation were required before symptoms of the leafspot diseases began to appear. On day 10 the trays were exposed to the misting system for approximately 15 minutes to resaturate the sand.

The following data were taken on the detached leaves for each pathogen:

a) Total number of lesions, counted at day 20
b) Estimate of lesion area in mm², taken as an average of five representative lesions at day 30
c) Latent period, defined as time in days after inoculation for 50% of lesions on a leaf to sporulate (calculated by counting the number of sporulating lesions every other day)
d) Sporulation, rated on a scale of 1 indicating no sporulation to 5 indicating heavy sporulation
e) Leaf area in cm², measured with a Li-Cor Model LI 3000 leaf area machine (Li Cor, Ltd., Lincoln, NB)

From these data two other variables were calculated:

a) Lesion number per 100 cm² of leaf area (total lesion number x 100/leaf area) and
b) Estimate of total necrotic area (lesion number x average lesion area x 10/leaf area).

Log_{10} transformations were used to normalize distributions for lesion number per 100 cm² leaf area and percent lesion area. Analysis of variance was performed for each variable and a Waller-Duncan multiple range test was used to compare entry means. The analysis was that of a factorial design such that the male and female main effect sum of squares estimated general combining ability and the male x female interaction sum of squares estimated specific combining ability. The total entry sum of squares was also partitioned into that due to reciprocal effects and heterosis. Heterosis was estimated as the deviation of the F_1 hybrids from the midparent mean. General combining ability effects were calculated for each parent as follows: $GCA_i = (T_i/N_i) - (T/N)$ where:

GCA_i = General combining ability for parent i
T_i = The total of parent i in hybrid combinations
N_i = The number of hybrid combinations for parent i
T = The total of all hybrid combinations
N = The total number of hybrid combinations.

Spearman rank correlations (17) were computed among the parameters measured within the detached leaf tests for each pathogen. Rank correlations of entry means were also computed between the parameters measured for early leafspot resistance and those measured for late leafspot resistance.

F_2 Field Test - The F_2 generations and parental lines of each cross were planted at the Peanut Belt Research Station, Lewiston, NC in a randomized complete block design with four replications for evaluation of leafspot resistance. Seeds were germinated in small peat pots and transplanted 2 weeks later into the field. Fungicides were not used to control leafspot. The plants were artificially inoculated with equal concentrations of *C. arachidicola* and *C. personatum* conidia approximately 60 days after planting to allow evaluation of resistance to both early and late leafspot. At the time of inoculation few lesions of early leafspot were observed so that competition with natural inoculum was considered minimal.

Inoculum was obtained by collecting conidia from infected plants in the greenhouse. The concentration of conidia of the two fungi collected was determined using a hemacytometer and then diluted to approximately 3,000 conidia/mL with water and Tween 80 (1 drop/100 mL H_2O) as a surfactant. Field inoculation was made with a Micron Ultra 8 low-volume sprayer (Micron Corp., P. O. 19698, Houston, TX 77024). Approximately 2 L of inoculum suspension was used to inoculate the 800 plants in the field. Two weeks later lesions of both early and late leafspot were observed on the plants.

On August 15, 1984 five leaves were sampled at random from midcanopy of each F_2 plants. Lesion number, average lesion size, and total leaf area were determined in the laboratory. Lesion number per 100 cm² leaf area and percent lesion area were calculated and a $\log_{10}$ transformation was used to normalize the distribution of the data. On September 26, 1984 each plant was visually rated for defoliation on a scale of 1-5: 1 = less than 5% defoliation, 2 = 5-15% defoliation, 3 = 15-30% defoliation, 4 = 30-60% defoliation, 5 = greater than 60% defoliation. The form of the analysis of the F_2 generation was the same as that used for the F_1 generation. The genotypic variances of the F_2 populations were obtained by subtracting the average variance among parental plants, as an estimate of environmental variance, from the total F_2 variance for each cross. Bartlett's test for homogeneity of variance was performed on the variances of parents. Due to significant heterogeneity of parental variances, some parents were excluded from the pooled estimates of environmental variances to obtain homogeneity. The late leafspot-resistant parents were excluded from the pooled estimate of environmental variance for lesion number per 100 cm² leaf area ($\log_{10}$) and percent lesion area. The parents NC 17090, NC 270806 and PI 269685 were excluded from the estimate of environmental variance for lesion size. Broad-sense heritabilities for each resistance parameter were calculated by dividing the estimated genetic variance by the overall phenotypic variance for each cross. The estimates of heritability were then pooled over crosses for each variable.

Results and Discussion

Combining Ability Analyses - General combining ability attributed to additive genetic variance was highly significant for all parameters of resistance to *C. personatum* measured in the greenhouse (Table 1). Specific combining ability or nonadditive genetic variance was not significant for any parameter. Walls (19) also reported that resistance to late leafspot measured in the greenhouse was predominantly controlled by additive gene effects. Reciprocal effects were found to be important for all parameters measured for late leafspot except lesion number. A comparison of the means of all reciprocal crosses revealed no general trend such that specific parents were found to be consistently better or worse over all crosses when used as a female. However, there were specific pairs of reciprocal crosses that were better with a parent used as a female rather than a male. There are no previous reports of reciprocal effects for late leafspot resistance. The mean of the F_1 hybrids deviated significantly from the midparent mean in the direction of the susceptible parent. This supports Nevill's (15) proposal that late leafspot resistance is controlled by recessive genes. However, because the combining ability analyses did not reveal significant nonadditive genetic variance, an alternative explanation is that there are more completely additive loci and/or alleles determining susceptibility than resistance in this population. Thus the mean of all F_1's would be skewed toward the susceptible parents. Walls (19) was also unable to fit Nevill's recessive loci model for all crosses in his combining ability analyses.

Table 1. Mean squares for general and specific combining abilities for parameters of resistance to *Cercosporidium personatum* and *Cercospora arachidicola* for the F_1 detached leaf evaluation.

	df	Lesion no./100 cm^2 of leaf area (log 10)	Avg lesion size	Necrotic area (log 10)	Sporulation rating	Latent period
		C. personatum				
GCA	6	0.13*	4.50**	0.39**	2.43**	9.93**
SCA	9	0.08	0.61	0.12	0.18	3.28
Error	233	0.06	0.57	0.10	0.24	2.28
Reciprocals	16	0.06	2.71**	0.37**	1.40**	38.83**
Heterosis[a]	1	0.28*	29.46**	4.25**	24.21**	605.00**
		C. arachidicola				
GCA	6	0.50**	0.71	0.41**	0.35	6.20
SCA	9	0.17*	0.49	0.21*	0.39	7.56*
Error	233	0.07	0.33	0.10	0.22	3.25
Reciprocals	16	0.10	0.72**	0.16	0.19	2.73
Heterosis[a]	1	0.01	0.31	0.00	0.00	0.07

[a]Measured by a single degree of freedom contrast of means of parent vs means of F_1 hybrids.

*,** Denote significance at p = .05 and .01, respectively.

In green house evaluations for resistance to *C. arachidicola*, only lesion number per 100 cm^2 leaf area and percent necrotic area exhibited significant general combining ability (Table 1). Specific combining ability or nonadditive genetic variance in the F_1 generation was also significant for these two parameters as well as for latent period. Yet, there was also no indication of significant heterosis for early leafspot resistance, as the mean of the F_1 hybrids was also not significantly different from the midparent mean. Reciprocal effects were significant for lesion size only. Again there are no previous reports of reciprocal effects for resistance to early leafspot.

A combining ability analysis of the F_2 generation in the field was performed for early leafspot resistance only, because there were few late leafspot lesions at the time of sampling. General combining ability was highly significant for all parameters of resistance to early leafspot measured in the field (Table 2). Specific combining ability was significant for lesion number, necrotic area, and defoliation. Hamid *et al.* (7) and Kornegay *et al.* (10) reported only significant general combining ability for early leafspot resistance evaluated in the field using lesion number. The mean of the F_2 plants was significantly different from the midparent mean in the direction of the susceptible parents for all parameters of resistance to early leafspot measured in the field. This suggests that resistance to early leafspot may be controlled by recessive genes. However, epistasis or interaction across loci may also cause heterosis. Genetic variance due to additive x additive epistasis is contained in both the general and specific combining abilities. Reciprocal effects were significant for lesion number and defoliation.

Table 2. Mean squares for general and specific combining abilities for parameters of resistance to *Cercospora arachidicola* for the F_2 field evaluation

	df	Lesion no./100 cm^2 of leaf area (log 10)	Avg lesion size	Necrotic area (log 10)	Defoliation
GCA	6	0.78**	12.32**	1.60**	8.36**
SCA	9	0.16*	1.98	0.33**	1.95**
Error	588	0.07	1.45	0.13	0.41
Reciprocals	16	0.13*	0.73	0.18	1.17**
Heterosis[a]	1	0.42**	21.47**	2.05**	0.69

[a]Measured by a single degree of freedom contrast of means of parents vs means of F_2 population.

*,** Denote significance at p = .05 and .01, respectively.

General combining ability effects for each parent were estimated using the F_1 generation evaluations for resistance to both early and late leafspot in the greenhouse and for the F_2 generation evaluations for resistance to early leafspot in the field (Tables 3 and 4). Large negative GCA effects are desirable for improving resistance as negative values indicate the mean of all hybrid combinations with parent i is less than the mean of all hybrid combinations across all parents. Although it is desirable to increase latent period, the scale for this variable was reversed to be consistent with the other components of resistance. The parents FESR 5-P2-B1 and GP-NC 343 were consistently the best parents for combining resistance to *C. personatum* as measured by all parameters examined in the greenhouse. However, NC 17090 produced progeny that supported less sporulation and longer latent periods than did all parental lines except FESR 5-P2-B1. The parents FESR 5-P2-B1 and GP-NC 343 were also the best parents in the greenhouse study for transferring genes to reduce lesion number and necrotic area due to *C. arachidicola* (Table 3). NC 17133(RF) was effective in reducing lesion size, GP-NC 343 produced progeny with lower sporulation and FESR 5-P2-B1 was most effective in increasing latent period for *C. arachidicola*. Estimates of GCA effects from the F_2 field test of early leafspot resistance again indicated that FESR

5-P2-B1 and GP-NC 343 were the best parents for producing progeny with reduced lesion number, lesion size and necrotic area (Table 4). PI 350680 produced progeny with the least defoliation.

Table 3. Estimates of general combining ability effects for parameters of resistance to *Cercosporidium perosonatum* and *Cercospora arachidicola* for the F_1 detached leaf evaluation

	Lesion no./100 cm^2 of leaf area (log 10)	Avg lesion size	Necrotic area (log 10)	Sporulation rating	Latent period
		C. personatum			
NC 17133(RF)	0.061	0.144	0.088	0.282	0.620
PI 350680	0.029	0.097	0.042	0.150	0.251
FESR 5-P2-B1	-0.071	-0.332	-0.127	-0.264	-0.467
NC 17090	-0.017	0.089	-0.001	-0.170	-0.405
PI 109839	0.001	-0.143	-0.015	0.056	-0.014
GP-NC 343	-0.036	-0.278	-0.074	-0.124	-0.077
NC 270806	0.000	0.394	0.064	0.087	0.251
PI 269685	0.036	0.003	0.028	-0.022	-0.154
LSD (.05)	0.130	0.376	0.194	0.238	0.770
		C. arachidicola			
NC 17133(RF)	0.088	-0.143	0.073	0.053	0.552
PI 350680	0.052	-0.086	0.038	-0.036	-0.071
FESR 5-P2-B1	-0.164	0.152	-0.101	0.001	-0.477
NC 17090	-0.008	0.069	0.019	-0.021	-0.009
PI 109839	-0.011	0.012	0.012	0.038	0.102
GP-NC 343	-0.089	-0.078	-0.107	-0.112	0.098
NC 270806	0.042	0.059	0.074	0.107	-0.097
PI 269685	0.038	0.000	0.037	-0.053	-0.104
LSD (.05)	0.096	0.220	0.119	0.179	0.656

Table 4. Estimates of general combining ability effects for parameters of resistance to *Cercospora arachidicola* for the F_2 field evaluation

	Lesion no./100 cm^2 of leaf area (log 10)	Avg lesion size	Necrotic area (log 10)	Defoliation
NC 17133(RF)	-0.037	0.199	-0.006	0.351
PI 350680	0.016	-0.020	0.019	-0.302
FESR 5-P2-B1	-0.084	-0.303	-0.147	-0.037
NC 17090	0.105	0.121	0.132	-0.030
PI 109839	0.059	-0.025	0.060	-0.107
GP-NC 343	-0.075	-0.254	-0.110	-0.123
NC 270806	0.022	0.493	0.087	0.284
PI 269685	-0.006	-0.229	-0.042	-0.061
LSD (.05)	0.085	0.391	0.113	0.195

If leafspot resistance is controlled entirely by recessive genes, resistant cultivars would be expected to possess recessive alleles for resistance to the leafspot fungi while susceptible cultivars would have dominant alleles at the corresponding loci. When a group of resistant lines are crossed to susceptible lines, the heterozygous hybrids would all be susceptible (only dominant alleles expressed) and there would be no differences among F_1 hybrids. However, significant differences were found among hybrids in the F_1 detached leaf tests for resistance to both leafspot diseases. It is possible that some recessive genes for resistance are present in the genome of the relatively susceptible parents which are expressed in the F_1 when combined with the corresponding alleles of the resistant parents. It is also possible that some genes responsible for expression of partial resistance may not be recessive but act additively across loci when combined in the F_1 hybrid generation. This would result in F_1 progeny better than the parents. This is supported by the fact that the GCA effects were better for some parents than expected based on parental means FESR 5-P2-B1 and GP-NC 343 were the parents in this study which appeared to possess the greatest number of genes acting in an additive manner for partial resistance to both fungi. These two lines consistently produced good progeny although they were not the most resistant lines based on mean parental performance. The parental cultivars PI 350680 and NC 17133 (RF) were the most resistant cultivars to late leafspot in all detached leaf trials but their hybrid progeny were more susceptible than progeny from less resistant parents. These two parents may possess recessive genes for resistance that are not expressed in the F_1 hybrids. NC 17133(RF) is the only parental line in this study which was also used by Nevill (15) in a study in which Nevill proposed that resistance to late leafspot is controlled by five recessive genes.

Parents did not rank consistently for all parameters of resistance to both leafspot diseases measured in the field and greenhouse. For example, in the F_1 late leafspot test, PI 109839 produced progeny with average lesion number but with much smaller lesion size, and PI 269685 was a good parent for increasing latent period in the progeny but was average for all other parameters (Table 3). FESR 5-P2-B1 produced progeny with longer latent periods and fewer lesions but average sporulation and increased lesion size in the F_1 test for early leafspot resistance (Table 3). This indicates there are different genes controlling specific components of resistance. The rank correlations of means of crosses and parents over parameters support this premise. In greenhouse evaluations of the F_1 generation, parameters for resistance to *C. personatum* generally correlated much better with each other than parameters for resistance to *C. arachidicola* (Table 5). Although the correlation coefficients among the parameters of resistance to *C. arachidicola* were significant based on the number of degrees of freedom, the coefficients were generally only moderate. Also ranked means of crosses for lesion number, lesion size and necrotic area measured in the F_2 field evaluation for early leafspot resistance were not significantly correlated to defoliation (Table 6).

Heritability Estimates - The broad-sense heritability for lesion number per 100 cm^2 of leaf area, necrotic area and defoliation was approximately 0.2 over all crosses indicating selection based on phenotypic differences of F_2 plants in the field would be difficult. In general, estimates of environmental variance were high compared to total F_2 variances, suggesting that homogeneous parental plots were less buffered to environmental influence than the heterogeneous plots of F_2 plants. There were individual crosses with higher heritability estimates for some parameters such that selection of F_2 plants may be effective in some crosses.

Effectiveness of the Detached Leaf Evaluations - The question must be answered as to whether the detached leaf evaluations for resistance to leafspot diseases are effective in estimating resistance in the field before selections can be made on greenhouse evaluations only. The means of crosses and parents were compared for parameters measured in the greenhouse for the F_1 generation

Table 5. Rank correlation of F_1 means[a] for parameters of resistance to *Cercosporidium personatum* and *Cercospora arachidicola* in the detached leaf test

	[LLNP] Lesion no./100 cm^2 of leaf area (log 10)	[LS] Avg lesion size	[LNA] Necrotic area (log 10)	[SR] Sporulation rating	[LP] Latent period
			C. personatum		
LLNP	x	.447**	.869**	.666**	-.558**
LS		x	.774**	.605**	-.631**
LNA			x	.798**	-.729**
SR				x	-.781**
LP					x
			C. arachidicola		
LLNP	x	.061	.895**	.187	-.409*
LS		x	.447*	.528**	-.399*
LNA			x	.402*	-.547**
SR				x	-.512**
LP					x

[a]Based on cross means.

*,** Denote significance at p = .05 and .01, respectively, where the degrees of freedom = 31.

Table 6. Rank correlation of F_2 means[a] parameters of resistance to *Cercospora arachidicola* measured in the field.

	[LLNP] Lesion no./100 cm^2 of leaf area (log 10)	[LS] Avg lesion size	[LNA] Necrotic area (log 10)	[DEF] Defoliation rating
LLNP	x	.561**	.923**	.245
LS		x	.812**	.392*
LNA			x	.360*
DEF				x

[a]Based on cross means.

*,** Denote significance at p = .05 and .01, respectively.

with field evaluation for resistance to early leafspot (Table 7). The comparisons were made between two different generations which confounds genotypic variation between F_1 and F_2 generations along with environmental effects. The lack of rank correlation in this case cannot be totally attributable to environmental changes; however, significant correlations found between latent period and sporulation recorded in the greenhouse with defoliation in the field indicates that latent period and sporulation are the best parameters for predicting defoliation from early leafspot in the field. Walls (19) found that latent period, sporulation and lesion diameter were the most effective parameters measured in the greenhouse for estimating field resistance to late leafspot while Johnson (9) found similar results for early leafspot.

Table 7. Rank correlation of means for parameters of resistance to *Cercospora arachidicola* between F_1 detached leaf and F_2 field evaluation (F_1 detached leaf test)

	[LLNP] Lesion no./100 cm^2 of leaf area (log 10)	[LS] Avg lesion size	[LNA] Necrotic area (log 10)	[SR] Sporulation rating	[LP] Latent period
LLNP	.153	.156	.241	.306*	-.165
LS	.159	-.107	.160	.318*	-.091
LNA	.126	.078	.209	.329*	-.131
Defoliation rating	.085	.224	.226	.538**	-.455**

*,** Denote significance at p = .05 and .01, respectively.

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