Theor Appl Genet (1986) 73:228–235

Diallel and generation means analyses for the components of resistance to *Cercospora arachidicola* in peanut*

C. C. Green and J. C. Wynne

Crop Science Department, North Carolina State University, Raleigh, NC 27695-7629, USA

Received June 18, 1986; Accepted July 21, 1986
Communicated by J. MacKey

Summary. The inheritance of the components of partial resistance to *Cercospora arachidicola* Hori in peanut (*Arachis hypogaea* L.) was examined in two five-parent diallels and in the six generations of two single crosses in greenhouse tests. The Griffing (1956) analysis indicated general combining ability (GCA) to be of most importance, yet large ratios of SCA/GCA sum of squares suggested nonadditive genetic variance as well. Reciprocal effects were found for lesion area and lesion number/10 cm² leaf area. The importance of nonadditive genetic variance was substantiated by the lack of fit for the additive-dominance model in the Hayman's analysis (1954a, b). Further evidence from the Hayman's analysis indicated that epistasis may be important in determining the inheritance of some of the components of resistance. Additive gene effects alone accounted for the genetic variability observed among the generation means from two single crosses for all components of resistance except latent period. There was evidence that epistasis was an important mode of gene action for the inheritance of latent period.

Key words: Early leafspot – *Arachis hypogaea* L. – Groundnut

Introduction

Early leafspot of peanut (*Arachis hypogaea* L.) caused by *Cercospora arachidicola* Hori is among the major constraints to higher yields of peanuts worldwide. Yield reductions as great as 50% have been reported where disease control measures were not practiced (Gibbons 1980; Jackson and Bell 1969; Mercer 1976). Chemical control of early leafspot, although effective, is a costly practice in the United States and is often not feasible in many developing countries of the world. Host plant resistance is thus a valuable tool in a disease management program. The present emphasis in the development of disease-resistant cultivars is in the use of partial resistance. Partial resistance is defined as resistance that reduces the rate of an epidemic. Generally partial resistance is controlled by many genes and is thus considered to be more durable against adaption by the pathogen population. Parlavliet (1979) stated that several resistance components contribute to the reduction in the rate of an epidemic with the most important components being (1) reduction in infection frequency or lesion number, (2) lengthening of latent period and (3) a decrease in spore production.

The development of resistant cultivars is enhanced by a knowledge of the inheritance of the resistance. Hamid et al. (1981) and Kornegay et al. (1980) both evaluated the F_2 generation of a six parent diallel for resistance to early leafspot and reported only significant general combining ability (GCA) for lesion count which is attributed to additive genetic variance. Anderson (1985) reported the analysis of the F_2 generation from a 4×4 (males=4, females=4) factorial mating design and showed significant GCA, specific combining ability (SCA) (attributed to nonadditive genetic variance), and significant reciprocal effects for lesion count. Anderson also examined several other components of resistance to early leafspot and found significant GCA for average lesion size, necrotic area/leaf and defoliation in addition to significant SCA for necrotic area/leaf and defoliation. Additive genetic variance is desirable as it can be selected upon and differences due to additive gene effects can be fixed in homozygous lines. Nonadditive genetic variance includes dominance and epistatic effects of which only additive×additive epistatic effects can be fixed in homozygous lines. Previous reports on the inheritance of resistance to early leafspot in early generation material did not attempt to separate nonadditive genetic effects into dominance and epistasis.

* Paper No. 10172 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27601, USA

The diallel cross is a mating design that provides a systematic approach to studies of continuous variation. It also enables the identification of crosses with good selection potential as well as identifies good parents for inclusion in additional crossing programs. Arguments against the utility of the diallel cross in self-pollinated crops have stated that the diallel analyses provide no more information than the parental means themselves. However, Hamid et al. (1981) and Anderson (1985) found parents that performed significantly better (higher resistance in the progeny) than predicted based on mean parental performance.

Two methods proposed for the analyses of data from diallel crosses in self-pollinators include the approaches of Griffing (1956) (method 1, model 1) and Hayman (1954a, b). Hayman (1961) stated that combining ability (Griffing analysis) does not contain the maximum amount of information about the action of genes by which the parents differ and that combining ability is as much a statistical concept as a genetic concept. Mather and Jinks (1971, 1977) used Hayman's approach to outline a more extensive study of the variation resulting from crosses of inbred lines and provide a genetic interpretation of the analysis.

The objective of this study was to examine the inheritance of the components of partial resistance to early leafspot in peanut with the goal of understanding the types of gene action governing resistance. This study includes the results of the F_1 analysis of two five-parent diallels utilizing both the Griffing and Hayman methods of analyses. A generation means analysis as outlined by Mather and Jinks (1977) to test the additive-dominance genetic model is also presented for two crosses (one from each five-parent diallel).

Materials and methods

1 Diallel analyses

The 10 parental lines included in this study were the cultivars 'Florigiant', 'NC 6', 'NC 7' and 'NC 5', breeding lines GP-NC 343 and NC 3033 and the exotic cultivars 'Kanyoma', 'PI 269685', 'PI 270806' and 'PI 109839'. The 10 parental lines included a range in levels of resistance to early leafspot with the widely grown cultivars 'Florigiant', 'NC 6' and 'NC 7' generally being the most susceptible. The 10 parental lines were randomly divided into two groups of five parents. Group I included 'Florigiant', 'Kanyoma', GP-NC 343, 'NC 6' and 'PI 269685' and group II included NC 3033, 'NC 5', 'PI 270806', 'PI 109839' and 'NC 7'. The lines within each group were crossed in all possible combinations producing two complete five-parent diallels with reciprocals.

The F_1 generation for each diallel was grown on a greenhouse bench in a randomized complete block design with four replications. The two diallels were planted and evaluated 2 weeks apart to reduce labor demands. Approximately 10 weeks after planting a detached leaf technique described by Melouk and Banks (1978) was used to evaluate the genotypes. The fourth fully expanded leaf from the terminal bud was detached from each of two laterals for each of the plants. The same randomization as established on the greenhouse bench was maintained in the detached leaf test. Each entry within a block was represented by a two-leaf plot. Leaves from diallel I were inoculated with approximately 21,000 conidia/ml. The conidia were collected from leaves obtained from unsprayed 'Florigiant' plants maintained at the Sandhills Research Station, Jackson Springs, NC. Leaves from diallel II were inoculated with 40,000 conidia/ml produced in culture as described by Ricker (1984). A higher inoculum concentration was used because a loss in inoculum efficiency had been observed for inoculum produced in culture. Inoculation was achieved using a Devilbiss atomizer attached to an air pump run at 6.9×10^4 Pa pressure. The upper surface of each leaf was misted for 4 s with the atomizer held at a distance of 20 cm from the leaf surface. The leaves were maintained in 1 × 10-cm test tubes containing Hoagland's solution (Hoagland and Arnon 1950; Ricker 1984). The test tubes with the leaves were held in holes on wood boards enclosed in plastic-covered, moist chambers. The moist chambers were kept under a mist system (misting 30 s every 3 min) to maintain high relative humidity. The leaves were misted directly using a hand mister with distilled water three times daily for the first 72 h following inoculation. The following components of resistance were measured for each entry:

1. Lesion number/leaf – recorded at 26 days after inoculation.
2. Standardized lesion number = lesion number/10 cm^2 leaf area determined as [(lesion number/leaf)/leaf area] × 10.
3. Lesion area (mm_2) = the average of three largest lesions/leaf.
4. Defoliation at 45 days after inoculation recorded as the number of leaflets lost/(total number of leaflets/plot).

Latent period was also determined for each entry by regressing the mean percent sporulating lesions (recorded every other day, day 22–34) versus days after inoculation. The regression equation for each entry was then used to predict the number of days after inoculation (predicted X) until 50% of the lesions that appeared by day 26 are sporulating (L_{50}).

A combining ability analysis was performed on all components of resistance except latent period. Latent period was not included because a single mean predicted X value (L_{50}) was obtained for each entry from the replicated sporulation data. Latent period was, however, included in all other analyses. A log transformation of lesion number was used to stabilize the variance. The statistical model used in the diallel analysis was that of Griffing's (1956) method I, model I with reciprocal effects included. General combining ability effects were computed for each parent for all components of resistance and genetic correlations were computed based on GCA effects.

In addition to the combining ability analysis, further information was obtained by utilizing the WrVr analysis described by Hayman (1954b) where the Vr's are the array variances and the Wr's are the covariances of the mean phenotypes in an array with the nonrecurrent parent. This method tests the adequacy of the additive-dominance model to describe the genetic variation.

2 Generation means analysis

The inheritance of the components of resistance to *C. arachidicola* was examined in two crosses, 'Kanyoma' × 'PI 269685' (cross 1) and NC 3033 × 'PI 270806' (cross 2). The parents (P_1, P_2) F_1, F_2 and two backcrosses of the F_1 to the parents (BC_1, BC_2) of each cross were evaluated for resistance using the detached leaf technique as described for the diallel study. Each cross was represented by four randomized sets of 50 plants each. Each of the four sets per cross consisted of the following:

5 plants each of P_1 and P_2
5 F_1 plants
10 plants each of BC_1 and BC_2
15 F_2 plants.

The segregating generations (F_2, BC_1, BC_2) were represented by more plants to better estimate their means. The two crosses were planted 2 weeks apart to reduce labor demands. Ten weeks after planting, plants were inoculated with 25,000 spores/ml. The inoculum was collected from 'Florigiant' plants maintained in moist chambers in the greenhouse (Ricker 1984). The data collected were the same as those for the diallel study.

Generation means analysis was conducted for each component of resistance measured. Each of the six mean phenotypes per cross ($\overline{P}_1$, $\overline{P}_2$, $\overline{F}_1$, $\overline{F}_2$, $\overline{BC}_1$, $\overline{BC}_2$) can be described in terms of the midparent (m) which depends on the general conditions of the observations, the additive component [d] and the dominance component [h] where:

[d] = the sum over loci of all d's which measure the departure of each homozygote from the midparent m and
[h] = the sum over loci of all h's which measure the departure of the heterozygote from the midparent m (Mather 1949).

Estimates of the model parameters (m, [d], [h]) were obtained from the six equations describing the mean phenotypes by a weighted least squares solution. The six means were weighted by the reciprocal of their corresponding variance. A joint scaling test as proposed by Cavalli (1952) was used to test the fit of the additive dominance model. In addition, individual scaling tests as defined by Mather (1949) were computed to compare with the results of the joint scaling test. The three individual scaling tests are:

$$A = 2\overline{BC}_1 - \overline{P} - \overline{F}_1$$
$$B = 2\overline{BC}_2 - \overline{P} - \overline{F}_1$$
$$C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$$

where A, B and C should equal zero if the additive-dominance model adequately describes the genetic variance.

Results

1 Diallel analysis

The combining ability analysis for the components of resistance (excluding latent period) in two five-parent diallels is summarized in Table 1. The GCA mean squares were significant for lesion area in diallel I and lesions/10 cm², lesion area and defoliation in diallel II. Significant SCA effects were found for lesion area in diallel I. Reciprocal effects were observed for lesions/leaf and lesion area in diallel I and lesions/10 cm² in diallel II. The sum of squares attributable to SCA was greater than for GCA for all components of resistance in diallel I (Table 1). The GCA and SCA sum of squares was approximately equal for all components of resistance in diallel II except lesions/leaf for which the SCA sum of squares was 10 times that of the GCA sum of squares. Reciprocal effects accounted for approximately 50% of the genotype sum of squares in both diallels for all resistance components except lesion area and defoliation in diallel I.

The range in means of the hybrids for the components of resistance exceeded that of the parents for lesions/leaf, lesion area, defoliation and latent period (L_{50}) in diallel I and lesions/leaf and defoliation in diallel II (Table 2). Results of the combining ability analysis suggest that the range of variability in means for some of the components of resistance is in part due to genetic sources. As expected, the two widely grown cultivars, 'Florigiant' (diallel I) and 'NC 7' (diallel II) were generally the most susceptible parents in this study.

Parental means over crosses were used to compute GCA effects for each parent (Table 3). Large negative values for GCA effects are desirable for all components of resistance except latent period for which large positive GCA values indicate a good parent. The ranking of the parents according to GCA effects was not highly correlated with their ranking according to parental means for any of the components of resistance except latent period (diallel I $r = 0.8$, diallel II $r = 0.9$) for both diallel groups. This indicates that selection of parents based on parental performance per se may not result in the best possible hybrids. Based on GCA

Table 1. Combining ability analyses for components of partial resistance to *Cercospora arachidicola* in two five-parent diallels

		Diallel I				Diallel II			
		Log. les./ leaf	Log les./ 10 cm²	Lesion area (mm²)	% Defoliation	Log les./ leaf	Log les./ 10 cm²	Lesion area (mm²)	% Defoliation
GCA	4	2.92	5.60	33.87**	255.86	0.64	30.50*	14.30**	3,839.8**
SCA	10	2.35	5.54	21.48*	197.53	2.72	11.06	5.05	1,632.2
Recipr.	10	4.61*	5.22	22.24**	296.88	2.19	20.08*	1.70	1,351.6
Error	72	1.83	3.04	8.23	185.24	1.70	10.02	2.78	831.3
		% Genotype sum of squares attributable to GCA, SCA and reciprocal effects							
GCA		14.35	17.14	23.65	17.24	5.00	28.15	45.88	33.98
SCA		28.90	42.60	37.50	32.76	52.56	25.52	40.50	36.11
Recipr.		56.75	40.26	38.85	50.00	42.44	46.33	13.62	29.91

*,** Denote significance at the 0.05 and 0.01 probability levels, respectively

Table 2. Parental means and range in means of the hybrids of two five-parent diallels for the components of resistance to *Cercospora arachidicola*

Entry	Lesions/ leaf	Lesions/ 10 cm²	Lesion area (mm²)	% Defoliation	L_{50} [a]
	Diallel I				
Hybrids	2.2–17.7	3.0–19.5	2.8–12.2	0–14.3	26.9–38.4
'Florigiant'	12.6	20.7	8.4	8.9	27.1
'Kanyoma'	4.1	4.1	7.7	7.1	30.2
GP-NC 343	3.9	4.7	3.8	8.9	32.0
'NC 6'	1.9	2.6	5.5	0	31.2
'PI 269685'	9.8	8.0	8.2	3.1	30.7
	Diallel II				
Hybrids	12.9–47.7	17.5–54.3	4.4–8.9	3.1–37.0	28.4–31.8
NC 3033	19.6	21.2	4.4	0	33.9
'NC 5'	16.7	30.6	6.4	6.2	29.3
'PI 270806'	37.9	39.8	9.0	25.0	29.2
'PI 109839'	35.6	54.1	5.6	26.6	29.2
'NC 7'	43.4	74.5	6.3	26.6	28.4

[a] L_{50} = latent period measured as predicted number of days after inoculation until 50% of the lesions that appeared by day 26 are sporulating

Table 3. Estimates of general combining ability (GCA) effects[a] for components of resistance to *Cercospora arachidicola* for the parents of two diallels

Parent	Log les./ leaf	Log les./ 10 cm²	Lesion area (mm²)	% Defoliation	Latent period (L_{50})
	Diallel I				
'Florigiant'	−0.22	−0.60	1.40	−4.48	−1.68
'Kanyoma'	0.08	−0.26	1.00	0.21	−2.19
GP-NC 343	−0.32	0.03	−1.46	3.33	1.96
'NC 6'	−0.09	0.12	−0.23	−1.88	0.55
'PI 269685'	0.56	0.70	−0.70	2.81	1.41
	Diallel II				
NC 3033	−0.11	−0.72	−1.09	−19.06	2.56
'NC 5'	0.07	0.37	0.40	7.50	−0.28
'PI 270806'	0.18	−0.85	0.99	−5.52	−0.63
'PI 109839'	−0.23	−0.62	−0.10	3.85	0.01
'NC 7'	0.08	1.82	−0.20	13.23	−1.68

[a] Large negative GCA effects are desirable for all components of resistance except latent period for which large positive GCA effects are desirable

effects, GP-NC 343 was the best parent in diallel I for lesions/leaf, lesion area and latent period, whereas 'Florigiant', unexpectedly, had the lowest GCA effects for lesions/10 cm² and defoliation.

Examination of the hybrid means revealed that the cross of GP-NC 343 × 'Florigiant' for lesions/10 cm² and the crosses of 'Kanyoma' × 'Florigiant' and GP-NC 343 × 'Florigiant' for defoliation ('Florigiant' as the male in all three crosses) resulted in the most resistant F_1's of all 20 hybrids (reciprocals included) for these components of resistance. The parental line NC 3033 was the best parent in diallel II for lesion area, defoliation and latent period, whereas 'PI 109839' and 'PI 270806' had the lowest GCA values for lesions/leaf and lesions/10 cm², respectively.

Genetic correlations determined as correlations among GCA effects were computed for the components of resistance to *C. arachidicola* (Table 4). In general, latent period and lesions/10 cm² were significantly correlated with all other components of resistance in

Table 4. Correlation coefficients among the general combining ability effects for the components of resistance to *Cercospora arachidicola* in two five-parent diallels

	Log lesions/ 10 cm²	Lesion area (mm²)	% Defoliation	Latent period (L_{50})
Log lesions/leaf-I[a]	0.50**	0.10	0	−0.30
II[b]	−0.10	0.50**	0.20	−0.80**
Log lesions/10 cm²-I		−0.70**	0.50**	0.60**
II		−0.30	0.90**	−0.40*
Lesions area (mm²)-I			−0.90**	−0.90**
II			0.10	−0.40*
Defoliation-I				0.70**
II				0.70**

[a] Diallel I correlation coefficients
[b] Diallel II correlation coefficients
*,** Denote significant correlation at the 0.05 and 0.01 probability levels, respectively

Table 5. Wr/Vr regression test of the additive-dominance genetic model for the components of resistance to *Cercospora arachidicola* in two five-parent diallels

	Diallel I			Diallel II		
	b Wr/Vr	SE b (±)	t[a]	b Wr/Vr	SE b (±)	t
Log lesions/leaf	0.36	0.11	3.3*	0.46	0.04	12.0**
Log lesions/10 cm²	0.51	0.14	3.5*	0.42	0.11	3.8**
Lesion area (mm²)	0.26	0.07	3.9**	0.49	0.02	22.5**
Defoliation	0.64	0.06	11.3**	0.43	0.08	5.3*
Latent period (T_{50})	0.43	0.02	17.9**	0.52	0.01	67.6**

[a] Comparison with tabular value for t with 8 degrees of freedom
*,** Denote significance at the 0.05 and 0.01 probability levels, respectively

both diallels. However, the sign (+ or −) on the correlation coefficients was not consistent for the correlation of latent period with lesions/10 cm² for diallels I and II. The correlation in diallel I was positive, indicating that genotypes with longer latent periods had higher numbers of lesions/10 cm². The association was the opposite in diallel II with genotypes with longer latent periods having fewer lesions/10 cm². Lesion area was highly negatively correlated with defoliation in diallel I indicating genotypes with larger lesion areas had higher defoliation.

Hayman's statistical tests using Wr and Vr were performed to investigate whether an additive-dominance genetic model was adequate to describe the genetic variation for the components of resistance. In general, (Wr+Vr) was consistent over arrays for most components of resistance except defoliation in both diallels, whereas (Wr−Vr) was very inconsistent over arrays for all components in diallels I and II. The slopes for the regression of Wr versus Vr were significant as indicated by the t-value and the slopes differed significantly from zero as well as unity for all components of resistance (Table 5). This indicates the inadequacy of the simple additive-dominance model, thus the components of variation and the average degree of dominance were not estimated.

2 Generation means analysis

Generation means for the parents (P_1, P_2), F_1, F_2 and backcrosses (BC_1, BC_2) (Table 6) for two crosses were used to test the additive-dominance genetic model. Results of Cavalli's (1952) joint scaling test indicate that the additive-dominance model is adequate in describing the variability for all components of resistance except latent period in both crosses (Table 7). The individual scaling tests (Table 7) are in agreement with the results of the joint scaling test except for lesion count, lesions/10 cm² and lesion area in diallel II. The individual scaling test B for lesions/leaf and lesions/10 cm² and the A scaling test for lesion area deviated significantly from zero, indicating some lack of fit of the additive-dominance model as tested by the expected relationships of the generation means. Estimates for the gene effects (m, [d], [h]) were obtained for all the components of resistance in both crosses except latent period for which the additive-dominance model was not adequate according to both the joint and individual scaling tests (Table 8). Estimates of the sum additive

Table 6. Observed means of parents (P_1, P_2), F_1, F_2 and backcrosses (BC_1, BC_2) for the components of resistance to *Cercospora arachidicola* in two crosses

	Les./leaf		Les./10 cm²		Les. area (mm²)		% Defoliation		Latent period (L_{50})	
	Cross 1[a]	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
P_1	24.5	57.4	27.2	54.5	9.4	13.4	45.0	0	22.5	27.7
P_2	38.6	39.5	42.6	42.8	8.4	17.7	85.0	21.0	23.4	24.6
F_1	34.0	42.5	37.2	47.1	8.6	14.8	88.9	25.0	22.7	27.4
F_2	30.8	44.3	35.8	45.7	8.6	14.2	89.8	26.0	22.8	25.7
BC_1	33.5	52.0	38.4	58.4	9.3	12.9	87.5	7.9	23.7	27.7
BC_2	32.2	53.0	38.8	57.9	8.6	16.8	69.2	25.0	23.3	26.1

[a] Cross 1 is 'Kanyoma' × 'PI 269685' and cross 2 is NC 3033 × 'PI 270806'

Table 7. Joint scaling test and individual tests (A, B, C) of the fit of the additive-dominance genetic model for the components of resistance to *Cercospora arachidicola* in two crosses

	Les./leaf		Les./10 cm²		Les. area (mm²)		% Defoliation		Latent period (L_{50})	
	Cross 1[a]	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
	Joint scaling test									
χ^2	1.46[b]	3.66	1.07	4.96	0.58	1.88	2.95	1.09	75.48*	85.73*
	Individual scaling tests									
A[c]	8.39 (±13.16)	4.03 (±16.35)	12.49 (±15.60)	15.25 (±19.01)	0.59 (±1.27)	−2.32* (±2.24)	0.41 (±0.44)	−0.09 (±0.18)	2.23* (±0.10)	0.33* (±0.10)
B	−8.19 (±13.04	24.03* (±14.58)	−2.26 (±15.93)	25.95* (±16.04)	0.21 (±1.34)	1.16 (±2.86)	−0.35 (±0.45)	0.04 (±0.28)	0.44* (±0.11)	0.26* (±0.11)
C	−8.09 (±22.52)	−4.52 (±23.59)	−0.98 (±27.43)	−8.58 (±24.46)	−0.75 (±2.31)	−3.61 (±4.37)	0.52 (±0.80)	0.34 (±0.48)	−0.33* (±0.19)	−4.17* (±0.18)

[a] Cross 1 is 'Kanyoma' × 'PI 269685' and cross 2 is NC 3033 × 'PI 270806'
[b] Calculated chi-square (χ^2) compared to tabular value with 3 degrees of freedom
[c] Where $A = 2\overline{BC_1} - \bar{P}_1 - \bar{F}_1 = 0$; $B = 2\overline{BC_2} - \bar{P}_2 - \bar{F}_1 = 0$; $C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_2 = 0$
* Denotes significant deviation from zero

Table 8. Estimates of the gene effects in two crosses evaluated for the components of resistance to *Cercospora arachidicola*

Estimates of the gene effects[a]	Lesions/leaf		Lesions/10 cm²		Lesion area (mm²)		% Defoliation	
	Cross 1[b]	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2	Cross 1	Cross 2
m	29.98 (±3.91)	48.42 (±4.48)	34.26 (±4.45)	49.23 (±4.53)	8.93 (±0.34)	15.18 (±0.80)	0.63 (±0.12)	0.08 (±0.12)
[d]	−3.78 (±3.41)	6.68 (±4.35)	−5.42 (±3.97)	4.32 (±4.49)	0.51 (±0.32)	−2.73 (±0.75)	−0.10 ±0.11)	−0.17 (±0.09)
[h]	3.27 (±8.09)	−2.56 (±8.85)	5.16 (±9.34)	1.03 (±8.89)	−0.30 (±0.69)	−0.92 (±1.43)	0.34 (±0.25)	0.20 (±0.23)

[a] where m = midparent value as influenced by the general conditions of the observations.
[d] = the sum over loci of the additive effects
[d] = the sum over loci of the dominance effects
[b] Cross 1 = 'Kanyoma' × 'PI 269685'; cross 2 = NC 3033 × 'PI 270806'

gene effects [d] were significantly different from zero for all components of resistance in both crosses except for defoliation in cross 1. Defoliation in cross 1 was the only component with a significant estimate of the sum dominance effects [h]. The estimates of [h] for all other components of resistance in both crosses included zero in the range of the estimate. The signs on the estimates of [d] were a function of which parent was assigned as parent 1 (P_1). For example, the estimate of [d] was negative in cross 1 for lesions/leaf where the more resistant parent was P_1 and [d] was positive for this same component in cross 2 where the more resistant parent was P_2.

Discussion

Based on significance tests in the combining ability analysis, additive genetic variance (GCA) was of greater importance than nonadditive genetic variance for the components of partial resistance to *C. arachidicola*. However, the proportions of the sum of squares attributable to SCA compared to GCA were large enough to suggest a substantial amount of genetic variability was unaccounted for by additive genetic variance. Significant reciprocal effects were found suggesting that cytoplasmic effects may be of importance in determining lesion number and lesion size. Examination of the means of reciprocal crosses revealed no consistent trends with the exception that Florigiant generally produced more susceptible progeny when used as a female rather than as a male. The results of this study are generally in agreement with the study by Anderson (1985), particularly with Anderson's report of significant reciprocal effects in the F_1 and F_2 generations. Kornegay et al. (1980) also reported significant GCA effects for lesion number and defoliation measured in the F_1 as well as significant SCA and reciprocal effects for defoliation. However, the SCA and reciprocal effects for defoliation were not observed in Kornegay's F_2 analysis.

The lack of correlation between the ranking of GCA effects and that of the parental means for the components of resistance also suggested that additive genetic variance alone did not account for all the genetic variability. The best parents for increasing resistance to *C. arachidicola* based on GCA effects included GP-NC 343 in diallel I for lesions/leaf, lesion area and latent period and NC 3033 in diallel II for lesion area, defoliation and latent period. Others (Anderson 1985; Hamid et al. 1981; Kornegay et al. 1980) have reported GP-NC 343 and NC 3033 to be good parents for reducing lesion number and defoliation, respectively, in the progeny. Anderson (1985) also reported that GP-NC 343 had good combining ability for reduced necrotic area as well. There were parents that produced progeny that performed better than expected based on mean parental performance. This could be explained if the favorable genes are dispersed among the parents, thus the hybrids would possess a greater number of favorable genes for increasing resistance than the parents. The increased resistance in the hybrid progeny could be a result of additivity over loci and/or complementary interaction (epistasis) between loci. Sokol and Baker (1977) conducted a simulation study to examine the influence of the dispersion of favorable loci between parents on the ratio of SCA/GCA sum of squares for the following genetic models: (1) additive, (2) additive plus dominance, (3) additive plus additive × additive and (4) additive plus dominance × dominance. Sokol and Baker (1977) reported an increase in the ratio of SCA/GCA sum of squares as the loci become more dispersed (negatively correlated) between parents in a diallel for all of the above models (models 2–4) except the additive model. The SCA/GCA ratio was large for all components of resistance in this study, possibly due to dispersion of favorable loci between parental lines that interacted in the hybrid progeny.

Most of the genetic correlations among the components of resistance were significant in both diallel I and diallel II. Yet some of the associations among the components of resistance were not the same in diallel I as in diallel II. For example, latent period was positively correlated with lesions/10 cm² ($r = 0.60$) in diallel I, whereas the correlation was negative in diallel II ($r = -0.40$). Also, lesion area was significantly correlated with lesions/10 cm² and defoliation in diallel I but not diallel II. This suggests the components of resistance are controlled by different genes rather than the same genes acting pleiotropically. Thus it should be possible to incorporate multiple components of resistance into a single line.

Hayman's approach to diallel analysis was also used to test the fit of the additive-dominance model. This approach is dependent on the fulfillment of several basic genetic assumptions, including (1) the lack of reciprocal differences among crosses and (2) that, dominance apart, the genes should be independent of each other in their contribution to the means, variances and covariances. Genes can show nonindependence in two ways. Firstly, genes may interact (epistasis) in producing their effects and, secondly, they may show nonrandom distribution among the parental lines, in particularly complete association and dispersion. Two broad tests were employed, the regression of Wr on Vr and the consistency of (Wr–Vr) over arrays. All slopes (b values) for the regression of Wr on Vr for the components of resistance deviated significantly from unity indicating a lack of fit of the additive-dominance model, thus a failure of the basic assumptions. The slopes were, however, significant (non-zero) indicating there was gene action other than accounted for by the simple additive-dominance model. Reciprocal effects were detected in the combining ability analysis for lesions/leaf and lesion area in diallel I and lesions/10 cm² in diallel II. The inconsistency of (Wr–Vr) over arrays also indicated nonindependence of nonallelic genes. There was no single parent that could be eliminated from the analysis for all components of resistance to restore homogeneity to the (Wr–Vr) arrays. More consistency over arrays for (Wr + Vr) was observed for most of the components of resistance except defoliation in both diallels. This indicates a lack of dominance which results in a significant slope for the Wr/Vr regression but one which deviates from unity. The lack of dominance would suggest that the large SCA sum of squares observed in the combining ability analyses can be accounted for by an additive-plus-epistasis genetic model where the genes are dispersed among the parents as demonstrated by Sokol and Baker (1977).

The results of the generation means analysis for the two crosses indicated the additive-dominance model accounted for the major portion of variation among generations for the components of resistance except

latent period. Estimates of the additive component [d] were significantly different from zero, whereas the estimates of the dominance component [h] included zero for all components of resistance for which gene effects were estimated except defoliation in cross 1. This indicates a lack of dominance at individual loci or a lack of directional dominance across loci. This is further substantiated by the fact that the F_1 means are approximately equal to the midparent values for all components of resistance except defoliation and latent period. The lack of fit of the additive-dominance model for latent period again indicates non-independence of genes due to interaction across loci and/or dispersion of alleles between the parents. The significance of the C scaling test indicates epistasis is important in the inheritance of latent period. An additional generation such as the F_3 would allow testing of a model which included an interaction (epistasis) component.

In conclusion, the components of resistance to *C. arachidicola* are controlled by additive as well as nonadditive gene effects in some cses. Epistasis may account for the nonadditive genetic variance where the additive-dominance model was inadequate in describing the genetic variability. There was also evidence that reciprocal effects are important in determining the inheritance of lesion area and lesion number. It should be possible to incorporate several components of resistance into one line and to select for increased levels of resistance, particularly in crosses with NC 3033 and GP-NC 343.

Acknowledgement. This research is part of the senior author's PhD dissertation and was partially supported by the Peanut CRSP, USAID grant number DAN-4048-G-SS-2065-00. Recommendations do not represent an official position or policy of USAID.

References

Anderson WF (1985) Combining ability and heritability of resistance to early leafspot (*Cercospora arachidicola* Hori) and late leafspot [*Cercosporidium personatum* (Berk. and Curt.) Deighton]. MSc Thesis, Department of Crop Science, North Carolina State University, Raleigh

Cavalli LL (1952) An analysis of linkage in quantitative inheritance. In: Reeve ECR, Waddington CH (eds) Quantitative inheritance. HMSO, London, pp 35–144

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. Aust J Biol Sci 9:463–493

Gibbons RW (1980) The ICRISAT groundnut program. In: Proc Int Workshop on Groundnuts. ICRISAT, Patancheru, AP, India, pp 12–16

Hamid MA, Isleib TG, Wynne JC (1981) Combining ability analysis of Cercospora leafspot resistance and agronomic traits in *Arachis hypogaea* L. Oleagineux 36:605–610

Hayman BI (1954a) The analysis of variance of diallel tables. Biometrics 10:235–244

Hayman BI (1954b) The theory and analyses of diallel crosses. Genetics 39:789–809

Hayman BI (1961) Notes on diallel-cross theory. In: Hanson WE, Robinson HF (eds) Statistical genetics and plant breeding. Pub No 982, National Academy of Sciences, pp 571–578

Hoagland DR, Arnon DI (1950) The water culture method for growing plants without soil. Calif Agric Exp Stn Circ 347

Jackson CR, Bell DK (1969) Diseases of peanut groundnut cultivars in Malaysia. Oleagineux 31:69–72

Kornegay JL, Beute MK, Wynne JC (1980) Inheritance of resistance to *Cercospora arachidicola* and *Cercosporidium personatum* in six virginia-type peanut lines. Peanut Sci 7:4–9

Mather K (1949) Biometrical genetics. Methuen, London

Mather K, Jinks JL (1971) Biometrical genetics. Cornell University Press, Ithaca, New York

Mather K, Jinks JL (1977) An introduction to biometrical genetics. Cornell University Press, Ithaca, New York

Melouk HA, Banks DJ (1978) A method of screening peanut genotypes for resistance to Cercospora leafspot. Peanut Sci 5:112–114

Mercer PC (1976) Effect of defoliation on yield of two groundnut cultivars in Malawi. Oleagineux 31:69–72

Parlevliet JE (1979) Components of resistance that reduce the rate of epidemic development. Annu Rev Phytopathol 17: 203–222

Ricker MD (1985): Components of resistance of peanut to early leafspot (*Cercospora arachidicola* Hori). MSc Thesis,, Department of Plant Pathology, North Carolina State University Raleigh

Sokol MJ, Baker RJ (1977) Evaluation of the assumptions required for the genetic interpretation of diallel experiments in self-pollinated crops. Can J Plant Sci 57:1185–1191