Components of Rust Resistance in Peanut Genotypes

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ABSTRACT

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Components of resistance to peanut rust were evaluated in 144 genotypes with the detached-leaf technique. All components of disease resistance—infection frequency, incubation period, lesion diameter, percentage of leaf area damage, and sporulation index—were significantly correlated with each other and with mean field rust scores. Incubation period was negatively correlated with all other components, which were positively correlated with one another. Significant differences among genotypes were observed for each component. The greatest variability among genotypes was observed for incubation period and percentage of leaf area damage. Of 144, 17 genotypes had a low sporulation index (1.3–2.5) and long incubation period (17.1–21 days). Components of resistance were further examined in 20 selected genotypes (based on sporulation index and incubation period levels), including the rust-susceptible cultivar TMV 2. Different components of resistance were not found in all genotypes; complementation of components was evident in genotypes ICG 10890 and 10881. The interrelationships among the components are described, and the usefulness of the incubation period and sporulation index is discussed in relation to selection for rust resistance.

Additional keywords: *Puccinia arachidis*, slow rusting.

Peanut rust, caused by *Puccinia arachidis* Speg., is a serious problem worldwide, causing substantial losses in crop yield in many regions (3–5,15,17,18). Rust is recognized by the orange pustules (uredinia) that appear on the lower surfaces of the leaves and rupture to expose masses of reddish-brown urediniospores. Infected leaves become necrotic and dry up but tend to remain attached to the plant. The pathogen perpetuates, spreads, and produces severe disease outbreaks by means of its urediniospores. Large yield losses occur if the crop is also attacked by early and late leaf spot. Recent outbreaks of peanut rust in Asia and Africa have led to considerable efforts to manage this disease, mainly through host-plant resistance and chemical control.

Research on the identification of peanut (*Arachis hypogaea* L.) resistance to rust has received increasing attention over the past 15 years, and a number of rust-resistant genotypes have been reported (2,12,15,16). Components of resistance have been studied for a limited number of genotypes (6,14). Subrahmanyam et al (14) reported significant differences in infection frequency, incubation period, pustule diameter, and percentage of leaf area damage among 30 genotypes with different levels of rust resistance. They reported that the genotypes within groups of highly resistant, resistant, moderately resistant, and susceptible genotypes had similar values for components of rust resistance. They also reported high correlations among components. Liao et al (6) studied components of resistance in 23 genotypes, including 12 resistant, four moderately resistant, and seven susceptible genotypes, using whole-plant and detached-leaf inoculation techniques. They also reported similar results for these components as well

as for sporulation index within the two broad groups of resistant and susceptible genotypes, but these components were not complementary in all genotypes. This indicated that in some genotypes certain components complemented each other for resistance reactions, but others did not.

The resistance identified in different genotypes is partial, similar to the slow-rusting type described in cereals, which reduces the rate of disease development. Because components of genotype-rust interactions are not fully complementary, the utilization of resistance sources in a breeding program requires detailed investigations into components of resistance in various rust-resistant genotypes. The objectives of the present study were to evaluate 143 rust-resistant genotypes for components of rust resistance and to examine possible interrelationships among the components.

MATERIALS AND METHODS

Genotypes. Components of rust resistance were studied in 143 resistant genotypes and one susceptible cultivar, TMV 2 (16; V. K. Mehan, P. M. Reddy, P. Subrahmanyam, D. McDonald, and A. K. Singh, *unpublished data*). The reactions of these 143 rust-resistant genotypes have been rated from 2 to 5 on a 9-point disease scale (1 = no disease, 3 = 6–10% foliage damaged, 5 = 21–30% foliage damaged, 7 = 41–60% foliage damaged, and 9 = 81–100% foliage damaged) (13) used in field screening trials. The detached-leaf technique (7) was used in this study.

Experimental material. Peanut genotypes were grown in 15-cm-diameter plastic pots containing a mixture of red sandy soil, river sand, and farmyard manure (2:1:1, v/v/v) in a glasshouse at 25–30 C. Four seeds were sown in each pot. Five pots were used for each genotype. Forty days after sowing, fully expanded healthy leaves (quadrafoliate), second from the top on the main stem, were collected. The detached leaves were arranged with petioles inserted in sterilized sand in plastic trays and covered with polyethylene covers. Leaves of each genotype were arranged in a randomized complete-block design in three replications, with two leaves in each replication. To acclimatize the leaves, these trays were kept in Percival incubators (Percival Co., Boone, Iowa) at 25 C with a 12-h photoperiod for 48 h.

Inoculum and inoculation. Inoculum of *P. arachidis* was produced on detached leaves of the susceptible cultivar TMV 2. Urediniospores taken from a single pustule on this cultivar were used to multiply the inoculum. This inoculum was obtained from rust-infected leaves of the cultivar TMV 2 grown at the ICRISAT Asia Center farm, Patancheru, India. The inoculated leaves, arranged in plastic trays (containing sterilized river sand), were incubated in a Percival incubator at 25 C with a 12-h photoperiod. The trays were covered with a thin polyethylene sheet. Urediniospores from sporulating lesions were collected in glass vials, using a cyclone spore collector, and stored at 4 C until further use.

A urediniospore suspension was made in sterile distilled water to which surfactant, Tween 80, was added (spore suspension at 0.1 ml/100 ml), and the spore concentration was adjusted to 10^5 spores per milliliter, as measured by a hemacytometer. Germination of urediniospores was greater than 90%. For the germination test, a few drops of urediniospore suspension were placed on sterilized glass slides that were placed in petri plates lined with moist filter paper. The plates were incubated in the dark at 25 C for 4 h. After incubation, the percentage of germination was estimated by counting the number of germinated urediniospores under a microscope.

The leaves were inoculated by spraying the urediniospore suspension on the adaxial and abaxial leaf surfaces, using a plastic atomizer, and the trays were placed in Percival incubators.

Measurement of components. The components examined include infection frequency, incubation period (time taken for the appearance of 50% of the total pustules from the time of inoculation), lesion diameter (excluding necrotic, yellow area), percentage of leaf area damaged, and sporulation index (on a 1–5 scale, where 1 = no sporulation evident; 2 = 1–25% lesion area covered with spores; 3 = 26–50% lesion area covered with spores; 4 = 51–75% lesion area covered with spores; and 5 = 76–100% lesion area covered with spores). Sporulation refers to the percentage of uredinium that contained spores. A rating of 5 indicates that the uredinium was fully open, and the entire uredinium was covered with urediniospores.

From 7 days after inoculation, the leaves were examined every day for pustules/urediniosori. When the number of urediniosori stopped increasing, the leaf areas were measured with a leaf area meter (Lukas Scientific Co., Lincoln, NE). Infection frequency (number of pustules per square centimeter of leaf area) was calculated by dividing the total urediniosori by leaf area. Lesion diameters were measured under a microscope 30 days after inoculation; 10 arbitrarily selected lesions were used for each leaf, and the mean lesion diameter was calculated. Leaf area damage and sporulation index also were assessed at 30 days after inoculation. Leaf area damage was estimated by comparing leaves with diagrams depicting leaves with known percentages (0.5, 1, 2, 5, 10, 20, 35, 50, 75, and 100%) of their areas affected. Ten arbitrarily selected lesions on each leaf were used to assess the sporulation index, which was based on a visual observation of sporulating lesions under a microscope (6).

Components of resistance were examined further in 20 selected genotypes. These included 15 with low sporulation index (1.3–2.5) and long incubation period (17.5–21 days); four (ICG 11080, 7897, 3527, and 7340) with medium-to-short incubation period (15.5–8.8 days) and high-to-low sporulation index (4.7–2.3); and the susceptible cultivar TMV 2 (short incubation period [9.8 days] and high sporulation index [4.7]). This experiment was repeated.

Statistical analyses. An analysis of variance (ANOVA) was carried out separately for each component of resistance on 144 genotypes. Correlations between different components of rust resistance and mean rust scores (in field screening trials over several seasons) of these genotypes were calculated. Differences

TABLE 1. Analysis of variance of components of rust resistance in 144 peanut genotypes

		Mean square				
	df	Infection frequency[a]	Incubation period (days)	Lesion diameter (mm)	Leaf area damaged (%)	Sporulation index[b]
Genotype	143	35.96**[c]	26.88**	0.0088**	340.25**	1.83**
Error	286	7.89	3.45	0.0025	41.93	0.48
Grand mean		5.5	15.1	0.30	9.5	3.3
SE		1.62	1.08	0.028	3.73	0.40
CV (%)		51.0	12.3	16.5	68.0	21.0
Range (genotypes)		0.8–15.0	8.8–21.0	0.17–0.42	1.2–47.5	1.3–5.0
TMV 2 (susceptible check)		12.3	9.8	0.54	71.7	4.7

[a]Number of lesions per square centimeter.
[b]On a 1 to 5 scale, where 1 = no sporulation and 5 = 76–100% sporulation.
[c]** indicates significance at $P < 0.01$.

among the 20 selected genotypes for each component of resistance were tested statistically from pooled ANOVA over two experiments. The genotypes for each component were ranked; the genotypes with low values for infection frequency, lesion diameter, leaf area damage, and sporulation index and high values for incubation period were given high ranks, whereas the genotypes with high values for infection frequency, lesion diameter, leaf area damage, and sporulation index and low values for incubation period were assigned low ranks. The mean ranking, based on all components, was computed for each genotype.

Considering incubation period and sporulation index as the most important components of resistance, the 144 genotypes were classified into three groups: long, medium, and short and high, medium, and low, respectively. This was done based on our experience from several experiments on these components of resistance in various genotypes with different degrees of rust resistance. For incubation period the ranges 9 to 13, 13.1 to 17, and 17.1 to 21 days were considered short, medium, and long, respectively. In the case of the sporulation index, the ranges 1.0 to 2.5, 2.6 to 4.0, and 4.1 to 5.0 were considered low, medium, and high.

RESULTS

Components of resistance. Significant differences ($P < 0.01$) among genotypes were observed for all components of resistance (Table 1). The magnitude of F values indicated large variations among genotypes for incubation period and leaf area damage.

Of 144 genotypes, only seven (ICG 1707, 4995, 7895, 10096, 10916, 11293, and 11567) had infection frequency values close to or higher than (11.9–15.0 pustules per square centimeter of leaf area) the susceptible cultivar TMV 2 (12.3 pustules per square centimeter of leaf area). Two (ICG 1707 and 4995) of these seven genotypes and four other genotypes (ICG 1703, 7296, 7340, and 10010) had incubation period values (8.8–9.7 days) not significantly different from that of TMV 2. Seventy-two genotypes had low leaf area damage (<5%). Two (ICG 10096 and 10916) showed substantial leaf area damage (44.2–47.5%) but significantly less than TMV 2. All genotypes had significantly smaller lesion diameters (0.17–0.42 mm) than did TMV 2 (0.54 mm). Sixty-eight (47.2%) genotypes had a lesion diameter greater than 0.30 mm, and four (ICG 7882, 10032, 10881, and 10890) had very low lesion diameters (0.17–0.20). Seventeen (11.8%) genotypes showed low sporulation index ratings (1.3–2.5), and 17 (11.8%) showed high sporulation index ratings (>4.5). Seventy-two (50%) genotypes showed <5 infection frequency. A few genotypes (ICG 10029 and 6340) had low infection frequency, leaf area damage, and lesion diameter but high sporulation index and short incubation period. Genotypes ICG 7296 and 10013 showed high infection frequency, moderate lesion diameter, leaf area damage, and incubation period but low sporulation index. Two genotypes (ICG 11088 and 11182) showed low infection frequency, lesion diameter, and leaf area damage values and high incubation period values but moderate sporulation index values (>3.5).

Full information on components of rust resistance for all 144 genotypes is not given in this paper. We would be pleased to provide such information on request. The seed of these genotypes can be obtained from ICRISAT.

Correlations among components. Significant correlations ($P < 0.01$) were found among the components of resistance (Fig. 1A–J). The highest correlation was observed between infection frequency and leaf area damage ($r = 0.705$; $P < 0.01$). All components were positively correlated among themselves, except incubation period, which had negative correlations of similar magnitude with all other components. Incubation period alone accounted for 44, 39, 37, and 37% of the variability in lesion diameter, leaf area damage, infection frequency, and sporulation index, whereas sporulation index accounted for 15, 19, and 34% of the variability in infection frequency, lesion diameter, and leaf area damage, respectively.

Correlations between rust scores in field trials and components. Mean rust scores in field screening trials were significantly and negatively correlated with incubation period and positively correlated with the other components (Fig. 2A–E). High correlations were observed with incubation period ($r = 0.685$; $P < 0.01$) and sporulation index ($r = 0.570$; $P < 0.01$).

Incubation period and sporulation index. The 144 genotypes were classified into three groups: long, medium, and short and high, medium, and low levels of incubation period and sporulation index, respectively, as shown in Table 2. Nearly 12% of the genotypes were found most desirable with low sporulation index (1.0–2.5) and long incubation period (17.1–21 days). Of the 90 genotypes in the medium sporulation index group, 30% showed a long incubation period. Of 144 genotypes, 19%, including TMV 2,

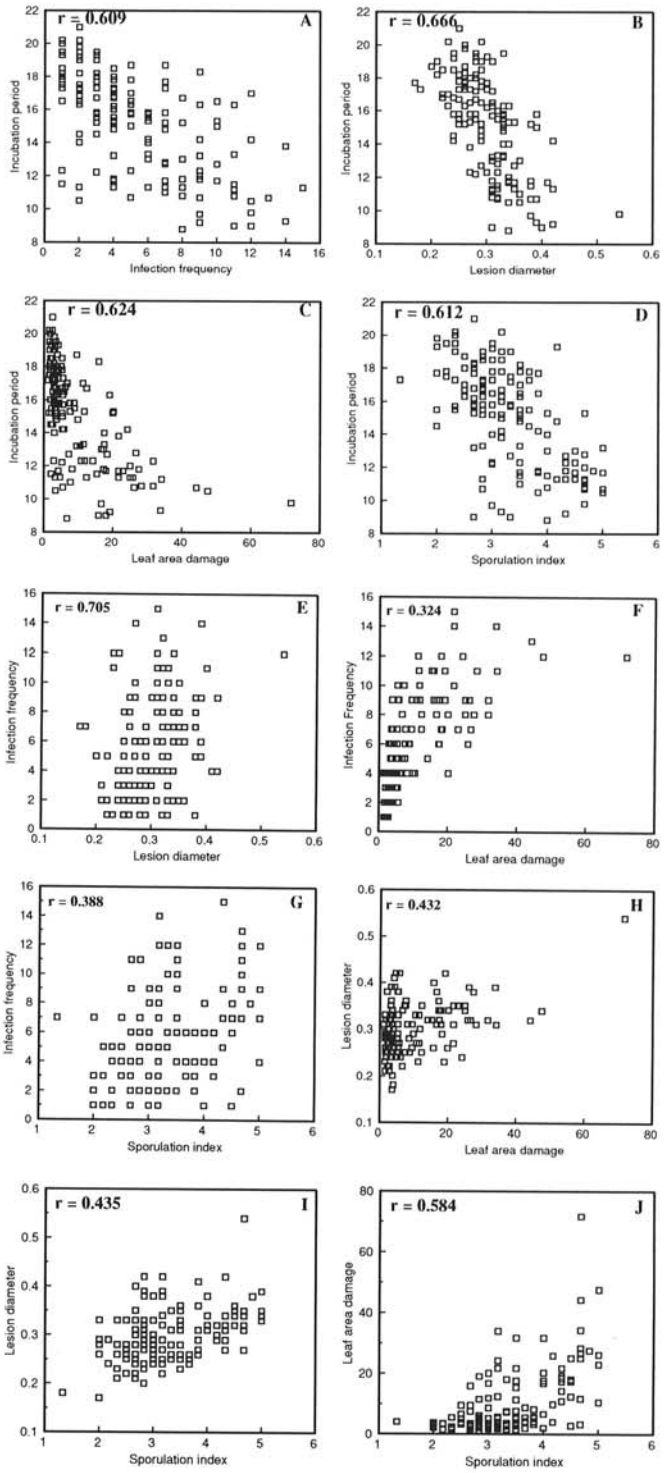

Fig. 1A–J. Scatter diagrams showing the relationships between the components of rust resistance in 144 genotypes (r = correlation coefficient; ** indicates significance at $P < 0.01$).

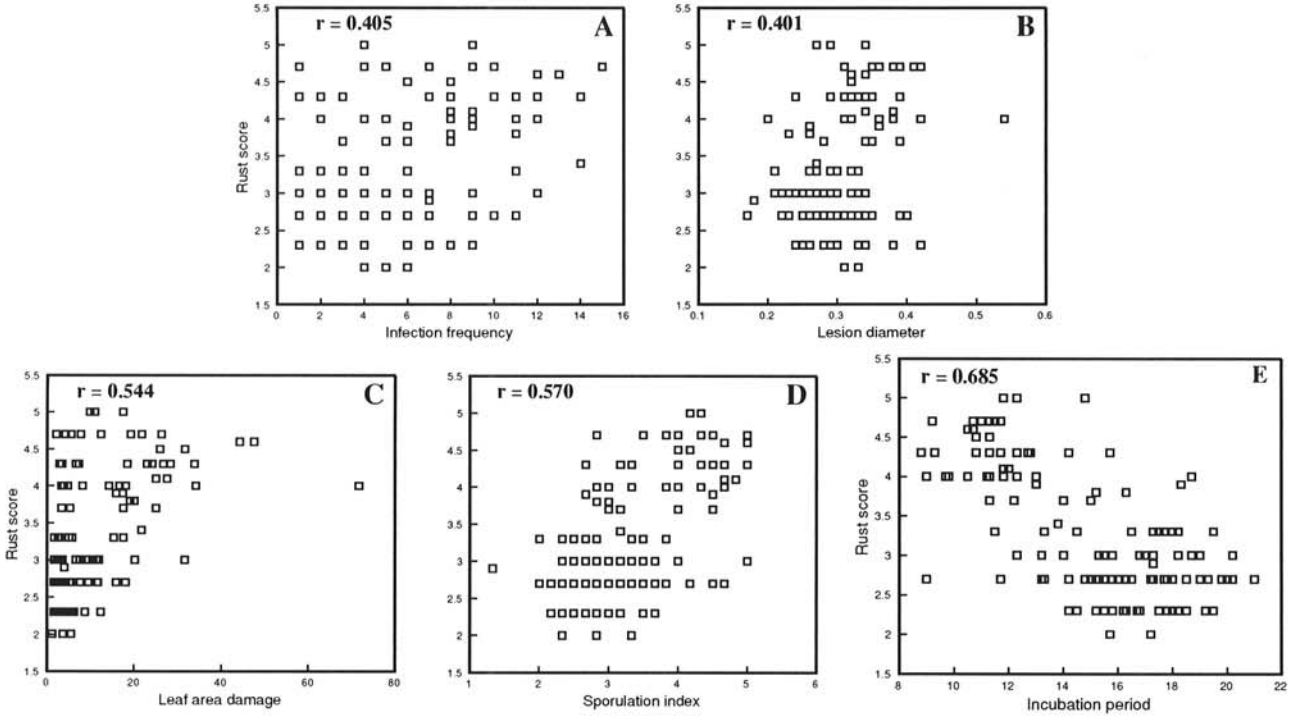

Fig. 2A–E. Scatter diagrams showing the relationships between rust scores in field trials and components of rust resistance in 144 genotypes (r = correlation coefficient; ** indicates significance at $P < 0.01$).

TABLE 2. Frequency distribution of incubation period and sporulation index of 144 peanut genotypes evaluated for components of rust resistance

Incubation period	Sporulation index			
	Low (1.0–2.5)	Medium (2.6–4.0)	High (4.1–5.0)	Total
Short (9–13 days)	0	16	27	43
Medium (13.1–17 days)	4	47	5	56
Long (17.1–21 days)	17	27	1	45
Total	21	90	33	144

had a high sporulation index and short incubation period. No genotype had both a low sporulation index and short incubation period. Only one genotype (ICG 11183) had a long incubation period (19.3 days) and high sporulation index (4.2).

Components of resistance in selected genotypes. Pooled analysis over two experiments revealed significant genotypic differences for all components in 20 selected genotypes. No significant differences were observed between experiments for all components, except infection frequency. Interactions between genotypes and experiments for all components except incubation period were nonsignificant. Hence, the mean values of different components for each genotype are presented in Table 3.

Pooled analysis on these genotypes, excluding the susceptible cultivar TMV 2 and the two other genotypes (ICG 3527 and 7340) that had low incubation period and high sporulation index values, also revealed similar results on genotype-experiment interactions for all components.

The differences between selected genotypes and the susceptible cultivar TMV 2 were highly significant for all components. The means of the ranks over the components for each genotype are presented in Table 3. Twelve of the 20 genotypes had average ranks below 10. The susceptible cultivar TMV 2 had the highest rank, 15. The genotype ICG 10890 was preferable with a mean rank of 1. This genotype was also significantly superior for incubation period over the rest of the selected genotypes.

For the 20 genotypes, results of all components, except incubation period, were mostly similar to those obtained in the earlier experiment (conducted with 144 genotypes) with the same genotypes. Slight variations between the experiments in the values of incubation periods were noted; however, trends in results were similar. All these selected resistant genotypes are Valencia (*fastigiata*) type (Table 4).

DISCUSSION

In studies of partial resistance to cereal rusts, Zadoks (19) reported that components of disease resistance reinforced one another. This would imply that all resistant cultivars would show small numbers of lesions, reduced lesion size, long incubation period, low leaf area damage, and sparse sporulation. In the present studies with a large number of genotypes, components of resistance were not fully complementary in many of the genotypes. This was evident in several of the selected genotypes. Some genotypes (e.g., ICG 11080) showed low infection frequency, lesion diameter, and leaf area damage values and high incubation period values, but high sporulation index values, whereas others showed high infection frequency, lesion diameter, and leaf area damage values, but low sporulation index. In only two genotypes (e.g., ICG 10890 and 10881), did rust resistance components tend to reinforce one another. These two genotypes showed much lower infection frequency, lesion diameter, leaf area damage, sporulation index values, and higher incubation period values than all other genotypes. It is emphasized that some genotypes may have partial resistance due to all components, whereas others have partial resistance due to some of the components. Thus, while there may be a correlation among components (reinforcement), certain lines contribute genes for different traits in crosses used to develop lines with better resistance. Disease development in such genotypes is likely to be slower, causing little damage to the foliage over the course of the disease epidemic during a cropping period. Such genotypes are useful in resistance-breeding programs. Several other genotypes, such as ICG 10032, 10052, 10567, 10928, 10933, 10014, and 10940, should also prove useful as resistance donors; they have long incubation periods (16.2–16.8 days), low-to-medium sporulation indexes (2.4–2.7) and low leaf area damage (5.7–6.8%).

TABLE 3. Components of rust resistance in 20 selected peanut genotypes

Genotype	Infection frequency	Incubation period	Lesion diameter	Leaf area damaged (%)	Sporulation index	Mean rank[a]
ICG 10890	2.6	18.7	0.18	2.0	2.0	1
ICG 10881	4.1	17.0	0.24	3.1	2.3	3
ICG 10014	3.5	16.2	0.23	4.0	2.7	4
ICG 10940	3.9	16.8	0.26	5.5	2.6	4
ICG 10031	4.3	16.0	0.28	4.2	2.7	6
ICG 10032	4.7	16.4	0.26	5.7	2.5	6
ICG 10052	4.3	16.4	0.28	6.2	2.7	6
ICG 10928	4.5	16.6	0.27	6.4	2.7	6
ICG 7882	5.1	15.6	0.25	5.7	2.7	7
ICG 10567	4.7	16.2	0.24	6.5	2.7	7
ICG 10933	5.0	16.3	0.25	6.8	2.4	7
ICG 11080	4.9	16.5	0.24	7.5	3.8	8
ICG 10022A	5.3	15.5	0.27	8.1	2.5	9
ICG 10067	6.0	16.0	0.28	7.7	2.7	10
ICG 10889	5.3	15.1	0.30	7.4	2.7	10
ICG 11108	5.5	15.7	0:28	9.5	2.9	10
ICG 7897	6.4	15.1	0.31	12.8	2.7	12
ICG 3527	5.4	11.6	0.41	19.6	4.4	13
ICG 7340	7.0	10.8	0.38	22.0	4.4	14
TMV 2	13.5	8.5	0.54	68.3	5.0	15
Mean	5.3	15.4	0.29	10.9	3.0	
SE for:						
Genotype	0.75	0.33	0.02	1.9	0.16	
LSD (5%)[b]	2.07	0.42	0.040	5.23	0.46	
	(1.72)	(0.94)	(0.034)	(3.99)	(0.47)	

[a]Mean rank was calculated by averaging the individual ranks for each component.
[b]Figures in parentheses are least significant difference (LSD) values calculated after excluding TMV 2, ICG 3527, and ICG 7340.

The results of five genotypes in the experiment with 144 genotypes (ICG 1707, 7882, 7897, 7898, and 7900) for infection frequency, incubation period, and leaf area damage were comparable with those obtained by Subrahmanyam et al (14). These researchers used 30 genotypes, 19 of which were used in the present studies. Considerable differences in infection frequency, incubation period, and leaf area damage were noted between these two studies for the other 14 genotypes. Two genotypes, ICG 1697 (NC Ac 17090) and 2716 (EC 76446 (292)), differed markedly for incubation period and infection frequency; both genotypes gave shorter incubation periods (14.2 and 11.5 days) in the present studies than in the previous studies (19.3 and 17.5 days). The possible causes of this variation are the pathogen population, variation in temperature and humidity, and different methods used for studying the components. Subrahmanyam et al (14) used whole plants to study the components in a glasshouse at temperatures ranging from 25 to 30 C, whereas the present study employed the detached-leaf inoculation method. Fluctuations in temperatures in the glasshouse can substantially influence components of resistance, particularly incubation period and leaf area damage. It is noteworthy that the susceptible cultivar TMV 2 showed much greater leaf area damage (>60%) in the present study compared to the 18.1% reported by Subrahmanyam et al (14); results for incubation period and infection frequency were similar in both studies. Liao et al (6) have reported high leaf area damage (82–83%) in this cultivar using both methods. However, their reported value of infection frequency for TMV 2 is much higher than the values observed in our study. Infection frequency is significantly correlated with leaf area damage, and high infection frequency (>20 cm^{-2}) is expected to lead to very high leaf area damage (>80%).

The significant relationships between rust scores recorded in field screening trials and components of resistance measured in the laboratory indicate that the latter can be successfully used in identifying rust-resistant genotypes. Similar observations have been reported by Subrahmanyam et al (14) and Liao et al (6). Whereas genotypes with low (2.0–3.0) and high (>8) rust scores tended to show uniformity in giving low values of lesion diameter, leaf area damage, and sporulation index and high values of incubation period and high values of lesion diameter, leaf area damage and sporulation index and low values of incubation period, respectively, there existed some overlap between groups of genotypes with moderate rust scores (3.1–5.0) with respect to these components. It is believed that long incubation period and low sporulation index slow down rust development and production of urediniospores in the field. In this context, incubation period and sporulation index are particularly useful and high correlations between rust scores and these two components high-

TABLE 4. Descriptions and field scores of selected peanut genotypes tested for components of rust resistance

Genotype		Botanical variety	Seed color	Rust score[a]
Number	Cultivar			
ICG 3527	USA 63	*fastigiata*	Purple	4.7
ICG 7340	WCG 182 198/66	*fastigiata*	Tan	4.3
ICG 7882	PI 314817	*fastigiata*	Tan	3.3
ICG 7897	PI 405132	*fastigiata*	Purple	2.7
ICG 10014	PI 476145	*fastigiata*	Tan	2.7
ICG 10022A	PI 476151	*fastigiata*	Dark purple	2.3
ICG 10031	PI 476168	*fastigiata*	Tan/purple	2.3
ICG 10032	PI 476168	*fastigiata*	Tan	3.0
ICG 10052	PI 476182	*fastigiata*	Tan	2.3
ICG 10067	PI 476191	*fastigiata*	Purple	2.7
ICG 10567	No. 2	*fastigiata*	Tan	3.3
ICG 10881	PI 475957	*fastigiata*	Red	2.7
ICG 10889	PI 476016	*fastigiata*	Red/purple	3.3
ICG 10890	SPA 406 Red	*fastigiata*	Red	2.9
ICG 10928	PI 476160	*fastigiata*	Tan	2.7
ICG 10933	PI 476166	*fastigiata*	Tan	2.7
ICG 10940	PI 476173	*fastigiata*	Tan/purple	2.3
ICG 11108	PI 476195	*fastigiata*	Light purple	2.7
ICG 11080	PI 476169	*fastigiata*	Tan	2.7
ICG 221	TMV 2[b]	*vulgaris*	Tan	8.7

[a]Mean rust scores (on a 1–9 scale) over several seasons (16).
[b]Susceptible.

light their importance. Several studies on cereal rusts have highlighted the importance of sporulation in disease epidemics (9–11). Significant negative correlations of incubation period with all other components clearly delineate the role of incubation period in slowing down rust development. A longer incubation period appears to be associated to other components, particularly infection frequency, lesion diameter, and leaf area damage.

The fact that components of rust resistance are not fully complementary is highlighted by several genotypes (e.g., ICG 11080) whose long incubation period tend to show high sporulation index and vice versa. Therefore, it is emphasized that the utilization of sources of resistance in a breeding program requires a detailed understanding of the components of resistance. Liao et al (6) indicated very high heritability of incubation period and sporulation index. This implies that these components are determined largely by genotype, and these components can be relied on in selecting for resistance. It is important to develop a breeding strategy in which different useful components of resistance are combined to enhance the existing levels of resistance in the cultivated groundnuts.

Variation in infection frequency was considerable in many of the genotypes studied in repeated experiments, although the inoculation method and inoculum concentrations were the same. Therefore, infection frequency does not appear to be a reliable component in selecting genotypes for resistance. Several researchers (1,8) have reported similar results in studies of components of resistance to late and early leaf spot pathogens (*Phaeoisariopsis personata* and *Cercospora arachidicola*).

As several genotypes with consistent differences in components of resistance (e.g., incubation period, sporulation index, lesion diameter, and leaf area damage) have now been identified, it would be useful to investigate the genetics of the different components of rust resistance.

LITERATURE CITED

1. Chiteka, Z. A., Gorbet, Z. A., Shokes, F. M., Kucharek, T. A., and Knauft, D. A. 1988. Components of resistance to late leaf spot in peanut. I. Levels of variability—Implications for selection. Peanut Sci. 15:25-30.
2. Cook, M. 1972. Screening for resistance to peanut rust in the green house and field. Plant Dis. Rep. 56:382-386.
3. Felix, S., and Ricaud, C. 1977. Occurrence and fungicidal control of groundnut rust in Mauritius. Rev. Agric. Sucr. Ile. Maurice. 56:110-114.
4. Harrison, A. L. 1973. Control of peanut leaf rust alone or in combination with Cercospora leaf spot. Phytopathology 63:668-673.
5. Ghughe, S. S., Mayee, C. D., and Godbole, G. M. 1981. Assessment of losses in groundnut due to rust and tikka leaf spot. Indian Phytopathol. 34:179-182.
6. Liao, B. S., Waliyar, F., Subba Rao, P. V., and McDonald, D. 1990. Components of resistance to rust in some newly identified peanut genotypes. Oil Crops China 3:9-13.
7. Nevill, D. J. 1979. An investigation of the disease reaction to *Cercosporidium personatum* in *Arachis hypogaea*. Trop. Grain Legume Bull. 15:18-22.
8. Nevill, D. J. 1981. Components of resistance to *Cercospora arachidicola* and *Cercosporidium personatum* in groundnuts. Ann. App. Biol. 99:77-86.
9. Parlevliet, J. E. 1975. Partial resistance of barley to leaf rust, *Puccinia hordei*. 1. Effect of cultivar and development stage on latent period. Euphytica 24:21-27.
10. Parlevliet, J. E. 1979. Components of resistance that reduce the rate of epidemic development. Annu. Rev. Phytopathol. 17:203-222.
11. Parlevliet, J. E., and Van Ommeren, A. 1975. Partial resistance of barley leaf rust, *Puccinia hordei*. II. Relationship between field trials, microplot tests and latent period. Euphytica 24:293-303.
12. Porter, D. M., Smith, D. H., and Rodriguez-Kabana, R. 1982. Peanut diseases. Pages 326-340 in: Peanut Science and Technology. H. E. Pattee and C. T. Young, eds. American Peanut Research and Education Society, Inc., Yoakum, TX.
13. Subbarao, P. V., Subrahmanyam, P., and Reddy, P. M. 1990. A modified 9-point scale for assessment of rust and late leaf spot of groundnut. 2nd Int. Congr. French Phytopathol. Soc. French Phytopathological Society, Montpellier, France.
14. Subrahmanyam, P., McDonald, D., Gibbons, R. W., and Subba Rao, P. V. 1983. Components of resistance to *Puccinia arachidis* in peanuts. Phytopathology 73:253-256.
15. Subrahmanyam, P., Mehan, V. K., Nevill, D. J., and McDonald, D. 1980. Research on fungal diseases of groundnut at ICRISAT. Pages 193-198 in: Proc. Int. Workshop Groundnuts. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.
16. Subrahmanyam, P., Rao, V. R., McDonald, D., Moss, J. P., and Gibbons, R. W. 1989. Origins of resistance to rust and late leaf spot in peanut (*Arachis hypogaea* Fabaceae). Econ. Bot. 43:444-455.
17. Subrahmanyam, P., Reddy, L. J., Gibbons, R. W., and McDonald, D. 1985. Peanut rust: A major threat to peanut production in the semiarid tropics. Plant Dis. 69:813-819.
18. Subrahmanyam, P., Williams, J. H., McDonald D., and Gibbons, R. W. 1984. The influence of foliar diseases and their control by selective fungicides on a range of groundnut (*Arachis hypogaea* L.) genotypes. Ann. Appl. Biol. 104:467-476.
19. Zadoks, J. C. 1972. Modern concepts of disease resistance in cereals. Pages 89-98 in: The Way Ahead in Plant Breeding. Proc. 6th Eucarpia Congr. F. G. H. Lupton, G. Jenkins, and R. Johnson, eds. The European Association for Research in Plant Breeding, Cambridge.