Susceptibility of Peanut Leaves to *Cercosporidium personatum*

Marion Cook

Former graduate student, University of the West Indies, Jamaica. Present address: c/o EMRO, c/o WHO/OMS, 1211-Geneva-27, Switzerland.

Based on a thesis submitted by the author to the University of the West Indies in partial fulfillment of the requirements for the Ph.D. degree.
The author is indebted to the University of the West Indies for granting an award to read for this degree and thanks Peter Hunt, former lecturer in mycology and plant pathology, University of the West Indies, Jamaica, for constant guidance during this study.
Accepted for publication 25 November 1980.

ABSTRACT

Cook, M. 1981. Susceptibility of peanut leaves to *Cercosporidium personatum*. Phytopathology 71:787-791.

Germination of *Cercosporidium personatum* conidia did not differ on the leaves of 12 peanut cultivars that were investigated. Although abaxial leaf surfaces retained more conidia and subsequently had more penetration of stomata by germ tubes than did adaxial surfaces, the resulting leaf spot density did not differ. There were indications of a hydrotropic response in stomatal penetration. Variations in stomatal density and stomatal length were not related to resistance to infection. The leaves of peanut plant introductions PI 259747 and PI 341879, both highly resistant to *C. personatum*, showed a positive regression of leaf spot density on leaf age. A necrotic-type defense reaction appeared to be operative. The leaves of the 10 other cultivars, ranging from highly resistant to highly susceptible to *C. personatum*, displayed a differential susceptibility to infection related to leaf size; regardless of leaf or plant age, a positive regression of leaf spot density on leaflet area was demonstrated for each of these cultivars. Knowledge of the variation in leaf susceptibility both within and between cultivars enabled standardization in leaf sampling during preliminary screening for resistance to leaf spot caused by *C. personatum*.

Additional key words: *Arachis hypogaea*, *Cercospora arachidicola*, leaf wettability.

Early maturing sequentially branched peanut (*Arachis hypogaea* L.) cultivars are generally more susceptible to leafspot caused by *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton (syn. *Cercospora personata* (Berk. & Curt.) Ellis and Everhart) than are later-maturing alternatively branched cultivars that exhibit various degrees of resistance (9). However, the nature of this resistance has not been fully elucidated. Hemingway (14) suggested that sequentially branched early maturing cultivars are more susceptible to infection because they have a higher proportion of stomata of "penetrable size" on the adaxial leaf surface. Jenkins (17) reported that infection was accomplished through either leaf surface, but Hemingway (13) concluded that the great majority of infections originated from the adaxial surface. D'Cruz and Upadhyaya (8) and Gibbons and Bailey (10) reported that resistance in wild *Arachis* species appeared to be associated with small stomatal apertures. Hassan and Beute (12) found a wild *Arachis* species, a wild species' hybrid, and a Virginia-type peanut cultivar that had smaller mean stomatal apertures on the adaxial leaf surfaces and were less susceptible to *C. arachidicola* after exposure to weathering than when grown continuously in the greenhouse. However, although all other cultivars investigated were also less susceptible after exposure, they had larger mean stomatal aperatures on the adaxial leaf surfaces than plants of the same cultivars that were not exposed to weathering. Mazzani et al (19) observed that in the field cultivars

0031-949X/81/08078705/$3.00/0

with stomatal length 16 μm or longer were no more affected by *Cercospora* species than those in which it was 14–15 μm. Abdou et al (1) found that germ tube growth was directed toward stomata on highly susceptible Arachis varieties and to a much lesser extent on moderately susceptible varieties; they found no directional response on varieties immune to *C. personatum* and/or *C. arachidicola*. Abdou et al (1) also noted that in moderately susceptible varieties resistance after penetration was associated with cell wall swelling and thickening in advance of and around the infection site, and in highly resistant varieties with the deposition of pectic substances on cell walls and in intercellular spaces.

Mazzani et al (19) observed that leaf spot counts were higher on cultivars with large, light green leaves. The leaves of alternately branched cultivars tend to be smaller and to have more palisade tissue than those of sequentially branched cultivars. Hemingway (14) proposed that this greater amount of palisade tissue may account for the slower rate of leaf spot growth on leaves of alternately branched cultivars and for their darker green foliage. Smartt (25) found one sequentially branched cultivar with dark green foliage that was resistant to leaf spot, and one alternately branched cultivar with pale green foliage that was highly susceptible. The finding of Yenni (27) that healthy tissues of all cultivars tested had a higher magnesium content than diseased tissues, and of Bledsoe et al (3) that a low level of magnesium was either directly or indirectly responsible for increased susceptibility to leaf spot may support this proposal (magnesium being a constituent of the chlorophyll molecules). Higgins (16) concluded that differences in cultivar resistance to *Cercospora* species were attributable to differences in maturity or productivity rather than to physiological or morphological differences. *C. personatum* is the more prevalent and destructive of these two leaf spot pathogens in Jamaica.

This study of the susceptibility of peanut leaves to *C. personatum* was undertaken to investigate these conflicting reports.

MATERIALS AND METHODS

Of 36 cultivars that had been observed by the author in the field for resistance to natural infection by *C. personatum*, three that were highly resistant, PI 259747, PI 341879 (both Tarapoto, of early maturity and with erect growth habit) and NC 5 (medium/semierect); three that were moderately resistant, NC 4X (medium/erect), NC 13 (medium/semierect) and V 56R (late/runner); three that were slightly resistant, PI 314817 (early/erect), VB 67 (medium/semierect) and V 61 R (late/runner), and three that were highly susceptible, Starr, Jamaican Valencia, and Jamaican Spanish (all early/erect) were studied further.

Seeds of these cultivars were sown in 20-cm-diameter plastic pots in a greenhouse. Daily minimum and maximum temperatures were about 20 and 28 C, respectively. Four weeks after seedling emergence, from five plants of each cultivar, leaves that had just opened, 0 days old, and leaves that were 7, 14, and 21 days old on the main axes (at nodes 10, 8, 6, and 4 from the base, respectively) were harvested and inoculated. To ensure uniform inoculation the leaflets were detached. The four leaflets of each leaf were placed on damp filter paper in the same petri dish; two leaflets were arranged with their abaxial surfaces exposed and two with their adaxial surfaces exposed. Separate dishes were used for each leaf.

Conidia of *C. personatum* were collected in the morning from leaves of field-grown plants free of rust (caused by *Puccinia arachidis*) and leaf spot caused by *C. arachidicola*. The conidia were suspended in water in a knapsack sprayer in the evening and sprayed onto the exposed leaflet surfaces until a density of approximately 100 conidia per square centimeter was attained on microscope slides interspersed among the dishes. No surfactant was used. The dishes were covered and placed in strong indirect light in the greenhouse. Water was added as needed to keep the filter papers damp.

To study conidia retention and germination and subsequent leaf penetration, the leaflets from one plant of each cultivar were cleared and stained as described previously (4). Leaflets of the other plants were inspected daily for signs of leaf spot development. Susceptibility to infection was assessed after 21 days and the number of leaf spots per 10 cm^2 of leaf surface was recorded; this area is approximately the size of an average fully expanded leaflet. At this stage of development the leaf spots on all leaves were similar in size, about 3 mm in diameter. Leaflets from plants at 6 and 10 wk after emergence were inoculated and evaluated by the same procedures as for 4-wk-old plants. On each occasion, leaves from the main axes of another five plants for each cultivar were sampled.

From four 6-wk-old plants of each cultivar, leaves aged 7, 21, and 35 days (at nodes 12, 8, and 4 from the base, respectively) were used for stomatal density estimations. Leaves that had just opened were not studied because their leaflets were in a state of rapid expansion; leaflet expansion is usually accomplished within 7 days. For each leaf examined, the density of stomata on the abaxial surface was determined from half of the lamina of one of the distal leaflets and the density on the adaxial surface from the other half. Each half of the lamina was cut away from the midrib when required. The abaxial surface was studied first on two of each set of four replicate leaflets and the adaxial surface first on the other two. The surface being investigated was viewed directly under the microscope by using reflected light. For each half lamina, counts were made in 30 microscope fields of view (field diameter = 0.41 mm) and the mean stomatal density per square millimeter was determined. Stomatal lengths were measured with an ocular micrometer.

RESULTS

The retention of conidia was much lower on adaxial leaf surfaces than on abaxial surfaces, and older leaves of all cultivars retained fewer conidia than younger leaves at each sampling time. Percentage germination of conidia 8 hr after inoculation was always high (>90%) irrespective of leaf surface or leaf age on all cultivars. Germ tubes mostly grew from terminal cells of conidia and directional growth was observed from the first day after inoculation by germ tubes close to stomata. Four days after inoculation, a large proportion of the germ tubes on both surfaces of all leaves had successfully penetrated stomata, even on the highly resistant cultivars. Macroscopic symptoms of infection appeared on leaves of all cultivars within 4 days as minute necrotic spots. Most of these enlarged and sporulation was noted about 2 wk after inoculation. The results for the 6-wk assessment of conidia retention and subsequent leaf spot development are summarized for six of the cultivars in Table 1.

It was apparent from the leaf spot counts on abaxial and adaxial leaf surfaces that there were no real differences in susceptibility of the two surfaces. The standard deviations of mean leaf spot counts increased with the increasing means. Counts were transformed to square roots, which stabilized the variance. Analysis of variance of the transformed data for each cultivar confirmed that no significant differences in susceptibility existed between leaf surfaces. The leaf surface results were therefore pooled.

The leaves of the highly resistant Tarapoto accessions PI 259747 and PI 341879 increased slightly in susceptibility to infection with increasing age. The youngest and oldest leaves of the other cultivars were the least susceptible to infection at each sampling time. This pattern of susceptibility reflected that for leaf size, the apical and basal leaves being the smallest on the plants. In Fig. 1 the transformed leaf spot data are plotted against leaf age for 4- and 6-wk-old plants of six of the cultivars. Also in Fig. 1, leaflet area is plotted against leaf nodal position for these cultivars. The results for the 10-wk assessment for each cultivar were comparable with the 6-wk assessment. The apical leaves and the expanded leaves that had opened after 6 wk were similar in size and susceptibility to the leaves at nodes 14 and 12, respectively, of the 6-wk sample. Leaves that had opened before 6 wk were similar in size and susceptibility to those at the same nodes in the 6-wk sample, except the leaf at node 14, which had now expanded and was as susceptible as the leaf at node 12.

For the Tarapoto accessions, the regressions of the transformed leaf spot density data on leaflet age for 4-, 6-, and 10-wk-old plants were shown by analysis of covariance not to differ significantly. Therefore, the 4-, 6-, and 10-wk assessments were combined for both

of these accessions; the correlation between leaf spot density and leaflet age was very high, r = > 95, $P = 0.001$, for each accession.

Among the other cultivars, the regressions of the transformed leaf spot density data on leaflet size for 4-, 6-, and 10-wk-old plants were shown by analysis of covariance not to differ significantly. Therefore, the 4-, 6-, and 10-wk assessments were combined for each of these cultivars; the correlation between leaf spot density and leaflet area was very high, r = > 90, $P = 0.001$, for each cultivar. The combined 4- and 6-wk assessments have been plotted for five of these cultivars in Fig. 2. Unexpectedly, the square root transformation rectified the data.

Microscopic examination of leaf sections showed the cells in the region of aborted infections in Tarapoto leaves to be brown and

TABLE 1. Retention of conidia and resulting leaf spot development on leaves[a] of 6-wk-old plants of six peanut cultivars differing in susceptibility to *Cercosporidium personatum*

Cultivar	Leaf nodal pos.[b]	Conidia/cm² leaf surface		Leaf spots/10 cm² of leaf surface	
		Abaxial	Adaxial	Abaxial	Adaxial
Starr	14	102	27	7.2	7.9
	12	63	19	13.4	11.7
	4	34	21	7.1	7.1
V 61R	14	75	24	6.3	5.2
	12	38	18	10.6	10.6
	4	19	15	5.8	5.7
NC 13	14	86	23	3.8	3.9
	12	47	14	7.5	7.3
	4	23	20	3.8	3.4
NC 4X	14	92	25	1.1	2.3
	12	59	19	5.9	5.4
	4	28	20	0.8	1.1
NC 5	14	83	26	0.6	0.8
	12	46	21	1.0	2.1
	4	20	16	1.1	0.6
PI 259747	14	87	29	0.0	0.0
	12	51	22	0.0	0.2
	4	23	25	0.8	1.7

[a] Leaves from one plant of each cultivar used for conidial retention estimations, and leaves from four plants used for mean susceptibility determinations.
[b] Leaves numbered in sequence from base of main axis of the plant.

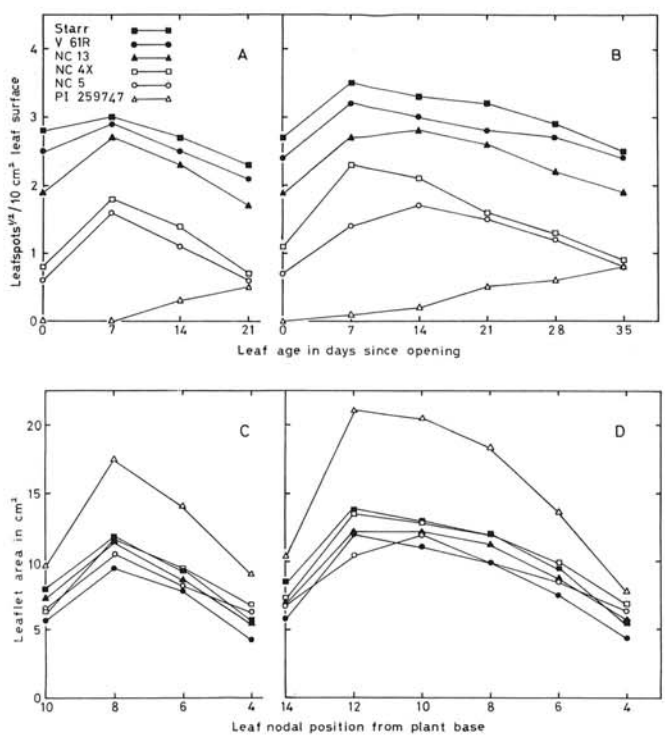

Fig. 1. Relationship of *Cercosporidium personatum* leaf spot density to leaf age for plants of six peanut cultivars aged **A,** 4 and **B,** 6 wk at inoculation of detached leaflets, and the relationship of leaflet size to nodal position from the base of the main axis for plants of the same cultivars at **C,** 4 and **D,** 6 wk.

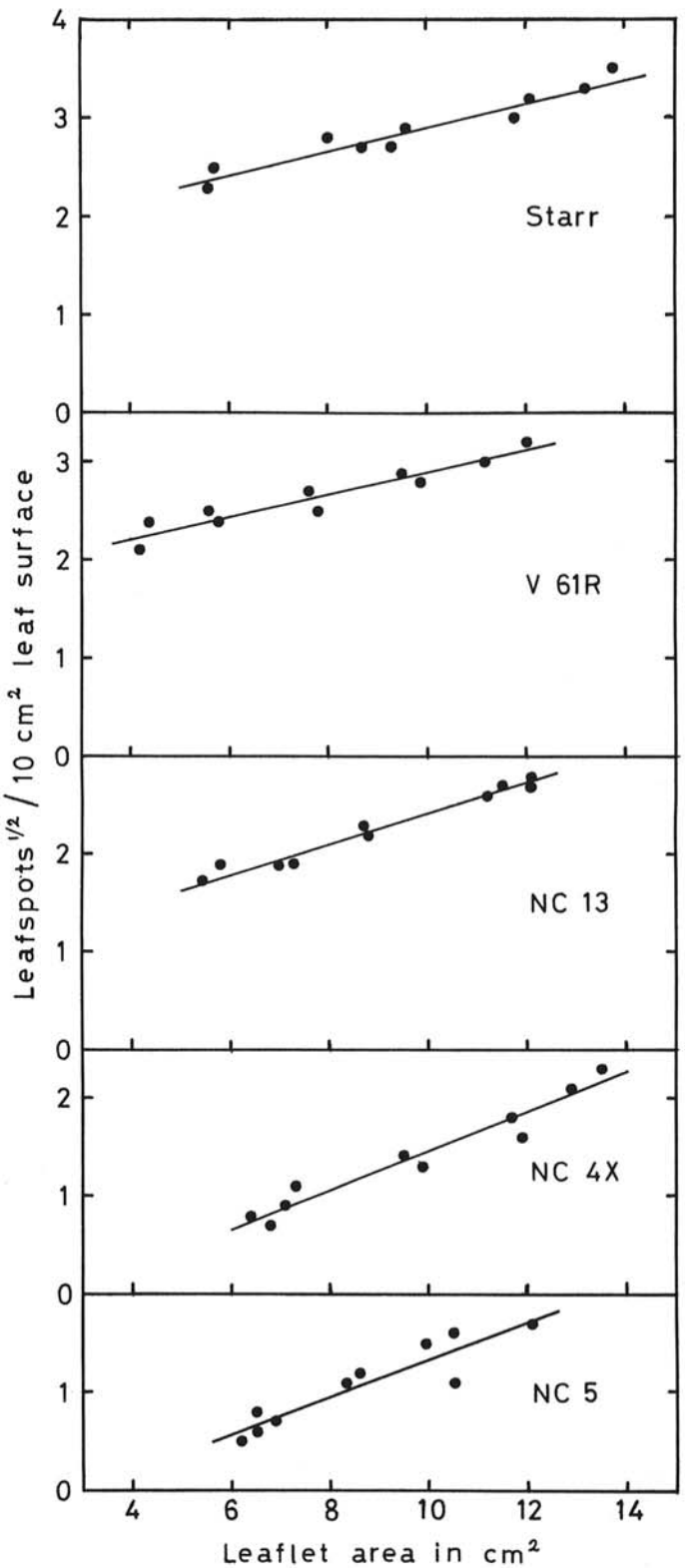

Fig. 2. Relationship of *Cercosporidium personatum* leaf spot density to leaflet area for five peanut cultivars; pooled transformed data for plants 4 and 6 wk old at inoculation.

shriveled. The cells in large leaves were larger and their walls appeared thinner than in small leaves but no differences between cultivars could be detected.

Variations in stomatal density among cultivars were small, as were variations between adaxial and abaxial leaf surfaces. However, there were significant differences ($P = 0.05$) among the leaves of any one cultivar; the higher a leaf was on the main axis, the lower was its stomatal density. Stomatal length measurements ranged between approximately 13 and 17 μm. Although there were no differences in mean stomatal aperture lengths between adaxial and abaxial leaf surfaces, there were slight differences among cultivars and leaves lower on the main axis tended to have stomata with shorter apertures. The stomatal density and length estimates are given for six of the cultivars in Table 2.

The cultivars retained the same relative susceptibility ratings as in the field at the 6- and 10-wk sampling times, but the results for the 4-wk samples were not consistent with those at 6 and 10 wk (Table 3). Only the leaves below the second node from the apex but above the 10th node from the base were included in the 6- and 10-wk assessments because they were comparable in size to those of the adult plant. The leaves of the 4-wk samples were smaller than those of the adult plant and only the leaf at the third node below the apex was assessed. The leaves at the first and second nodes below the apex were omitted because they were expanding.

DISCUSSION

The differential retention of conidia by the leaves was due to a differential rate of runoff of spray droplets. The adaxial surfaces of peanut leaves are always highly water repellent, but the abaxial surfaces of younger leaves are more wettable than those of older ones (5). That the leaf surfaces did not differ in susceptibility was unexpected. It is apparent that some factor had a greater influence on leaf spot development than inoculum density. The inoculum deposition was comparable to that by a suspension of 15,000 conidia per milliliter. This deposits about 60 conidia per square centimeter on the abaxial surface of the most wettable leaves of Starr (retention by this surface being about 4 mg/cm^2), and gives a comparable deposit on both surfaces of all other leaves when a surfactant is used (5). The most susceptible leaves of Starr at 6 and 10 wk in this study retained about 60 conidia per square centimeter. Although further investigation showed that lower mean leaf spot counts were obtained with lower inoculum densities, which is in accordance with the findings of Hassan and Beute (12) for *C. arachidicola*, with higher densities there was little change in mean counts, even when both surfaces of the leaves were inoculated. The highest leaf spot counts attained on individual leaflets of Starr were ~38, density 27 per 10 cm^2, compared with the highest density in this screening on a leaflet of Starr of 24.7 per 10 cm^2 (leaf mean = 18.3, sample mean = 12.5). The regressions for the cultivars of leaf spot density on leaflet area all extrapolated to a common leaf spot density point of about 30 per 10 cm^2 (range 28–34). It would seem that mean densities are not obtainable above this value. Assuming maximum leaf spot diameter to be about 6 mm, the theoretical upper density limit for full-sized leaf spots is 35 per 10 cm^2.

That the youngest and oldest leaves of the cultivars, except the Tarapoto accessions, at each sampling time were the least susceptible to infection is in accordance with the observations of Shanta (24). However, for any one of these cultivars, this effect appears to be related to leaf size rather than age. Leaflets of expanded leaves increase in area with ascending position on the main axis of the plant until plants are about 6 wk old. Leaflets of leaves opening after this time are comparable with each other in size when fully expanded. Schneider and Sinclair (23) found diffusates on the apical and basal leaves of cowpea (*Vigna unguiculata*) cultivar Lalita that inhibited conidial germination of *Cercospora canescens*. However, Abdou et al (1) found no significant differences in germination of conidia of *C. personatum* on leaves of various peanut cultivars. In the present work, likewise, no differences in germination were observed on leaves of resistant and susceptible cultivars, nor on resistant and susceptible leaves of the same cultivar.

Hemingway's (13) evidence that most infections originated through the adaxial surface may indicate a hydrotropic response. Under certain atmospheric conditions, water on the water-repellent adaxial surfaces will dry or recede, whereas a film of water will remain on the abaxial surfaces. With *Cercospora beticola* (22), *Cercospora musae* (11), and *Cercospora medicaginis* (2) penetration of host tissue is low under continuous wetting regimes. Rathaiah (22) found with *C. beticola* that penetration of the host was enhanced by interruption of leaf wetting with a daily 6-hr dry interval. He proposed that this enhanced penetration under interrupted wetting was due to hydrotropism, which directed germ

TABLE 2. Stomatal densities, stomatal lengths, and leaflet areas of leaves[a] of six peanut cultivars differing in susceptibility to *Cercosporidium personatum*

Cultivar	Leaf nodal pos.[b]	Mean stomatal density[c]	Mean stomatal length[d]	Mean leaflet area[e]	Mean leaf spot count[f]
Starr	12	119	15.4	13.8	17.3
	8	146	15.4	12.1	12.7
	4	158	15.1	5.7	4.0
V 61R	12	116	15.3	12.0	12.7
	8	154	15.2	9.9	8.3
	4	164	15.0	4.4	2.5
NC 13	12	121	15.3	12.1	9.0
	8	153	15.4	11.2	7.7
	4	162	15.2	5.8	2.1
NC 4X	12	117	15.5	13.5	7.6
	8	154	15.4	11.9	3.9
	4	155	15.2	7.1	0.7
NC 5	12	116	15.3	10.5	1.6
	8	150	15.3	9.9	2.3
	4	168	15.2	6.5	0.5
PI 259747	12	115	15.6	21.1	0.2
	8	146	15.5	18.3	1.3
	4	151	15.5	8.7	1.1

[a] Leaves from four plants of each cultivar used for stomatal density and stomatal length estimations, and leaves from another four plants used for susceptibility determinations.
[b] Leaves numbered in sequence from base of main axis of plant.
[c] Mean density per square millimeter.
[d] Mean length in micrometers.
[e] Mean area in square centimeters.
[f] Mean leaf spot count per leaflet.

TABLE 3. Relative susceptibility of 12 peanut cultivars to infection by *Cercosporidium personatum* in the field and greenhouse

Cultivar	Leaflets infected in field[a] (percent at 12th week)	Mean leaf spot count in greenhouse[b] 21 days after inoculation at 4 wk	6 wk	10 wk
Jamaican Spanish	88	10.3	16.9	17.6
Starr	86	10.7	16.6	17.3
Jamaican Valencia	81	9.0	15.3	16.1
VB 67	75	9.2	14.9	15.7
V 61R	69	8.0	12.1	13.1
PI 314817	67	7.9	11.8	12.4
NC 13	54	8.6	9.3	9.5
V 56R	53	5.6	9.0	9.1
NC 4X	46	4.2	7.3	8.1
NC 5	38	2.8	2.7	3.7
PI 341879	25	0.0	0.2	1.9
PI 259747	22	0.0	0.4	1.7

[a] Susceptibility to natural infection assessed as percentage of leaflets bearing leaf spots 2 mm or greater in diameter.
[b] Mean count per leaflet for four replicate plants of each cultivar at each sampling time; the leaf at the third node below the apex of the main axis being sampled at 4 wk, and the leaves between the second node below the apex and the 10th node above the base at 6 and 10 wk.

tubes toward stomata. Abdou et al (1) did not note directional growth of germ tubes towards stomata until 8 days after inoculation; prior to this time the inoculated plants had been kept in conditions near 100% relative humidity. In the present study, germ tube growth towards stomata was observed from the first day after inoculation. That the relative humidity in the petri dishes was not always 100% was evidenced by the disappearance of condensation from the inner surface of the petri dish lids during a part of each day. Condensation remained in the lids of petri dishes enclosed in plastic bags. Directional growth of germ tubes was not observed on leaves in such dishes, and few leaf spots developed within 21 days.

Stomatal density and stomatal length had no effect on the susceptibility to infection of the cultivars investigated. Stomatal counts were highest on the least susceptible leaves and although stomatal apertures tended to be longer on the most susceptible leaves, variations among cultivars were slight and could not account for susceptibility differences.

The differential susceptibility to infection observed among leaves of each cultivar studied was due to factors that limited growth of the pathogen within the leaf; the number of successful stomatal penetrations of the host by the pathogen was always much greater than the resulting number of leaf spots. With the Tarapoto accessions the appearance of the cells in the region of aborted infections indicated the involvement of a necrotic type of defense reaction. Cell wall structure or cell size or both may have been involved in the susceptibility of the other cultivars. That the pathogen can experience difficulty in cell penetration was indicated by the frequent angular appearance of leaf spots due to limitation in their spread by leaf veins.

Detached leaves from field plants inoculated during further investigations were less susceptible to *C. personatum* than those from greenhouse plants. The leaflets tended to be smaller on plants in the field, and the interval between leaf opening was longer. However, consistent results in the relative susceptibility of cultivars were always obtained whether plants were grown in the field or greenhouse. Although Hassan and Beute (12) found plants exposed to weathering 2 wk before inoculation to be less susceptible to infection by *C. arachidicola* than those grown continuously in the greenhouse, they found that many of the peanut cultivars differed markedly in relative susceptibility in the field; eg, Starr was among the most resistant in the greenhouse but among the most susceptible in the field. This may have been due to the postinoculation treatment of the plants, which were covered with plastic bags and placed in a mist chamber for 8 days. The inconsistencies may help elucidate the mode of resistance to *C. arachidicola*. Host colonization by the pathogens differs; leaf cells are killed in advance of the hyphae of *C. arachidicola*, which then invade the dead cells, whereas the hyphae of *C. personatum* penetrate between the cells and send haustoria into the living cells (1,17). Resistance to the two pathogens is inherited independently (15,18). However, although cultivars can differ in susceptibility to the pathogens (6,7), many react similarly (1). Of nine cultivars the author investigated in the field in common with Hassan and Beute (12), all scored comparably in relative percentage of leaflets infected. Defoliation was not assessed as the use of detached leaflets in the greenhouse study precluded investigation of leaflet abscission. Melouk and Banks (20) used whole leaves in their screening technique; this is preferable when inoculation apparatus is available.

That *C. personatum* usually makes its appearance late in the season may be due to the low susceptibility of leaves of field-grown plants younger than 6 wk. Since each conidial cycle takes 10 days or more, depending on the race of the pathogen (21,26), and as the leaves at lower nodes are barely susceptible to infection, primary infection usually will not occur before the plants are about 6 wk old. Thus, secondary infection will be of little importance before 8 wk.

The need for standardization in leaf sampling during preliminary screening of cultivars for resistance to *C. personatum* is shown by this work. Plants should not be screened before 6 wk because they have no foliage comparable to that of the adult plant. With plants $\geq$6 wk of age, leaves below the second node from the apex, but above the 10th node from the base of the main axis may be sampled; likewise, the leaves just below the second node from the top of side branches may be sampled. The leaves at the first and second nodes below the apices give inconsistent results because they are still expanding. It is probably advisable to exclude these also when screening for resistance to *C. arachidicola*.

The time required for the plants to mature must be taken into consideration when screening for resistance; with late-maturing cultivars there is a longer time period in which secondary infection can occur.

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