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Mechanisms of Resistance to *Sclerotinia minor* in Selected Peanut Genotypes

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ABSTRACT

Sclerotinia minor (Jagger) Kohn is a serious and increasingly prevalent pathogen of peanut (*Arachis hypogaea* L.). Peanut stem tissues were reported to differ in their resistance to *S. minor*, but field performance is not always correlated with laboratory evaluations of resistance to Sclerotinia diseases in other crops. Differences in genotype performance in field and laboratory results may reflect differences in mechanisms of resistance. The objective of this study was to characterize mechanisms of resistance to *S minor* in selected peanut genotypes by using agar culture tests, wounded and nonwounded stem inoculations, and field trials. For the culture test, sap was expressed from five genotypes with different levels of field-resistance to *S. minor*. Each extract was incorporated into an agar medium, which was overlaid with a dialysis membrane. The fungus produced distinctive infection hyphae on the media. Genotype extracts differentially affected size of terminal and secondary hyphae and the number of hyphae per organized cluster. Nine genotypes were evaluated for resistance to *S. minor* in two stem inoculation tests. Inoculation sites were wounded in the first method, and were not wounded in the second method. Significant differences in lesion size were found with both methods, but more differences were found among genotypes in the nonwounded inoculation. Genotype performance in culture and stem inoculation tests was not correlated with performance in the field. These studies demonstrated that although some genotypes had resistance to stem colonization by *S. minor*, other mechanisms account for most of the resistance expressed in the field.

SCLEROTINIA MINOR is a serious and increasingly prevalent pathogen of peanut in the USA, especially in Virginia and North Carolina (Porter and Beute, 1974, Beute et al , 1975), Oklahoma (Wadsworth and Melouk, 1985), and Texas (Woodard and Simpson, 1993). Management of Sclerotinia blight of peanut is difficult. Growers must use combinations of cultural practices, fungicides, and partially resistant cultivars to reduce disease losses

Lumsden and Dow (1973) showed that two isolates of *Sclerotinia sclerotiorum* (Lib) de Bary produced specialized infection hyphae during pathogenesis of bean (*Phaseolus vulgaris* L) One of these isolates produced small sclerotia characteristic of *S. minor*, and Lumsden (1979) later referred to this isolate as *S. minor*. For both species, hyphae found at the margins of lesions were larger than normal, contained granular cytoplasm, and were oriented in parallel clusters, resulting in the formation of an organized infection front In contrast, hyphae on resistant scarlet runner bean (*P. coccineus* L.) were small and not organized into an infection front (Dow and Lumsden, 1975). This phenomenon was reproduced in vitro on cellophane-covered bean extract medium, whereas clusters produced on cellophane-covered cornmeal extract agar (*Zea mays* L. is not a host of *Sclerotinia* spp; Held and Haenseler, 1953) contained only a few, small hyphae (Lumsden, 1975) These results suggested that substances present in host tissue may be required for production of infection hyphae. Exogenous nutrients have been known to affect pathogenesis by *Sclerotinia* spp since de Bary first investigated nutrient influence on formation of appressoria and penetration of hosts (Lumsden, 1979)

Sclerotinia minor attacks all peanut tissues, but stem infections account for most disease losses. Stem inoculation has been used to evaluate resistance to *Sclerotinia* spp. in several crops, including sunflower (*Helianthus annuus* L , Sedun and Brown, 1989), alfalfa (*Medicago sativa* L.; Pratt and Rowe, 1994), bean (Hunter et al., 1981), and soybean [*Glycine max* (L.) Merr ; Chun et al., 1987] Although field performance is not always correlated with laboratory evaluations of resistance in other crops (e.g., Chun et al , 1987), peanut stem tissues were reported to differ in their resistance to *S. minor* (Melouk et al , 1992) and detached peanut stems were used effectively in evaluations of fungicides for efficacy against *S. minor* (Brenneman et al., 1988).

Performance of peanut genotypes in the field is governed by several factors. Avoidance of disease due to plant canopy characteristics may influence infection efficiency on several hosts (e.g., Schwartz et al., 1978), including peanut (Coffelt and Porter, 1982). In general, spanish-type peanut (*A. hypogaea* ssp. *fastigiata*) has more resistance to Sclerotinia blight than virginia types (*A. hypogaea* ssp. *hypogaea*; Porter et al., 1975). Whether field resistance in spanish types results from upright growth habit, from early maturity, or from greater resistance of plant tissues to the pathogen is unclear, but the resistance is heritable (Wildman et al., 1992) A spanish cultivar with partial resistance to Sclerotinia blight has been released (Smith et al., 1991).

Higher levels of Sclerotinia blight resistance are needed in cultivars of virginia-type peanut, and understanding the mechanisms that contribute to resistance could allow for more efficient screening methods. The objective of the current studies was to characterize and compare efficacy of different mechanisms of resistance to *S. minor* in selected peanut genotypes by using plant extracts in agar culture, wounded and nonwounded stem inoculations, and field trials.

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Abbreviations: PDA, potato dextrose agar, AUC, areas under the curve.

MATERIALS AND METHODS

The isolate of *S minor* was obtained from diseased peanut plants grown in Suffolk, VA, in 1986 and was cultured on potato dextrose agar (PDA, Difco Laboratories, Detroit, MI), except as indicated Tissue extracts from five peanut genotypes were evaluated for their effects on growth of *S minor* in culture The genotypes used differed in levels of field resistance to Sclerotinia blight and included Chico (Bailey and Hammons, 1975), a spanish genotype with high levels of field resistance to Sclerotinia blight The virginia genotypes included 'VA 81B' (Coffelt et al , 1982), a cultivar that expresses field-resistance to Sclerotinia blight in North Carolina and Virginia, 'NC 7' (Wynne et al , 1979), a high-yielding cultivar grown extensively in North Carolina and Virginia; NCVA 871414, a highly susceptible breeding line, and NC 3033 (Beute et al , 1976), a germplasm line that is used extensively in multiple-pathogen resistance breeding at North Carolina State Univ., Raleigh, NC, and has moderate levels of resistance to several soilborne pathogens

Plants were grown in the greenhouse under supplemental florescent lighting (12-h day length, range in light from 27 μmol m^{-2}s^{-1} at night to 750 μmol m^{-2}s^{-1} during midmorning) At 13 wk after germination, aboveground portions were removed and tissue extracts were collected Extracts were filtered, sterilized in a Millipore filter apparatus (0 2-μm filter, Gelman Sciences Inc , Ann Arbor, MI), and mixed 1 1 by volume with sterile, cooled molten 1% water agar These solutions were poured into 60 by 15 mm petri plates Sterile dialysis membrane tubing (mwco 12 000 to 14 000) was used to cover the surface of solidified agar media A 1-cm-diam plug of *S minor* was placed in each plate, and plates were incubated for 24 h at 20°C The number of hyphae per infection cluster were counted and lengths and diameters of infection hyphae and secondary hyphae were measured Plates from each genotype were arranged in a randomized complete-block design with four replications The experiment was conducted three times, and data were combined in analysis of variance following preliminary analysis Means were separated using Waller-Duncan *k*-ratio *t*-tests

Full, two-thirds, and one-third strength PDA was used to test the effects of nutrient concentration on development of fungal hyphae Cultures were transferred and incubated on plates prepared with dialysis tubing as previously described Infection hyphae and secondary hyphae were measured and data were regressed on medium concentration where appropriate

Lesion expansion was measured on wounded and nonwounded detached stems of nine peanut genotypes Five advanced breeding lines (NCVA 871609, NCVA 871612, NCVA 871613, NCVA 871414, and NCVA 871415), two virginia-type cultivars [NC 7 and 'Florigiant' (Carver, 1969)], and two field-resistant genotypes (Chico and VA 81B) were evaluated The breeding lines were selected from crosses of [Florigiant × 'Florunner' (Norden et al , 1969)] × Chico made in conjunction with a cooperative resistance breeding program at North Carolina State Univ and USDA-ARS, Suffolk, VA Inoculation experiments were performed separately for plants grown in the greenhouse and in the field at the Upper Coastal Plains Res. Stn , Rocky Mount, NC

In the evaluation of resistance on wounded stems, uniform lateral stems were removed from plants, and leaves and pegs were removed at their juncture with the stem (Brenneman et al , 1988) Stems were cut to 90 mm with an internode in the central portion One oat (*Avena sativa* L.) grain infested with *S. minor* was attached with an insect pin to the central portion of each stem, which wounded the stem Stems were placed in moist chambers and incubated under florescent lighting (40 to 60 μmol m^{-2}s^{-1}; mean 54 μmol m^{-2}s^{-1}) in growth chambers at 20°C for 7 d after inoculation

In a second resistance evaluation, detached stems were not wounded during inoculation (Melouk et al , 1992) Stem sections removed from field-grown plants were 20 cm long, sections removed from greenhouse-grown plants were 15 cm long The basal end of each stem was inserted 5 cm deep into washed sand in a 250-mL beaker and all petioles and pegs were removed 2 cm above their juncture with stems Detached stems were placed in a mist chamber for 48 h before they were inoculated An oat grain infested with *S minor* was placed between the stem and the remaining portion of a centrally located petiole, and the inoculation site was draped with a 2 by 5 cm piece of cheesecloth (Melouk et al , 1992) Beakers containing inoculated stems were placed in mist chambers in the greenhouse

Lesion lengths were measured at 24-h intervals, and areas under the curves (AUC) for lesion lengths, plotted with time, were estimated (Shaner and Finney, 1977) All stem inoculation experiments were conducted in randomized complete-block designs with 10 replications per genotype Each inoculation experiment was conducted twice for both field- and greenhouse-grown plants Data from the two experiments on field-grown stems were combined after preliminary analysis, subjected to analysis of variance, and means were separated by Waller-Duncan *k*-ratio tests with k = 100 where appropriate

Field studies were conducted at the Upper Coastal Plains Res. Stn , Rocky Mount, NC, during the 1990 and 1991 growing seasons Peanuts were planted in plots 8 5 m long and four rows wide, with a between-row spacing of 0.9 m and seed spacing of 25 4 cm The soil was a Norfolk loamy sand (fine-loamy, siliceous, thermic Typic Paleudult) infested with *S minor* Recommended agronomic practices were used with the following exceptions. copper sulfate (Kocide 404S) was applied at 4 7 L ha^{-1} on a 14-d schedule for the control of Cercospora leafspot [caused by *Cercospora arachidicola* S Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton] to eliminate the nontarget stimulatory affects of chlorothalonil (tetrachloroisophthalonitrile) on Sclerotinia blight (Porter, 1980, Hau and Beute, 1983) Also, intraplot traffic was eliminated, because vine injury may alter expression of resistance (Porter and Powell, 1978) Plots were weeded manually to avoid use of post-emergence herbicides or cultivation.

Numbers of infection loci per row were assessed by counting the number of 0 3-m sections of row having visual signs or symptoms of the disease at 145 d after planting Data were converted to proportions by dividing by the number of 0.3-m sections per row An arcsine transformation was used to stabilize variances of the proportion data before analysis of variance The Waller-Duncan procedure was used for comparison of means when appropriate

RESULTS

Sclerotinia minor produced distinct hyphal types on membranes placed on peanut extract agar. Extracts from different peanut genotypes differentially (P = 0.05) affected production and size of organized parallel hyphae (Table 1) The greatest number of hyphae per cluster but the smallest (length and diameter) terminal infection cells were produced on extracts from the field-resistant spanish germplasm Chico. Secondary cells were also small on extracts from Chico, although differences were

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Table 1. Hyphal characteristics of *Sclerotinia minor* cultured on water agar amended 1:1 with tissue extracts from five peanut genotypes and overlaid with dialysis membrane.

Genotype	Hyphae/cluster	Terminal cells		Secondary cells	
		Length	Diameter	Length	Diameter
		μm			
NCVA 871414	4.5 b†	214.4 a	12 6 a	75 4 a	10.7 a
VA 81B	3 6 c	205 9 a	11 7 b	62.1 b	10.7 a
NC 7	4.7 b	164.4 b	11.8 b	62 5 b	9 7 b
NC 3033	3.0 d	221.4 a	11 9 ab	57.3 b	9.4 b
Chico	5.9 a	130 1 c	10 7 c	54 7 b	9 6 b

† Data are means of three experiments. Means followed by the same letter are not different (P = 0 05) according to the Waller-Duncan k-ratio test with k = 100

not significant. The fewest hyphae per cluster were produced on extracts of the breeding line NC 3033, followed by extracts of the field-resistant cultivar VA 81B. Terminal cells also were large on extracts from these two lines Terminal hyphal cells were longest on extracts from NCVA 871414, NC 3033, and VA 81B and had greatest diameters on extracts from NCVA 871414 and NC 3033. Hyphal characteristics on extracts from NC 7 generally were intermediate

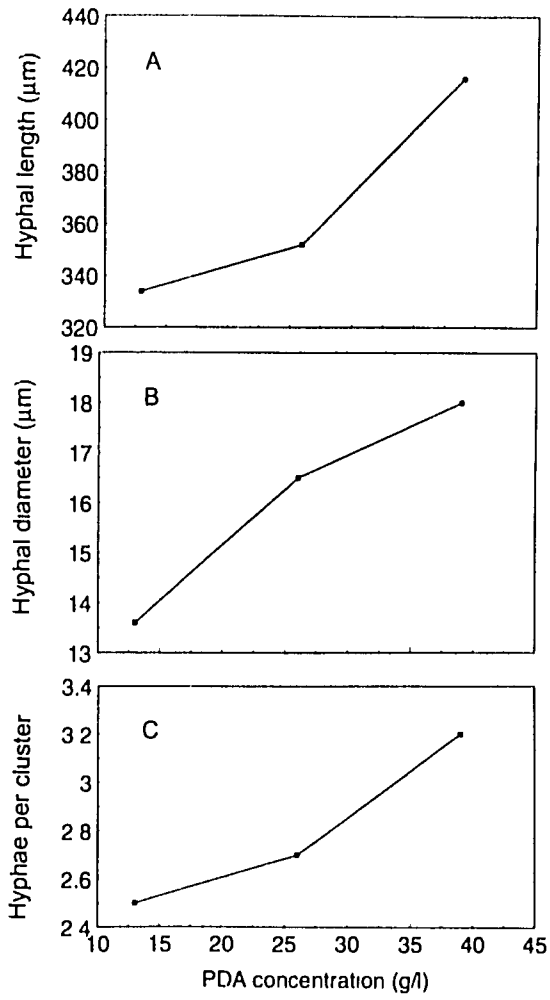

Fig. 1. Effects of concentration of potato dextrose agar (PDA; in grams dehydrated medium per liter deionized water) on (A) length, (B) diameter, and (C) number of clustered infection hyphae produced by *Sclerotinia minor* on a dialysis membrane overlaying the agar. The PDA concentration effects were significant (P = 0.05) for all variables.

Nutrient concentration in PDA media significantly affected the number of organized parallel hyphae per cluster, length of terminal infection hyphae, and diameter of terminal hyphae (Fig. 1). Cultures of *S. minor* grown on the full concentration medium produced the most parallel hyphae per cluster, longest terminal cells, and greatest hyphal diameter. The relationship between medium concentration and numbers of clustered hyphae was linear (P = 0 05), but significant deviation from linearity occurred in the response of hyphal length and diameter to nutrient concentration

Lesion development varied significantly on nonwounded stems detached from different genotypes of field-grown plants (Table 2). The AUC for lesion length was greater on stems of Chico than on the virginia-type cultivars NC 7 and VA 81B. The AUC for Florigiant was intermediate among the four cultivars tested. The breeding lines NCVA 871609 and NCVA 871613 had smaller AUC than Chico, NCVA 87612, and NCVA 871414. The AUC for lesion length on NCVA 871612 was greater than on the cultivars and was similar to the AUC for Chico

In the wounded-stem inoculation tests, AUC were larger and differences among genotypes were not as pronounced as in the nonwounded tests. The NCVA 871613 breeding line had significantly smaller lesions than Florigiant and Chico and the breeding lines NCVA 871609 and NCVA 871414 The AUC for VA 81B,

Table 2. Lesion development on detached stems of nine peanut genotypes inoculated with *Sclerotinia minor*.

Genotype	Areas under the curve†	
	Inoculation method	
	Nonwounded	Wounded
	mm-days	
NCVA 871609	39 d‡	117 a
NCVA 871612	136 a	108 ab
NCVA 871613	38 d	68 b
NCVA 871414	84 abc	115 a
NCVA 871415	78 bcd	97 ab
Florigiant	74 bcd	129 a
NC 7	48 cd	101 ab
VA 81B	55 cd	85 ab
Chico	111 ab	128 a

† Lesion length was measured daily for 7 d after inoculation and areas under the disease progress curves were calculated (Shaner and Finney, 1977).

‡ Data were means from two experiments and were transformed by square roots before analysis Back-transformed means are presented. Means followed by the same letter were not significantly different (P = 0.05) according to the Waller-Duncan k-ratio test with k = 100.

NCVA 871415, NCVA 871412, and NC 7 were intermediate (Table 2). No significant differences were found among stems detached from plants grown in the greenhouse in either assessment of resistance (data not shown).

Overall incidence of infection loci in the field varied between the two growing seasons. Averaged across all treatments, 42% of row increments (0.3 m long) contained diseased plants in 1990, compared with 69% in 1991. In 1990, disease incidence was greater on NC 7 than on Chico (Table 3). Disease incidence on the virginia-type cultivars Florigiant and VA 81B was intermediate to NC 7 and Chico. Among breeding lines in 1990, disease incidence on NCVA 871612 and NCVA 871415 was not significantly greater than on Chico, whereas NCVA 871609, NCVA 871613, and NCVA 871614 had greater incidence of Sclerotinia blight than Chico In 1991, Chico and VA 81B had the lowest disease incidence among the four cultivars Disease incidence on NC 7 and Florigiant exceeded 90% in 1991, and all breeding lines except NCVA 871414 had significantly lower levels of disease incidence than these genotypes The breeding lines NCVA 871609 and NCVA 871415 had levels of disease incidence that were not significantly greater than VA 81B (NCVA 871415 only) or Chico (both NCVA lines).

Rankings of genotypes by disease incidence in 1990 were not correlated with rankings for AUC in nonwounded ($r = -0.38$, $P = 0.31$) or wounded ($r = -0.29$, $P = 0.44$) inoculations of field-grown stems. Field rankings in 1991 also were not correlated with rankings for AUC in nonwounded ($r = -0.02$, $P = 0.97$) or wounded ($r = 0.33$, $P = 0.38$) inoculations of field-grown stems

DISCUSSION

Development of specialized hyphae on membrane-covered media containing peanut tissue extracts was similar to that previously reported for *Sclerotinia* spp on bean extract medium (Lumsden, 1975) Hyphal cells at the margin of the culture were arranged in clusters and were larger than the secondary cells (Table 1) Lumsden (1975) reported that differences in fungal development on susceptible (bean), resistant (scarlet runner bean), and nonhost (corn) plants could be reproduced on media containing extracts from these plants. Similarly, differences in responses of *S minor* to different peanut extracts could reflect differences in resistance to the pathogen in the source plants. Ranking of genotypes based on number of hyphae per cluster (VA 81B < NC 7 < Chico) corresponded most closely to rankings of each genotype on wounded stems, perhaps because wounding gives the pathogen access to the same substances present in expressed extract In nonwounded stems, physical barriers make these substances less available to the fungus

In previous experiments (Lumsden and Dow, 1973, Dow and Lumsden, 1975), both the numbers and sizes of hyphae per cluster were greatest on susceptible hosts The fungus produced the greatest number of clustered infection hyphae but the shortest and narrowest terminal cells on the same host medium (extracts from Chico) Quality or concentration of nutrients in tissue extracts probably differs less among genotypes of the same species than among different species or nonhosts These more subtle differences may account for the lack of correspondence between hyphal numbers and large cell size observed in these studies

Because potato (*Solanum tuberosum* L.) is a host of *S. minor*, commercially prepared PDA could be used to evaluate effects of nutrient concentration on production of infection structures. Changes in hyphal morphology and organization, in response to decreasing concentration of PDA (Fig 1), suggests that a portion of the differential effects of host extracts observed here and elsewhere (Lumsden, 1975) could be attributed to nutrient concentration.

Low to moderate levels of resistance to *S. minor* have been reported for Florigiant and VA 81B in field tests (Porter et al , 1975, Coffelt and Porter, 1982, Coffelt et al , 1982), but neither Florigiant nor VA 81B differed from NC 7 in evaluations of stem tissues for resistance in this study. Nonwounded stems of VA 81B and NC 7 were significantly more resistant to *S minor* than stems of Chico, however (Table 2) Field resistance in the spanish-type Chico probably is related to growth habit, early maturity, or both, rather than to resistance to colonization in stem tissues

Genotypes differed in resistance to stem colonization when stems were obtained from field-grown but not greenhouse-grown plants. Stems from greenhouse-grown plants may have differed from field-grown stems in cuticle structure, cell-wall composition, succulence, or similar stem properties that influenced susceptibility to *S minor* Only field-grown plants should be used in stem inoculation experiments.

Genotype differences in resistance to stem colonization did not play a large role in field performance of any entry evaluated. Chico and VA 81B did not differ in field performance even though they had different levels of resistance in intact stem inoculations. The NCVA 871613 breeding line exhibited the highest level of resistance overall in stem inoculations but had high levels of disease in the field in 1990. Differences in growth habit (Chappell, 1992) accounted for most of the differences in field resistance to Sclerotinia blight. Under the wet

Table 3. Incidence of Sclerotinia blight caused by *Sclerotinia minor* on peanut genotypes grown in field plots.

Genotype	Year 1990	Year 1991
	% row infected	
NC VA 871609	48 ab†	65 bcd
NC VA 871612	34 bc	73 bc
NC VA 871613	51 ab	71 bc
NC VA 871414	76 a	85 ab
NC VA 871415	38 abc	64 cde
Florigiant	31 bc	96 a
NC 7	47 ab	94 a
VA 81B	22 bc	42 c
Chico	16 c	48 de

† Data were transformed by square roots in 1990 and by arcsine-square roots in 1991. Back-transformed means are presented. Means followed by the same letter were not significantly different ($P = 0.05$) according to the Waller-Duncan k-ratio test with $k = 100$.

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conditions present in 1991, however, NCVA 871613 performed better than NC 7 or Florigiant. When conditions were very favorable for disease development in 1991, the effects of growth habit may have been less important and resistance in the stem tissues of NCVA 871613 may have been expressed in the field

Thinning and pruning experiments provided additional evidence for the influence of peanut canopy on disease development (Dow et al , 1988; Brune and Bailey, 1992) Canopy pruning, coupled with fungicide use, may play a larger role in disease management in the future (Brune and Bailey, 1992) If these practices are widely adapted, resistance to colonization in wounded stem tissue could become important

Although consistent differences in resistance to stem colonization were found in the genotypes evaluated, field results indicated that selection for open or upright canopy types should take precedence at this time in breeding for resistance to Sclerotinia blight in virginia-type peanut Growth habit and resistance to stem colonization may have both contributed to field resistance to Sclerotinia blight in VA 81B, however. Similar combinations of resistance mechanisms would be desirable in future cultivar development

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