

Effects of Rotations with Susceptible and Resistant Peanuts, Soybeans, and Corn on Inoculum Efficiency of *Cylindrocladium crotalariae* on Peanuts

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ABSTRACT

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Field microplots were infested with microsclerotia (ms) of *Cylindrocladium crotalariae* at about 35 ms/g soil. Susceptible Florigiant peanuts, resistant NC 3033 peanuts, soybeans (a host), and corn (a nonhost) were planted in all possible rotations in 1979 and 1980. Florigiant or NC 3033 were planted in microplots in 1981 after rotations established in 1979 and 1980. Postharvest inoculum densities in 1979 and 1980 for Florigiant and soybeans were similar and greater than for NC 3033 and corn. However, efficiency of ms to induce peanut root rot was high following NC 3033, intermediate following Florigiant, and low following soybeans. Variation in inoculum efficiency following different rotation crops was attributed to differences in ms genotype and phenotype, concentration of residual nitrogen in soil, and soil microflora.

Additional key words: *Arachis hypogaea*, *Glycine max*, *Zea mays*

Cylindrocladium black rot (CBR) of peanut (*Arachis hypogaea* L.) caused by *Cylindrocladium crotalariae* (Loos) Bell & Sobers occurs throughout peanut-growing areas in the southeastern United States (8,9). Losses are greatest in North Carolina and Virginia. Until 1982, rotation with nonhosts was the only management practice for fields infested with *C. crotalariae* (1,9). A peanut cultivar moderately resistant to *C. crotalariae* (NC 8C) was released in 1982 (16). In-furrow soil fumigation with metam-sodium is available to complement genetic resistance in heavily infested fields (1).

Agriculture is diverse in North

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Carolina and Virginia and rotations with peanut are flexible. Corn (*Zea mays* L.), tobacco (*Nicotiana tabacum* L.), and cotton (*Gossypium hirsutum* L.) are rotated with peanut, although corn is used predominantly. Peanut following soybean (*Glycine max* (L.) Merr.) has been discouraged because of *C. crotalariae* and other pathogens common on the two crops (1,8,9).

Inoculum density (ID) is one of several factors that affect CBR severity. Hadley et al (6) designated virulence of *C. crotalariae* effective for all cultivars as "general virulence" and virulence effective for an individual cultivar as "specific virulence." Certain *C. crotalariae* isolates had specific virulence on a resistant peanut line in greenhouse tests (3,6). In the field, a population from a single isolate became adapted on a resistant peanut line during monoculture but *C. crotalariae* populations composed of several isolates did not overcome resistance (3).

In addition to pathogen genotype, increased numbers of soil microflora were associated with decreased CBR on peanut (3). Soil microflora following different rotations varied in their effects on peanut plant growth (3). Supplemental nitrogen reduced CBR in field experiments.

Inoculum efficiency in this report refers to the various relationships

between inoculum density of the pathogen in soil and subsequent root rot severity. Inoculum efficiency reflects number of infections induced per microsclerotium. It can be used as a relative term (eg, high or low) or can be quantified with regression experiments (3).

CBR of peanuts was studied in field microplots to determine effects of rotations with susceptible and resistant peanuts, soybeans, and corn on the efficiency of microsclerotia (ms) of *C. crotalariae* to induce root rot on peanuts.

MATERIALS AND METHODS

Microplots 76 cm in diameter were established (2) in April 1979 in uninfested Norfolk loamy sand at the Central Crops Research Station in Clayton, NC. A composite of 12 isolates of *C. crotalariae* was chosen to infest the microplots (3). Six isolates had specific virulence for NC 3033 and six had specific virulence for Florigiant. Inoculum was increased in potato-dextrose agar (PDA) in darkness for 5 wk. The number of ms produced for each isolate was estimated by blending and sieving a random sample of plates (11). Inoculum was prepared by blending cultures at high speed in water for 1 min. On 2 or 3 June 1979, the ms-mycelium-PDA suspension, composed of equal portions of each isolate, was mixed into the upper 20 cm of soil in the microplot with shovels to obtain an approximate ID of 35 ms/g soil.

A randomized complete block was the experimental design, with treatments arranged in a $5 \times 4 \times 2$ factorial over 3 yr with four replicates. Factors in 1979 were CBR-susceptible Florigiant peanuts, resistant NC 3033 peanuts, Ransom soybeans, and Pioneer 3368A corn in infested soil and corn in uninfested soil for a control. Factors in 1980 (in all possible rotations with 1979 factors) were Florigiant, NC 3033, soybean, and corn. Factors in 1981 (in all possible rotations with 1979 and 1980 factors) were Florigiant and NC 3033.

Recommended management practices were followed (13), including recom-

mended fertilizer and lime,alachlor as herbicide, carbofuran as insecticide/nematicide, methomyl and carbaryl as insecticides, and chlorothalonil as leaf spot fungicide. Planting dates were 4 June 1979, 20 May 1980, and 15 May 1981. Seedlings were thinned to three per plot after emergence. Landplaster (1,120 kg CaSO₄/ha) was applied to the soil surface in July of each year in microplots planted to peanuts.

Root rot severity on peanut was estimated at harvest in October on a scale of 0–5, where 0 = no lesions and 5 = completely rotted roots (12). Ears of corn and pods of peanuts were harvested in October each year but soybean pods were left on the plants. In November, residues were cut into segments smaller than 15 cm and mixed into the top 20 cm of soil.

Soil samples were collected from each microplot with a vertical core-sampling tube (2 × 15 cm). In January 1980 and 1981, about 2.5 kg of soil was assayed from each plot. In May 1981 and January 1982, samples were about 0.5 kg. Postseason (January 1982) and pre-season (May 1981) IDs were estimated by elutriation and dilution plating (10). A logarithmic transformation of ID was used when necessary to stabilize variances and normalize data. A subsample January and May 1981 was analyzed for water-soluble nitrogen (mg nitrate/dm³).

In March 1982, 0.5-kg soil samples were taken from the four replicates of three treatments: plots planted with Florigiant or NC 3033 for three consecutive years (FFF and NNN) and plots planted with soybean for 1979 and 1980 followed by NC 3033 in 1981 (SSN). Five *C. rotalariae* isolates were collected

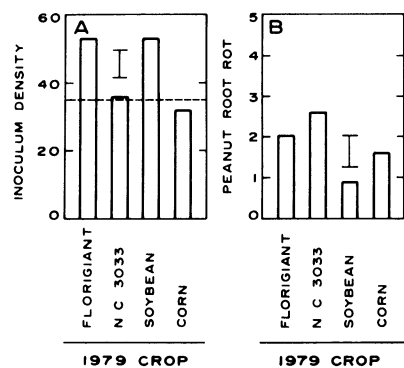


Fig. 1. Inoculum density (microsclerotia [ms] per gram of soil) in January 1980 and subsequent average of root rot over Florigiant and NC 3033 peanuts in October 1980 in microplots infested with *Cylindrocladium crotalariae*. CBR-susceptible Florigiant or resistant NC 3033 peanuts, soybeans, or corn had been grown in 1979. Root rot severity: 0 = no lesions and 5 = completely rotted roots. Bar represents Fisher's least significant difference (LSD) at $P = 0.05$. (A) Mean inoculum density in January 1980 for 1979 main effects. Dotted line at 35 ms/g represents approximate initial inoculum density in June 1979. (B) Mean root rot in October 1980 for 1979 main effects.

from each plot sampled. Cultures were transferred from isolation plates (10) and increased in PDA for 4 wk in darkness. Untreated field soil infested with 35 ms/g (11) was packed into plastic cylinders (i.d. 3.5 cm, length 15.5 cm) (3). Single 3-day-old seedlings of Florigiant or NC 3033 were transplanted in five cylinders for each isolate and subirrigated in the greenhouse at about 25 C for 5 wk.

Variance of root rot was estimated from each of the three rotation treatments for isolates (variance of general virulence) and isolate × cultivar interaction (variance of specific virulence) as described by Hadley et al (6). A ratio of variance of general virulence:variance of specific virulence was then calculated for FFF, NNN, and SSN treatments.

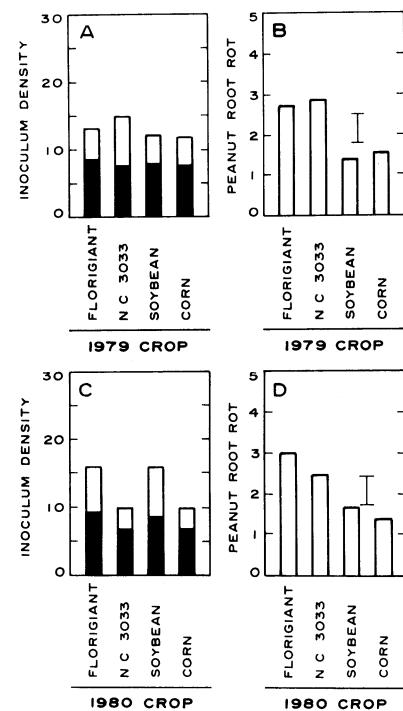


Fig. 2. Inoculum density (microsclerotia per gram of soil) estimated in January and June 1981 and subsequent average of root rot severity on Florigiant and NC 3033 peanuts in October 1981 in microplots infested with *Cylindrocladium crotalariae*. CBR-susceptible Florigiant or resistant NC 3033 peanuts, soybeans, or corn had been grown in all possible rotations in 1979 and 1980. Root rot severity: 0 = no lesions and 5 = completely rotted roots. Inoculum densities were transformed before analysis [$\log_{10}(\text{inoculum density} + 1)$] and the detransformed means presented are geometric means. Bar represents Fisher's least significant difference (LSD) at $P = 0.05$ and is for use with root rot severity. (A) Mean inoculum density in January 1981 (open column) and June 1981 (solid column) for 1979 main effects (not significantly different). (B) Mean root rot in October 1981 for 1979 main effects. (C) Mean inoculum density in January 1981 (open column) and June 1981 (solid column) for 1980 main effects. Least significant ratio at $P = 0.05$ was 1.26 for January data and 1.25 for June data. (D) Mean root rot in October 1981 for 1980 main effects.

RESULTS

Efficiency of *C. crotalariae* ms to induce peanut root rot (ie, ID relative to subsequent severity) in field microplots was high following resistant NC 3033, intermediate following susceptible Florigiant, and low following soybean. When inoculum efficiency was low on one peanut cultivar, it was also low on the other. Therefore, "peanut root rot" refers to severity averaged across both Florigiant and NC 3033. Root rot was not evaluated on soybean or corn.

Peanut root rot severity. Root rot was more severe on CBR-susceptible Florigiant than on resistant NC 3033 peanuts in 1979 and in 1980 and 1981, when peanuts were planted after identical prior rotations.

Average root rot on Florigiant and NC 3033 at harvest in 1980 varied according to which crop was grown in 1979. Root rot on peanuts following NC 3033 was more severe than following soybeans and corn (Fig. 1). Root rot was more severe on peanuts following Florigiant than on peanuts following soybeans.

Peanut root rot severity at harvest in 1981 was more severe if 1979 or 1980 crops were Florigiant and NC 3033 than soybeans and corn (Fig. 2).

Root rot severity on peanuts in 1981 differed among prior 2-yr rotations, ie, there was a significant 1979 × 1980 interaction. In general, peanut root rot in 1981 was greater if the 1980 crop was Florigiant than if it was soybeans or corn (Figs. 2 and 3). Root rot in 1981 was usually lowest following corn as the 1980 crop within all 1979 crops (except Florigiant), but the difference between corn and soybeans as 1980 crops was never significant within any 1979 crop. In fact, when the 1979 crop was Florigiant, root rot was significantly less following soybeans than following corn in 1980.

The 1979–1981 rotation with the least average peanut root rot in 1981 was corn-corn-peanuts; soybeans-corn-peanuts also had an average root rot severity of less than 1.0 (Fig. 3, Table 1).

The individual treatments resulting in the least peanut root rot in 1981 were soybeans-NC 3033-NC 3033, soybeans-soybeans-NC 3033, corn-corn-NC 3033, corn-corn-Florigiant, corn-soybeans-NC 3033, and soybeans-corn-NC 3033 (Table 1).

Inoculum density. A higher ID was found after 1979 crops of Florigiant and soybeans than after NC 3033 and corn (Fig. 1A). IDs after NC 3033 and corn were near and slightly less than initial levels, respectively.

Average IDs, in plots 3 mo after harvest of Florigiant, were always greater than after NC 3033. The proportionate differences became greater each year from 1980 through 1982 (Figs. 1A, 2C, and 4); however, this residual effect did not exceed 1 yr (Fig. 4A,B). The difference in ID 3 mo after the 1981

Table 1. Root rot severity on peanuts in October 1981 and inoculum density of *Cylindrocladium crotalariae* in January 1982 following a 3-yr rotation experiment in microplots with CBR-susceptible Florigiant peanuts, resistant NC 3033 peanuts, soybeans (a host), and corn (a nonhost)

Rotation ^a	Root rot ^b	Inoculum density ^c
FFF	4.8	31.2
FFN	4.0	9.4
FNF	3.1	7.5
FNN	2.0	3.1
FSF	1.3	14.5
FSN	1.5	11.0
FCF	3.9	12.5
FCN	1.4	6.6
NFF	4.1	30.2
NFN	3.3	17.6
NNF	4.7	37.7
NNN	2.1	9.6
NSF	4.0	55.5
NSN	1.3	4.1
NCF	2.4	7.1
NCN	1.2	3.5
SFF	2.9	19.6
SFN	1.4	10.5
SNF	2.8	18.3
SNN	0.0	5.6
SSF	2.6	29.6
SSN	0.1	2.6
SCF	0.8	4.9
SCN	0.6	3.7
CFF	2.4	7.5
CFN	1.4	7.5
CNF	4.1	15.2
CNN	1.0	2.2
CSF	2.3	25.7
CSN	0.5	5.8
CCF	0.4	3.9
CCN	0.3	2.3

Fisher's LSD_{0.05} 2.0 LSR_{0.05} 3.7^d
C.V. 67% C.V. 40%

^aFirst, second, and third letters of abbreviations refer to crops planted in 1979, 1980, and 1981, respectively, where F = susceptible Florigiant peanuts, N = resistant NC 3033 peanuts, S = soybeans (a host), and C = corn (a nonhost).

^bRoot rot severity in October 1981 on the peanut cultivar indicated by the last letter of the rotation abbreviation: 0 = no lesions and 5 = completely rotted roots.

^cMicrosclerotia per gram of soil estimated by elutriation and dilution plating in January 1982. Data was transformed before analysis [$\log_{10}(\text{inoculum density} + 1)$] and the detransformed means presented are geometric means.

^dLeast significant ratio ($P = 0.05$) to compare geometric means.

harvest of Florigiant compared with NC 3033 was greater when the 1980 crop was NC 3033 or soybeans than when it was Florigiant or corn (interaction $P < 0.07$) (Fig. 4D). IDs in January 1982 for all treatments are listed in Table 1.

Residual nitrogen. There was more than twice as much soil nitrogen (nitrate) 2 and 7 mo after incorporating debris in soybean plots than in Florigiant or NC 3033 plots (Fig. 5). Nitrate in plots 2 and 7 mo after incorporating soybean debris was 7.2 and 13.4 times the levels after corn, respectively. Nitrate in plots after Florigiant and NC 3033 was more than

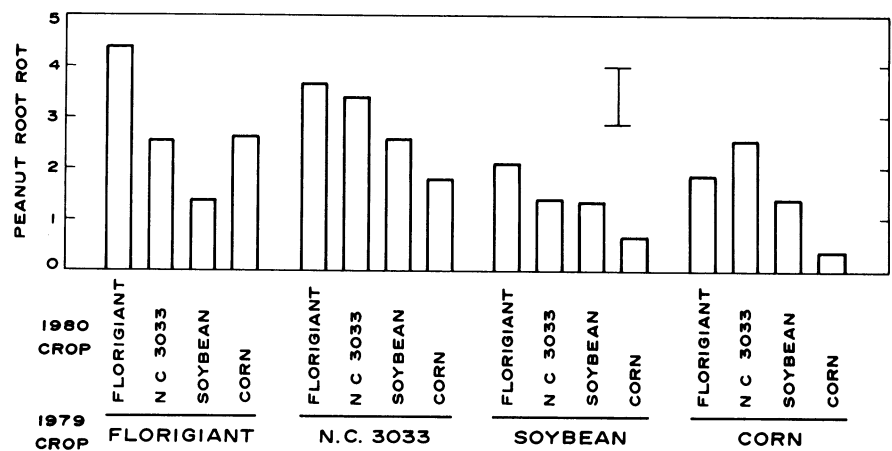


Fig. 3. Average of root rot over Florigiant and NC 3033 peanuts in October 1981 in microplots infested with *Cylindrocladium crotalariae*. In 1979 and 1980, all possible rotations of CBR-susceptible Florigiant and resistant NC 3033 peanuts and soybeans and corn were used. Root rot severity: 0 = no lesions and 5 = completely rotted roots. Bar represents Fisher's least significant difference (LSD) at $P = 0.05$ for 1979 × 1980 main effects interaction.

three times greater than after corn at both sampling dates.

Inoculum efficiency. Based on IDs in plots 4 mo before planting, peanut root rot severity was greater than expected 1 yr after growing NC 3033 (Figs. 1A,B and 2C,D). Peanut root rot severity was also greater than expected 2 yr after growing NC 3033 (Fig. 2A,B); however, peanut root rot severity after growing soybeans was less than expected, on the basis of IDs in plots 1 yr (Figs. 1A,B and 2C,D) and 2 yr (Fig. 2A,B) later.

Greater efficiency of ms to induce peanut root rot following NC 3033 also affected subsequent ID increase in susceptible crops when plots were assayed after 15 and 27 mo. IDs in plots 3 mo after every year's harvest were lower after growing resistant NC 3033 than susceptible Florigiant (Figs. 1A, 2C, and 4C), which agrees with Phipps and Beute (11). However, IDs in plots 15 mo after the 1979 or 1980 harvest of NC 3033 was similar to Florigiant (Figs. 2A and 4B) and 27 mo after the 1979 harvest; growing resistant NC 3033 actually resulted in higher IDs in plots than growing susceptible Florigiant (Fig. 4A).

The low efficiency of ms following soybeans affected subsequent postharvest ID. ID 3 mo after harvest of the 1979 crop of soybeans was greater than following NC 3033 (Figs. 1A and 2C). ID 15 mo after harvest was similar for soybeans and NC 3033 (Figs. 2A and 4B); however, IDs in plots 27 mo after harvest was less following soybeans than NC 3033 (Fig. 4A).

Virulence assay. Mean virulence in greenhouse tests over both peanut cultivars (seedlings of susceptible Florigiant and resistant NC 3033) for isolates recovered from soil after SSN and NNN was greater than FFF (Table 2). From separate analyses of root rot for isolates from different treatments, isolates after SSN had the greatest variance of general virulence (due to

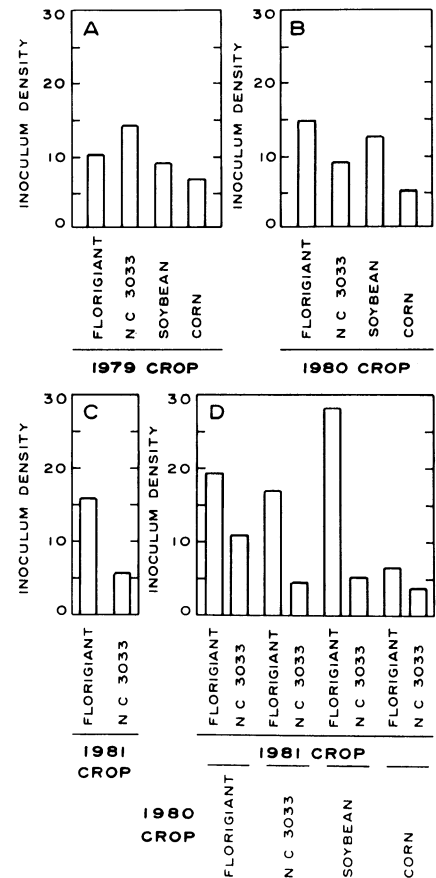


Fig. 4. Inoculum density of *Cylindrocladium crotalariae* (microsclerotia per gram of soil) estimated January 1982 where CBR-susceptible Florigiant and resistant NC 3033 peanuts, soybeans, and corn had been grown in various rotations in 1979, 1980, and 1981. Inoculum densities were transformed before analysis [$\log_{10}(\text{inoculum density} + 1)$] and the detransformed means presented are geometric means. (A) Mean inoculum density in January 1982 for 1979 main effects; least significant ratio (LSR_{0.05}) at $P = 0.05$ was 1.59. (B) Mean inoculum density in January 1982 for 1980 main effects; LSR_{0.05} was 1.59. (C) Mean inoculum density in January 1982 for 1981 main effects; LSR_{0.05} was 1.39. (D) Mean inoculum density in January 1982 for 1980 × 1981 main effects interaction ($P < 0.07$).

isolates) and the lowest variance of specific virulence (due to isolate \times cultivar interaction). Isolates after FFF had the lowest variance of general virulence and the greatest variance of specific virulence. The ratio of variance of general virulence to variance of specific virulence was 3.9:1, 18.8:1, and 36.6:1 for FFF, NNN, and SSN, respectively (Table 2).

DISCUSSION

Variation in efficiency of ms to induce peanut root rot following different rotation crops was apparently affected by ms genotype and phenotype, concentration of residual nitrogen in soil, and soil microflora.

Isolates of *C. crotalariae* were recovered from soil and increased in PDA to compare virulence (genotype) under uniform conditions (standardized

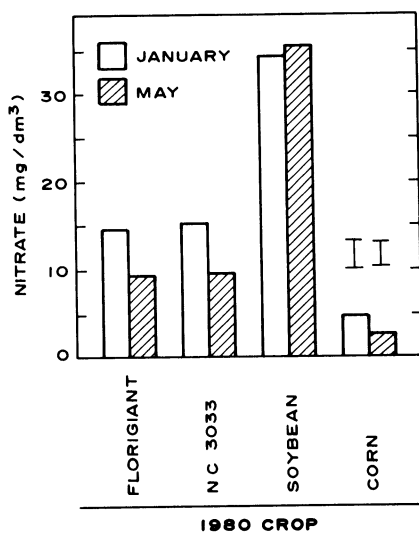


Fig. 5. Water-soluble nitrogen (nitrate) in soil samples collected in January and June 1981 where CBR-susceptible Florigiant and resistant NC 3033 peanuts, soybeans, and corn had been grown in 1980. Bars represent Fisher's least significant difference (LSD) at $P = 0.05$ for January and May samples, respectively.

Table 2. Mean virulence in greenhouse tests of 60 *Cylindrocladium crotalariae* isolates over two differential peanut cultivars (susceptible Florigiant and resistant NC 3033) and variances of general and specific virulence following 3 yr of growing Florigiant, 3 yr of growing NC 3033, or 2 yr of growing soybeans followed in year 3 with NC 3033

Rotation ^a	Mean root rot ^b	Variance		Variance ratio (G:S)
		General virulence ^c	Specific virulence ^c	
FFF	2.62	0.385	0.100	3.9:1
NNN	3.00	0.583	0.031	18.8:1
SSN	2.93	0.625	0.017	36.6:1

Fisher's $LSD_{0.05}$ 0.25
C.V. 21%

^a First, second, and third letters of abbreviations refer to crops planted in 1979, 1980, and 1981, respectively, where F = susceptible Florigiant peanuts, N = resistant NC 3033 peanuts, and S = soybeans. Five isolates were taken from each of four replicates of each treatment.

^b Root rot severity: 0 = no lesions and 5 = completely rotted roots. Mean is for 20 isolates per treatment over the two differential peanut cultivars, susceptible Florigiant and resistant NC 3033. Inoculum density for each combination was adjusted to 35 microsclerotia per gram of soil.

^c Variance of general virulence is that σ^2 due to isolates nested within field replicates; variance of specific virulence is that σ^2 due to cultivar \times [isolates nested within field replicates] interaction.

ID and ms size, same soil). General virulence (effective on both differentials) (6) was lower after FFF than after NNN and SSN (Table 2). Ranking of treatments NNN and FFF for effects on general virulence was consistent with observations of disease in microplots. However, the high general virulence of isolates after SSN contrasted with field observations where inoculum efficiency was low following soybeans.

Variance of specific virulence (more effective for one differential cultivar) (6) of isolates from ms in soil was 0.100 after FFF, 0.031 after NNN, and 0.017 after SSN. The interaction between root rot severity on the two peanut cultivars and field treatments was not significant; therefore, effects on general virulence were far more important than effects on specific virulence.

Size (phenotype) of ms may be a contributing factor to the phenomenon observed in this study of inoculum efficiency being high following NC 3033 and low following soybean. Under some conditions, ms of *C. crotalariae* following soybeans were smaller than ms following Florigiant (3). Following NC 3033, ID was generally low, and at low ID, ms size was increased (3). Small ms in greenhouse tests induced less severe root rot than large ms (3). Larger propagules would have more metabolic reserves to initiate lesions, to mitigate effects of plant-beneficial microflora, and to survive than would smaller ms.

Soil nitrogen concentration was more than twice as high after soybeans as after peanuts and was depleted after corn (Fig. 5), which is consistent with other work (14). Peanut root nodules are highly susceptible infection sites (7) and non-nodulating plants or plants with few nodules due to nitrogen fertilizer had reduced CBR severity and incidence (3). Peanuts planted after soybeans had roots with fewer nodules than after corn (M. C. Black, unpublished), and therefore, roots had fewer highly susceptible infection

sites. High soil nitrogen may also contribute to senescence of ms by accelerating microbial decomposition of cell walls (4). Nitrogenous soil amendments have suppressed many pathogens (4).

Wijetunga and Baker (15) induced suppressiveness with successive plantings of radish in soil infested with small but not with large propagules of *Rhizoctonia solani*. Suppressiveness of soil to *C. crotalariae* following soybeans may be due to the unique composition of the soil microflora and to the tendency of small propagules to be more sensitive to suppression (3).

Correlations reported previously between ID and severity of CBR (5) were improved when *Meloidogyne* and *Criconebella* nematode populations in soil were considered. Factors affecting inoculum efficiency in this study identify other sources of CBR variability.

Avoiding soybeans in rotations with peanuts is currently recommended for fields infested with *C. crotalariae* (1,8,9), and in this study, NC 3033-soybeans-Florigiant was not an acceptable rotation (Table 1). However, soybeans (a host) were used effectively in certain peanut rotations (soybeans-soybeans-NC 3033, soybeans-NC 3033-NC 3033, corn-soybeans-NC 3033, and soybeans-corn-NC 3033) (Table 1). NC 3033 peanut is not grown commercially because of low yield and small seed size.

Farmers with fields infested with *C. crotalariae* typically plant corn 1-3 yr and in some cases up to 7 yr after each peanut crop. Farmers who grow tobacco also plant that crop between peanut crops.

The lowest root rot severity on Florigiant in 1981 was for the rotation corn-corn-Florigiant (Table 1); this is in agreement with recommendations of planting corn before peanuts in infested fields. Acceptable rotations in infested fields using agronomically acceptable resistant peanuts might include corn-soybeans-corn-peanuts-corn or soybeans-corn-soybeans-peanuts-corn.

Some acreage planted with soybeans would allow growers more flexibility in managing labor and equipment at planting and harvest (soybeans are planted and harvested later than corn and peanuts) and would also reduce the need for supplemental nitrogen fertilizer for corn grown after soybeans. Rotations with soybeans should be evaluated further at other locations in soils infested with *C. crotalariae*.

Qualitative types of resistance to foliar pathogens may have prolonged usefulness if resistant and susceptible cultivars are planted alternately over years (17). This would not be suitable for managing *C. crotalariae* on peanuts, as seen in this study (NC 3033-Florigiant-NC 3033, NC 3033-NC 3033-Florigiant, Florigiant-NC 3033-Florigiant) (Table 1), because ms

remain in soil rather than being reintroduced every year.

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