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Effect of Within-field Variation in Soil Texture on *Heterodera glycines* and Soybean Yield[1]

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Abstract: The influence of soil texture on soybean yield in the presence of *Heterodera glycines* was investigated by comparing yields of susceptible cultivars with a resistant cultivar for 2 years. Soybean yield was negatively correlated with increasing sand content ($P = 0.05$). Yields of susceptible cultivars were suppressed with increasing sand content. Final nematode population densities were lowest in plots with greatest sand content. Soybean infection by SCN, as determined by the number of cysts 30 days after planting, was not consistently related to soil texture over 2 years. Initial nematode population density was positively related to soybean yield the first year and negatively related to soybean yield the second, probably a result of greater yield suppression by *H. glycines* in plots with greater sand content.

Key words: crop loss, *Heterodera glycines*, *Glycine max*, soil texture.

Soybean cyst nematode (SCN) *Heterodera glycines* Ichinohe is a major soybean pest in the United States (11,15,16). Soybean yield response to this pest may range from negligible to near crop failure (15). Genetic, edaphic, and environmental factors interact with initial nematode population density (Pi) in determining the extent of yield suppression. Soil texture is recognized as an important factor that affects both crop productivity and plant-parasitic nematode communities (8–10,17,18). Soil type influences the damage potential of several nematodes, including *H. glycines*, to soybean (14,17,19). Clay content affects the distribution of root-knot nematodes (8), and *Belonolaimus longicaudatus* Rau is restricted to soils with a sand content greater than 85% (12). The abundance of *Xiphinema americanum* Cobb was negatively correlated with clay content, whereas the abundance of *Helicotylenchus pseudorobustus* Steiner was positively correlated with clay content in midwestern U.S. soybean fields (9). Reproduction of *Heterodera schachtii* Schmidt on sugarbeet was greater in a silt loam than in a sandy loam, but the reverse was true for *Meloidogyne hapla* Chitwood (13).

Damage functions can be useful in predicting crop yield in the presence of plant-parasitic nematodes (2,7) but may need to be adjusted for soil texture. Researchers have determined damage threshold densities for SCN in the mid South (6) but have not incorporated soil texture into more refined damage models. Microplot experiments in North Carolina with different soil types showed a very low or zero tolerance limit to *H. glycines* in most cases (16). The slopes of the negative linear relationship between SCN eggs and soybean yield were not as steep in soils with high clay content compared to that observed in sandier soils (16). Soil texture largely determines soil moisture holding capacity and aeration (10,17,18) and is thus an important determinant of plant growth and yield, especially in areas subject to periodic drought. The effects of soil texture on plant growth also will be reflected in the structure and density of the plant-parasitic nematode community because of the obligate nature of the association (10,17).

Agriculturists generally recognize increased crop damage from plant-parasitic nematodes in sandier soils. Researchers observed higher *H. glycines* densities in sandier soils (5). There is, however, relatively little quantitative data on the effects of soil texture on *H. glycines* and its interaction with soybean yield. The purpose of this

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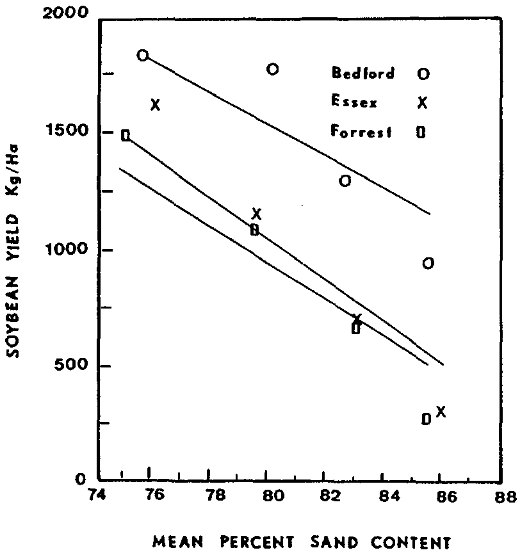

FIG. 1. Influence of sand content on yield of soybean cultivars Bedford, Forrest, and Essex in the presence of *Heterodera glycines*. Regressions are based on means of data for 2 years. Regression equations: Forrest Y = 7128 − 77.5X, R^2 = 0.62; P = 0.02; Essex Y = 7907 − 88.7X, R^2 = 0.64; P = 0.018; Bedford Y = 7093 − 69.0X, R^2 = 0.49, P = 0.0544.

research was to 1) evaluate the influence of soil texture on SCN and 2) quantify the effects of soil texture and SCN on soybean yield over a relatively narrow range of textures within individual fields.

MATERIALS AND METHODS

The experiments were conducted at the Rhodes farm of the University of Missouri, Delta Center near Clarkton, Missouri. The soil type was a Brosley fine sandy soil loamy, mixed thermic, arenic hapludalf. Sites selected exhibited a gradient in soil texture from one end to the other. The sand content decreased and silt content increased (Table 1). The sand content varied from 72 to 84% in 1984 and from 78 to 87% in 1985. Plots were arranged as a split plot with whole plots as texture levels and subplots as soybean cultivars with differential resistance to SCN. There were four replicates for each cultivar–soil texture block. The soybean cultivars Essex (susceptible), Forrest (resistant to SCN races 1 and 3), and Bedford (resistant to SCN races 3 and 4) were planted in four-row plots 6.1 m long with 0.96 m row spacing. Soybean yield, plant height, and preplant and postharvest samples for nematode analyses were taken from the two inside rows. Preplant nematode samples were taken the day of planting, and harvest soil samples were taken within a week of soybean harvest maturity. Soil samples were 15 2.5-cm-d soil cores taken to a depth of 15–20 cm and composited. The number of cysts in 1984 was determined from the average of two 100-g subsamples by elutriation (1). Cysts were extracted from a single 750-g sample by elutriation in 1985, and the eggs were counted after crushing cysts in a Ten-Broek tissue homogenizer. Ten plants were selected at random, five per row from the two outer rows of each plot, to determine the number of cysts per plant 30 days after planting in 1984 and 1985. Root weights were also determined at 30 days in 1985 but not in 1984. The sand, silt, and clay percentages in each plot were determined by the Bouyoucos method (4). Nematode data were transformed to $\log_{10}$ (X + 1) to standardize the variance for analyses. Untransformed data are presented in tables for clarity. The approximate amount of infection (number of cysts per plant 30 days after planting) was adjusted to the preplant cyst density in order to evaluate soil texture effects on soybean infection by SCN. The approximate adjusted infection rate (AIR_{30}) = ($\log_{10}$ cysts per plant at 30 days)/($\log_{10}$ preplant cyst + 1). Data were analyzed by analysis of variance (ANOVA), correlation, and regression analyses.

RESULTS AND DISCUSSION

Effects of cultivar and soil texture on seed yield: The number of cysts on Bedford was approximately 10% of the numbers recorded on either Essex or Forrest 30 days after planting (Table 1). Bedford yield was greater than either Forrest or Essex in all plots (Table 1). Soybean yield of susceptible cultivars approached those of resistant Bedford as sand content decreased (Fig. 1); the slopes, however, were not significantly different. The split-plot design established that sand was an important component of

TABLE 1. Sand content soybean yield and *Heterodera glycines* cyst and egg numbers/100 g naturally infested soil in 1984 and 1985.

Location	Cultivar	Soil texture (%)			Cysts/100 g soil		Eggs/100 g soil		Cysts/plant at 30 days	Seed yield (kg/ha)	Plant height (cm)
		Sand	Silt	Clay	Preplant	Harvest	Preplant	Harvest			
1984											
1	Bedford	84	12	4	64 aA	28 aB			11 cA	1,450 aAB	84 aC
1	Essex	84	12	4	58 aA	50 aB			198 aA	532 bb	42 cB
1	Forrest	84	12	4	55 aA	56 aB			99 bA	536 bC	54 bB
2	Bedford	80	16	4	39 aAB	78 aA			18 cA	1,654 aAB	97 aB
2	Essex	81	15	4	44 aAB	98 aA			131 aAB	794 bB	52 cA
2	Forrest	81	15	4	44 aAB	89 aA			87 ba	837 bC	61 bB
3	Bedford	76	19	5	41 aAB	65 bA			31 bA	1,840 aA	113 aA
3	Essex	75	20	5	42 aAB	108 aA			124 aB	1,346 bA	55 cA
3	Forrest	75	20	5	41 aAB	98 aA			123 aA	1,149 cAB	74 bA
4	Bedford	72	24	4	28 aB	53 bA			21 bA	1,667 aAB	104 aAB
4	Essex	73	23	4	35 aB	85 aAB			124 aB	1,398 bA	61 bA
4	Forrest	72	24	4	35 aB	79 aAB			112 aA	1,279 bA	78 bA
1985											
1	Bedford	87	10	3	6 aB	5 aB	350 aB	190 aA	72 bA	489 aC	78 aB
1	Essex	88	9	3	5 aC	4 aC	185 bC	60 aB	507 aB	110 bC	36 bC
1	Forrest	87	10	3	6 aC	3 aC	190 bC	70 aB	510 aA	49 bD	41 bB
2	Bedford	85	13	2	6 bB	11 aAB	270 bB	685 aA	68 bA	971 aB	83 aB
2	Essex	85	12	3	11 aBC	10 aBC	420 bBC	445 aA	664 aB	614 bB	41 bBC
2	Forrest	85	13	2	13 aB	14 aB	825 aA	790 aA	855 aA	511 bC	49 bB
3	Bedford	84	14	2	15 bA	9 bAB	690 bA	465 bA	78 cA	1,719 aA	102 aA
3	Essex	84	13	3	32 aA	17 abA	1,775 aA	500 bA	1,412 aA	969 bB	48 cAB
3	Forrest	84	13	3	16 bAB	29 aA	805 bA	1,505 aA	848 bA	1,038 bB	64 bA
4	Bedford	79	18	3	24 aA	13 aA	1,170 aA	545 aA	86 cA	1,982 aA	102 aA
4	Essex	79	18	3	15 bAB	15 aAB	745 bB	485 aA	1,019 aB	1,836 abA	56 cA
4	Forrest	78	19	3	29 aA	24 aA	1,260 aA	1,230 aA	840 bA	1,685 bA	69 bA

Means followed by the same letter are not significantly different ($P = 0.05$) for least significant difference (lsd). Lower case letters are for separation of cultivars within location and year; upper case are for separation of cultivar by location.

TABLE 2. Correlation coefficients of sand percentage, soybean yield (kg/ha), plant height (cm), preplant cyst density/100 g soil (PPc), final cyst density/100 g soil (PFc), cysts/plant 30 days after planting (CP_{30}), and approximate adjusted infection rate (AIR_{30}) for three soybean cultivars in 1984.

Cultivar	Variable	AIR_{30}	CP_{30}	PFc	PPc	Plant height	Yield
Bedford	Sand	−0.82**	−0.62**	−0.47	0.69**	−0.75**	−0.21
	Yield	0.45	0.43	NS	NS	0.42	
	Plant height	−0.69**	0.64**	0.79**	−0.46		
	PPc	−0.54*	NS	NS			
	PFc	0.46	0.45				
	CP_{30}	0.90**					
Essex	Sand	NS	0.46	−0.42	0.46	−0.83**	−0.85**
	Yield	NS	−0.60**	0.56*	−0.54*	0.74*	
	Plant height	NS	−0.52*	NS	−0.47		
	PPc	−0.73**	NS	NS			
	PFc	−0.47	−0.64**				
	CP_{30}	0.63**					
Forrest	Sand	−0.48	NS	−0.48	0.48	−0.92**	−0.82**
	Yield	0.63**	NS	NS	−0.70**	0.76**	
	Plant height	NS	NS	0.54*			
	PPc	−0.73**	NS	NS			
	PFc	NS	NS				
	CP_{30}	0.72**					

Correlation coefficients for 16 observations. Coefficients significant at $P \leq 0.01$ are denoted **; coefficients significant at $P \leq 0.05$ are denoted *; coefficients significant at $P \leq 0.10$ are unmarked.

soybean yield in the presence of *H. glycines*, since the cultivar × location interaction was significant ($P = 0.01$) both years when analyzed as a split plot (Table 1). Bedford, Essex, and Forrest have similar yield potential in the absence of SCN but differ somewhat in maturity. Soybean height followed a similar trend to seed yield (Table 1), and both were positively correlated (Tables 2, 3). Generally the relationship between plant height and sand content was stronger than the relationship between yield and sand content. A likely explanation for the better fit with plant height is that yield is a more complex phenomenon which is subject to stress throughout the season.

Essex and Forrest soybean yields were negatively correlated ($P = 0.0001$) with sand content in 1984 and 1985. Bedford yield was negatively correlated with sand content only in 1985, whereas plant height of Bedford was negatively correlated with sand content both years. The negative relationships between sand content and yield components were much stronger for the susceptible cultivars (Fig. 1). Root weight 30 days after planting was the same for all three cultivars in 1985 and was not affected by sand content.

Influence of sand content on H. glycines: The relationship of preplant densities of SCN cysts in 1984 and cysts and eggs in 1985 to sand content differed greatly between years. Initial SCN density and sand content were positively correlated ($P = 0.05$) in 1984 (Table 2) and negatively correlated in 1985 (Table 3) ($P = 0.05$). There was an inverse relationship between sand content and final population densities of SCN in both years ($P = 0.05$) (Tables 2, 3). The low final SCN densities at the higher sand content were probably related to greater host damage, a result of nematode infection and drought stress associated with higher sand content.

Soybean and H. glycines interactions: Yields of Essex and Forrest were negatively correlated with preplant cyst density (PPc), whereas the relationship between PPc and

TABLE 3. Correlation coefficients of sand percentage, yield, fresh root weight (g), plant height (cm), final egg population (PFe), final cyst (PFc), preplant eggs (PPe), cysts/plant 30 days after planting (CP_{30}), and approximate adjusted infection rate (AIR_{30}) for three soybean cultivars in 1985.

Cultivar	Variable	AIR_{30}	CP_{30}	PPc	PPe	PFc	PFe	Plant height	Root weight	Yield
Bedford	Sand	0.51*	NS	−0.67**	−0.50	−0.57*	−0.52*	−0.58*	NS	−0.71**
	Yield	−0.43	0.47	0.82**	0.67**	0.45	NS	0.89**	0.60*	
	Root weight	NS	0.68**	NS	0.44	NS	NS	0.55*		
	Plant height	NS	0.43	0.63**	0.46	0.45	0.42			
	PFe	NS	0.53*	NS	NS	0.91*				
	PFc	NS	0.58*	0.52*	NS					
	PPe	−0.62**	−0.45	0.52*						
	PPc	−0.63**	0.43							
	CP_{30}	NS								
Essex	Sand	NS	−0.42	0.44	−0.54*	−0.64**	−0.58*	−0.87**	NS	−0.94**
	Yield	NS	0.61**	0.58*	0.66**	0.73**	0.72**	0.83**	NS	
	Root weight	NS	NS	NS	NS	NS	NS	NS		
	Plant height	NS	NS	0.50	0.60*	0.68**	0.65**			
	PFe	−0.43	0.59*	0.72**	0.79**	0.90**				
	PFc	−0.49	0.62**	0.81**	0.81**					
	PPe	−0.64**	0.62**	0.91**						
	PPc	−0.69**	0.70**							
	CP_{30}	NS								
Forrest	Sand	0.74**	NS	−0.73**	−0.67**	−0.56*	−0.46	−0.65**	NS	−0.86**
	Yield	−0.81**	0.57*	0.88**	0.82**	0.73**	0.68**	0.82**	NS	
	Root weight	NS	0.55*	NS	0.44	0.42	NS			
	Plant height	−0.48	0.54*	0.62**	0.62**	0.66**	0.58**			
	PFe	−0.44	0.47	0.57*	0.68**	0.96**				
	PFc	−0.46	0.52*	0.60*	0.72**					
	PPe	−0.78**	0.64**	0.89**						
	PPc	−0.88**	0.70**							
	CP_{30}	NS								

Correlation coefficients for 16 observations. Coefficients significant at $P \leq 0.01$ are denoted **; coefficients significant at $P \leq 0.05$ are denoted *; coefficients significant at $P \leq 0.10$ are unmarked.

the yield of Bedford was not significant (Table 2) in 1984. In 1985 there were highly significant ($P \leq 0.01$) positive correlations between soybean yield and either preplant cyst (PPc) or egg density (PPe) for all cultivars (Table 3). The positive relation between yield and nematode density in this instance is a result of the very low SCN densities encountered with increasing sand. Final SCN densities were positively correlated with soybean yield both years (Tables 3, 4). The positive relations between yield and SCN final density was significant for all cultivars, but especially so for Forrest and Essex.

The numbers of cysts per plant 30 days after planting (CP_{30}) were much greater ($P = 0.01$) on both Essex and Forrest than on Bedford both in 1984 and 1985 (Table 1). The correlations of yield versus CP_{30} were positive for Bedford, negative for Essex, and nonsignificant for Forrest in 1984 (Table 2). The relation between CP_{30} and soybean yield was positive for all cultivars in 1985 because of lower preplant densities associated with increased sand content (Tables 1, 3).

Approximate adjusted infection rates (AIR_{30}) were not consistently related to soybean yield or sand content for susceptible Essex either year (Tables 2, 3). The relation between sand content and AIR_{30} was negative in 1984 but positive in 1985 for Forrest and Bedford. The discrepancy between AIR_{30} and sand content over the 2 years exemplifies the problems associated with measuring interactions of soil texture with nematode activity. Soil moisture and aeration are affected by texture (10,16,17), and different moisture regimes during the early growing season probably account for the reversed trends in infection between years. Excessively high moisture may inhibit nematode infection and soybean root growth because oxygen becomes limiting, whereas very low moisture tends to inhibit nematode activity. Sandier soils will have better conditions than loamier soils for nematode activity under high rainfall conditions. Lower rainfall will result in greater nematode activity in finer textured soils. Yields for Forrest and Bedford were positively correlated with AIR_{30} in 1984 and negatively correlated in 1985 (Tables 2, 3) reflecting the strong influence of sand on preplant nematode densities. Root weights of Forrest and Bedford were positively related to the number of cysts per plant in 1985, whereas the root weight of Essex was not. Similarly, Forrest and Bedford root weights were significantly correlated with yield and plant height, but there was no significant correlation between Essex root weight and any parameter measured (Table 3). The positive relationship between Forrest yield, root weight, and CP_{30}, though surprising, was reasonable. The greater numbers of cysts per plant were a result of higher preplant nematode densities and increased root weight encountered with lower sand content.

Correlations of nematode population data were different between the 2 years, reflecting important aspects of plant-parasitic nematode biology. Final population densities were not correlated with initial population densities in 1984 (Table 2) as a result of host damage associated with a combination of high initial nematode density in plots with high sand content. Final densities of SCN eggs and cysts and CP_{30} were positively correlated with initial densities in 1985 ($P \leq 0.01$) for all three cultivars (Table 3). Much of the discrepancy between 1984 and 1985 data can be attributed to much lower SCN densities in 1985 (Table 1). Density dependent rates of reproduction are common and may affect population fluctuations of *H. glycines* (3). A comparison of the three cultivars in respect to the relation between cysts per plant 30 days after planting (CP_{30}) and final population density (PFc or PFe) in 1984 was informative. The relation between CP_{30} and final density for Bedford was positive; the relation for susceptible Essex was negative; and Forrest, with some resistance, was intermediate. This last result is credible, since improved Bedford growth and yield would allow for increased final SCN densities as a result of its resistance. Additionally, CP_{30} accounts for some of the genetic variability of the SCN population, in regard to its ability to parasitize Bedford on a per plot basis, and this adds a genetic component to the regression model. The negative relation between Essex CP_{30} and final density shows the lack of resistance. The lack of fit of Forrest CP_{30} and final *H. glycines* population level probably is a residual effect of resistance to some portion of the SCN population.

Variation in soil texture within fields used in this study affected yields of both resistant and susceptible cultivars in the presence of *H. glycines*. The split-plot design was effective in delineating interactions between disease and soil texture (Table 1). The significant plot location × cultivar interaction both years indicates that susceptible cultivars are damaged more by SCN in coarser textured soils. This is especially evident, since SCN density was lowest in sandier plots in 1985 but still caused significantly greater yield suppression. We were unable to develop regression models incorporating both soil texture and nematode density over both years because nematode density gradients versus sand content gradients were opposite in the 2 years. Experiments with better controls may delineate texture–Pi relationships. Damage thresholds for *H. glycines* need to be developed over a number of years at many locations.

Lower SCN final population densities were associated with high sand content both years in our study. This result was expected, since soybeans were severely damaged in these plots. Santo and Bolander (13) found that reproduction of *Heterodera schachtii* was greater in soil containing higher silt content, whereas Dropkin et al. (5) found higher *H. glycines* densities associated with greater sand content. Soils used by Dropkin et al., however, were much higher in silt and clay than those encountered in our work. The results of our study and those of the other researchers (5,13) suggest that there is both an upper and lower limit in the optimum sand content for *Heterodera* species. This conclusion must be considered cautiously, since SCN damage to soybean was greatest with increasing sand content. Thus, the increased damage in sandier soils results in a lower equilibrium nematode density.

Damage functions must take into consideration soil texture and other environmental, edaphic, and genetic factors to improve reliability. A damage threshold developed for SCN on soybean in a silt loam in Missouri estimated a minimum yield of 0.80 (6) or approximately 20% yield suppression. Yield loss in our study, however, was on the order of 70–89% in a sandy loam based on yield of susceptible versus resistant cultivars. In very coarse textured soils a damage threshold based on sand content might actually provide more precise information.

Intrafield variation in soil texture and other edaphic variables has been shown to influence the distributions of plant-parasitic nematodes (8,9). Similarly, within-field variation also can influence plant health, yield, and damage caused by nematodes. Our results show that soybean yield suppression caused by *H. glycines* is greater with increasing sand content. Severe host damage, especially in coarse textured soils, can result in low nematode population densities.

LITERATURE CITED

1. Barker, K. R., committee chairman. 1978. Determining nematode population responses to control agents. Pp. 114–127 *in* E. I. Zehr, ed. Methods for evaluating plant fungicides, nematicides, and bactericides. St. Paul, MN: American Phytopathological Society.

2. Barker, K. R., and T. H. A. Olthof. 1976. Relationships between nematode population densities and crop responses. Annual Review of Phytopathology 14:327–353.

3. Bonner, M. J., and D. P. Schmitt. 1985. Population dynamics of *Heterodera glycines* life stages on soybean. Journal of Nematology 17:153–158.

4. Bouyoucos, G. J. 1951. A recalibration of the hydrometer method of making mechanical analysis of soils. Agronomy Journal 43:434–438.

5. Dropkin, V. H., C. H. Baldwin, T. Gaither, and W. Nace. 1976. Growth of *Heterodera glycines* in soybeans in the field. Plant Disease Reporter 60:977–980.

6. Francl, L. J., and V. H. Dropkin. 1986. *Heterodera glycines* population dynamics and relation of ini-

tial population to soybean yield. Plant Disease 70: 791–795.

7. Ferris, H. 1980. Nematology—status and prospects: Practical implementation of quantitative approaches to nematology. Journal of Nematology 12: 164–170.

8. Noe, J. P., and K. R. Barker. 1985. Relation of within-field spatial variation of plant-parasitic nematode population densities and edaphic factors. Phytopathology 75:247–252.

9. Norton, D. C., L. R. Frederick, D. E. Ponchillia, and J. W. Nyhan. 1971. Correlations of nematodes and soil properties in soybean fields. Journal of Nematology 3:154–163.

10. Norton, D. C. 1978. Ecology of plant-parasitic nematodes. New York: John Wiley and Sons.

11. Riggs, R. D. 1977. Worldwide distribution of soybean cyst nematode and its economic importance. Journal of Nematology 9:34–39.

12. Robbins, R. T., and K. R. Barker. 1974. Effects of soil type, particle size, temperature, and moisture on reproduction of *Belonolaimus longicaudatus*. Journal of Nematology 6:1–6.

13. Santo, G. S., and W. J. Bolander. 1979. Interacting effects of soil temperature and type on reproduction and pathogenicity of *Heterodera schachtii* and *Meloidogyne hapla* on sugarbeets. Journal of Nematology 11:289–291.

14. Schmitt, D. P., and K. R. Barker. 1981. Damage and reproductive potentials of *Pratylenchus brachyurus* and *P. penetrans* on soybean. Journal of Nematology 13:327–332.

15. Schmitt, D. P., and G. R. Noel. 1985. Nematode parasites of soybeans. Pp. 13–59 *in* W. R. Nickle, ed. Plant and insect nematodes. New York: Marcel Dekker.

16. Schmitt, D. P., H. Ferris, and K. R. Barker. 1987. Responses of soybean to *Heterodera glycines* races 1 and 2 in different soil types. Journal of Nematology 19:240–250.

17. Wallace, H. R. 1963. The biology of plant parasitic nematodes. London: Edward Arnold.

18. Wallace, H. R. 1971. Abiotic influences in the soil environment. Pp. 257–280 *in* B. M. Zuckerman, W. F. Mai, and R. A. Rohde, eds. Plant parasitic nematodes, vol. I. New York: Academic Press.

19. Windham, G. R., and K. R. Barker. 1986. Effects of soil type on the damage potential of *Meloidogyne incognita* on soybean. Journal of Nematology 18:331–338.