

Soybean and Soybean Cyst Nematode Response to Soil Water Content in Loam and Clay Soils

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ABSTRACT

Soybean cyst nematode (*Heterodera glycines* Ichinohe) (SCN) is a major pest of soybean [*Glycine max* (L.) Merr.] in the southeastern USA. The objective of this study was to determine the effect of wet and dry silt loam and clay soils on SCN development and corresponding soybean yield response in a greenhouse study. 'Tracy-M' soybean was grown in pots that contained either Dubbs silt loam (fine-silty, mixed, thermic Typic Hapludalf) or Sharkey clay (very fine, montmorillonitic, nonacid, thermic Vertic Haplaquept) surface soils that were watered to maintain adequate soil water potential (SWP) (-30 kPa SWP, wet treatment), or had water added at one-half the rate of the adequate treatment (dry treatment). Nematode treatments were either infested or noninfested. Experiments were conducted in 1987, 1988, and 1989, and new soil was infested each year. Number of cysts increased significantly with time in the wet silt loam treatment, stayed the same as the initial infestation in the dry silt loam treatment, and declined significantly in both the wet and dry clay treatments in all years of the study. Infestation by SCN caused a reduction in seed yields in both soils, but the decrease was less in the clay soil. Soil water content in each soil interacted with level of SCN infestation to influence soybean yield. The interaction was not dependent on similar SCN infestation levels between soils, or similar differences in SCN infestation between wet and dry soil treatments within soil. Yield declines associated with SCN infestation were highly correlated with number of seed. These results indicate that SCN will not maintain populations in fine-textured clay soil under greenhouse conditions, nor result in the magnitude of yield decline that often is measured in coarse-textured soil.

SOYBEAN CYST NEMATODE is injurious to soybean, and infests soils throughout the mid- and lower Mississippi River Valley and the southeastern coastal plain in the USA (Riggs and Schmitt, 1987). Studies have investigated effects of soil pore space, temperature, moisture, texture or type, and aeration on nematode population levels. These reports indicate that edaphic factors can significantly influence infestation, development, egg hatch, survival, migration, and infectivity of many nematode species.

Influence of soil moisture content on nematode development has been observed with *Rotylenchulus reniformis* Linford & Oliveira (Rebois, 1973), *Pratylenchus penetrans* (Cobb) Filipjev (Kable and Mai, 1968; Willis and Thompson, 1969), *Xiphinema americanum* Cobb (Lownsbery and Maggenti, 1963), and *Heterodera glycines* (Heatherly et al., 1982; Young and Heatherly, 1988). Eggs of *Meloidogyne hapla* Chitwood hatched equally at field capacity and permanent wilting point of soil, but the hatched nematodes were unable to migrate in the drier soil (Couch and Bloom, 1960). Similar results were reported for *Heterodera schachtii* Schmidt (Wallace, 1955). Wal-

lace (1958a,b) showed that distribution of soil water in the pores is an important factor in movement of juveniles of *H. schachtii* and *Ditylenchus dipsaci* (Kühn) Filipjev. Slack et al. (1972) reported that well-watered soil allowed *H. glycines* to maintain infectivity for a significantly longer period. Reduced development of *H. glycines* as indicated by low cyst numbers in an excessively wet (-18 kPa soil water potential) sandy loam soil (Heatherly et al., 1982) may be interrelated with limited O_2 level (Robbins and Barker, 1974; Wallace, 1955), fungal parasitism (Kerry et al., 1980), or reduced juvenile emergence from cysts (Slack and Hamblen, 1961).

Soil texture and its inherent properties of pore and particle size, and soil water holding properties are important factors that influence nematode behavior and damage potential. Soil type influences the damage potential of *P. penetrans* (Schmitt and Barker, 1981), *P. brachyurus* (Godfrey) Filipjev (Schmitt and Barker, 1981), *Meloidogyne incognita* (Kofoid and White) Chitwood (Windham and Barker, 1986), and *M. javanica* (Treub) Chitwood (Sleeth and Reynolds, 1955). *Heterodera glycines* damage to soybean is dependent on sand or clay content of soil (Dropkin et al., 1976; Koenning et al., 1988; Schmitt et al., 1987). Todd and Pearson (1988) recovered higher numbers of *H. glycines* females and eggs from a sandy loam soil than from silty loam soils 8 wk after introduction of similar numbers of eggs and juveniles; however, females and cysts increased in both soil types. Increased clay content adversely affects the mobility and distribution of *M. incognita* (Noe and Barker, 1985; Prot and Van Gundy, 1981), although the presence of some clay seemed preferable for nematode movement. Wallace (1958a) determined that *H. schachtii* is more mobile when pore diameter is 30 to 60 μ m, which is larger than most pores in a clay soil (Danielson and Sutherland, 1986). Movement of both *H. schachtii* and *D. dipsaci* is dependent on soil particle size, but the soil particle size associated with maximum mobility varies with species (Wallace, 1958b). Distribution of *Belonolaimus longicaudatus* Rau is limited to soils with $>80\%$ sand and $<10\%$ clay content, and this is apparently the primary limiting factor in its geographical distribution (Robbins and Barker, 1974). Norton et al. (1971) found that density of *Helicotylenchus pseudorobustus* (Steiner) Golden was positively correlated with clay content, but Ferris and Bernard (1971) found a negative correlation for *X. americanum* and *H. pseudorobustus* in soybean fields.

There are ≈ 7.8 million ha of land in the lower Mississippi River alluvial flood plain. About 50% of this area is comprised of soils that are predominantly clay (Brown et al., 1970), and the majority of this large clay area is planted to soybean. In fact, soybean is relegated primarily to these clay soils. There are no documented problems caused by *H. glycines* on this clay soil, but the assumption is that major problems caused by SCN

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will develop. The significance of an SCN infestation on such a large scale could be catastrophic; thus, a knowledge of the damage potential of SCN from such an occurrence is essential.

The objectives of this study were to determine the effect of clay and silt loam soils at two soil water contents on SCN reproduction and survival, and the corresponding soybean response.

MATERIALS AND METHODS

In January of 1987, 1988, and 1989, 32 pots (26-cm deep, 23 cm diam.) were filled to a depth of 16 cm with soils that were not infested with SCN. Pots were placed in a greenhouse and soils were watered to saturation. One-half of the pots received Dubbs silt loam surface soil, and the other half received Sharkey clay surface soil. About 1 wk later, soil had dried to a workable condition, and one-half of the pots of each soil were filled to within 5 cm of the top rim with soil of the same type, the soil having been infested with SCN (Race 14) at a rate to achieve about 700 cysts L⁻¹ in the top 15 cm after incorporation. Noninfested pots were filled similarly with the appropriate noninfested soil. Within 1 wk of nematode infestation, four 4- or 5-d-old seedlings of SCN susceptible Tracy-M soybean were transplanted into each pot. After establishment, seedlings were thinned to two uniform plants per pot. In 1987 and 1988, three 2.5-cm diam. by 15-cm deep soil cores were extracted from each infested pot at the time of transplanting to confirm the intended infestation level in each pot; in 1989, infested soil was sampled before being placed in the pots.

Mercury-manometer type tensiometers were inserted to a depth of 15 cm in one-half of the infested and noninfested pots of each soil. These pots were designated as a wet treatment. The remaining pots without tensiometers were designated as a dry treatment. Tensiometer readings were recorded between 0800 and 0900 central daylight time each morning.

Pots of the wet treatment were watered each morning to maintain SWP near -30 kPa. Pots of the dry treatment were watered with one-half of the amount that was applied to each wet treatment pot within a replicate, soil, and nematode infestation level. Average SWPs from the duration of the experiment and standard errors associated with each soil and nematode infestation level of the wet treatment are shown in Table 1. Textural composition and soil moisture characteristics of the Dubbs and Sharkey soils are given by Heatherly and Russell (1979). The wet treatment water contents at -30 kPa were approximately 0.28 and 0.37 m³ of water m⁻³ of soil for the Dubbs and Sharkey soils, respectively. For the dry treatment, water contents and SWPs were estimated to be about 0.18 m³ of water m⁻³ soil and -120 kPa for the Dubbs soil, and about 0.31 m³ of water m⁻³ soil and -180 kPa for the Sharkey soil.

The experiment had four replicates of the two soils, two soil water contents, and two nematode infestation levels in a randomized complete-block design with a factorial arrangement of treatments. A 16-h photoperiod was maintained with supplemental fluorescent lighting for 3 wk after transplanting in 1987, and for 4 wk after transplanting in 1988 and 1989. Daily minimum air temperatures were kept above 20 °C, and daily maximum air temperatures were kept above 30 °C. Bloom dates were 45, 48, and 53 d after transplanting in 1987, 1988, and 1989, respectively.

Just before maturity in 1987, and at about 60 d after transplanting in 1988 and 1989, soil samples for nematode analysis were collected from each pot by the same procedure that was used at the beginning of the experiment. Dry soil of the same soil was placed in each hole created by the sampling. The three cores taken from each pot for nematode

Table 1. Statistical parameters for soil water potential measurements at 15-cm depth in greenhouse pots filled with one of two soil types and either infested or not infested with soybean cyst nematode at Stoneville, MS.

Treatment†	Mean	SE
	kPa	
<u>1987</u>		
Loam, wet, infested	-23.8	0.23
Loam, wet, noninfested	-27.6	0.27
Clay, wet, infested	-19.4	0.35
Clay, wet, noninfested	-31.0	0.77
<u>1988</u>		
Loam, wet, infested	-22.9	0.38
Loam, wet, noninfested	-28.4	0.74
Clay, wet, infested	-29.6	0.99
Clay, wet, noninfested	-35.7	1.24
<u>1989</u>		
Loam, wet, infested	-27.5	0.47
Loam, wet, noninfested	-30.2	0.87
Clay, wet, infested	-26.6	0.74
Clay, wet, noninfested	-27.2	0.75

† Loam = Dubbs silt loam (Typic Hapludalf); clay = Sharkey clay (Vertic Haplaquept).

analysis were mixed, and a 0.225-L sample per pot was washed through 20- and 60-mesh sieves (0.85- and 0.25-mm openings, respectively). Cysts and females retained on the 60-mesh sieve were counted.

All seed was harvested at maturity. Number of 1-, 2-, and 3-seeded pods, and total number of pods per pot were recorded. All pods were dried at 70 °C for 48 h, and seed were then shelled and counted. Weight of seed from each pot was recorded, and average weight per seed was calculated. All data were analyzed with analysis of variance using both individual year and combined data. Simple correlation coefficients were calculated to determine the association between seed yield and yield components, and between number of seed and other yield components. Cyst data from the infested pots were analyzed by analysis of variance using both individual year and combined data. The difference in the number of cysts at the beginning of the experiment and at the second sampling was calculated for each pot. The cyst data were analyzed to determine the effect of soil and soil moisture level on change in number of cysts during the experiment and the significance of the changes. Means of all data were compared using significance of the *F* ratio or an LSD (*P* = 0.05).

RESULTS AND DISCUSSION

Nematode response

Number of cysts of SCN at the beginning of the experiment was not significantly different between soils or between soil water contents in any year, or in the combined analysis (Table 2). At the last sampling of each year's experiment, both soil texture (ST) and soil water content (SW) significantly affected (*P* = 0.05) number of cysts except in 1988, when only ST affected the number. Because the ST × SW interaction also was significant, only its effect will be discussed. In all analyses, number of cysts in the wet silt loam exceeded the number in the dry silt loam, whereas in the clay soil, the difference in number of cysts between the two soil water contents was never significant. The results from the silt loam soil are similar to those from previous research (Heatherly et al.,

Table 2. Number of cysts of soybean cyst nematode at beginning and at 60 d after planting or at end of greenhouse experiments in 1987, 1988, and 1989 at Stoneville, MS.

Soil type (ST) and soil water (SW)†	No. of cysts at beginning				No. of cysts at end‡				No. at end minus beginning			
	1987	1988	1989	Avg.	1987	1988	1989	Avg.	1987	1988	1989	Avg.
	cysts L ⁻¹											
Loam, wet	775	856	600	744	2067	1400	1292	1586	1292	544	692	842
Loam, dry	617	756	600	657	783	842	775	800	166	86	175	143
Clay, wet	892	689	593	725	267	192	558	339	-625	-497	-35	-386
Clay, dry	900	739	593	744	200	417	474	364	-700	-322	-118	-380
	LSD (0.05) or level of significance											
Between ST	NS	NS	NS	NS	**	**	**	**	**	**	**	**
Between SW	NS	NS	NS	NS	**	NS	**	**	*	NS	**	**
SW × ST	NS	NS	NS	NS	659*	429*	339*	351*	712*	287*	339*	269*

*,** Significant difference at the 0.05 and 0.01 levels of probability, respectively. NS = no significant difference or interaction at $P = 0.05$.

† Loam = Dubbs silt loam (Typic Hapludalf); clay = Sharkey clay (Vertic Haplaquept).

‡ Sampled before maturity in 1987; sampled at 60 days after planting in 1988 and 1989.

1982; Young and Heatherly, 1988). The difference in number of cysts between the wet silt loam and wet clay was significant, and was much greater than the difference between the dry silt loam and dry clay. The difference between the dry silt loam and dry clay was significant only in the combined analysis, but the trend was for greater numbers in the dry silt loam each year.

Analyses also were conducted to determine the effect of ST and SW on the change in number of cysts during the course of the experiment. Only the significant SW × ST interaction (Table 2) will be discussed. In the silt loam soil, the number of cysts at the beginning of the experiment and at the second sampling were significantly different ($P = 0.05$) between the two soil water contents, while the numbers were not different in the clay soil. In both the wet and dry soil treatments, the change in number of cysts was significantly different ($P = 0.05$) between soils.

In the wet silt loam, the increase in number of cysts was significant in all years and in the combined analysis, while the slight increase in number of cysts in the dry silt loam was not significant. Heatherly et al. (1982) reported similar results for a sandy loam soil. In the clay soil, number of cysts decreased significantly for both soil water contents in 1987 and 1988 and in the combined analysis. From these results, it appears that SCN populations will increase in a silt loam soil if available soil moisture is high, and maintain themselves if soil moisture is low.

These results also indicate that the nematode cannot maintain itself in the fine-textured clay soil, even with adequate soil water. Todd and Pearson (1988), using two soil textures (10% clay or 24–26% clay), found that number of SCN females and cysts had increased in both soils 8 wk after infestation, but the increase was less in the soils with greater clay content. Our results show a significant decline in number of cysts in the clay soil (57.5% clay) between the two samplings. The results of Wallace (1958a) indicate that the predominant pore size in clay soil (Danielson and Sutherland, 1986) could restrict nematode movement. Results from a companion study (Young and Heatherly, 1990) indicate fewer eggs per cyst are produced in the clay soil, possibly because of reduced mating between SCN males and females. Juveniles (18

µm diam.) invaded roots equally in both soils 5 to 10 d after transplanting in the companion study.

Soybean seed yield and yield components

Nematode infestation (NEM) and SW significantly affected seed yield in all years and in the combined analysis, and ST significantly affected yield in 1987, 1988, and in the combined analysis (Table 3). The SW × NEM interaction was significant in 1987, 1988, and in the combined analysis; the NEM × ST interaction was significant in all analyses; and the NEM × SW × ST interaction was significant in 1987 and 1988. Therefore, single-factor effects will not be discussed, because interactions involving all factors were significant in every analysis.

In 1987, the nematode-free, wet clay soil produced 20.2 g of seed pot⁻¹, which was higher than the 13.9 g pot⁻¹ produced by the nematode-free, wet silt loam soil. All other yields from clay and silt loam were nearly equal. The wet soil produced a greater yield than the dry soil except in the infested clay soil, where yields were similar in the wet and dry treatments. Yield from noninfested soil was significantly greater than from infested soil, regardless of ST or SW, but the magnitude of difference was greater between the wet infested and wet noninfested treatments of the clay soil. Apparently, initial populations were sufficient to restrict yield even though the number of cysts was reduced at the end of the experiment in 1987 (Table 2). Previous experiments (Young and Heatherly, 1990) showed that the number of cysts of SCN in clay soil at 30 d after transplanting had not declined significantly below initial infestation levels, but the number of eggs per cyst in clay soil was significantly below the number in silt loam soil after 30 d. By 60 d after transplanting, both number of cysts and eggs per cyst in the clay soil were significantly below the number in the silt loam soil. Thus, early-season stress may be imposed by SCN in clay soils with high initial infestations.

In 1988, yields from the clay soil were higher in all cases, but the difference of 15.4 g pot⁻¹ between ST in the wet infested treatment was almost twice as large as the difference of 8.8 g pot⁻¹ in the dry infested treatments. Nematode infestation had the greatest effect

Table 3. Yield of soybean grown with and without soybean cyst nematode at two soil water contents in loam and clay soil in a greenhouse at Stoneville, MS, in 1987, 1988, and 1989.

Nematode (NEM) and soil water (SW) levels†	1987			1988			1989			Combined		
	Soil type (ST)‡			Soil type			Soil type			Soil type		
	Loam	Clay	Avg.	Loam	Clay	Avg.	Loam	Clay	Avg.	Loam	Clay	Avg.
	g pot ⁻¹											
Inf., wet	7.8	6.8	7.3	2.4	17.8	10.1	11.2	14.4	12.8	7.1	13.0	10.0
Inf., dry	2.8	4.2	3.5	0.6	9.4	5.0	2.4	10.3	6.4	2.0	8.0	5.0
Avg.	5.3	5.5		1.5	13.6		6.8	12.4		4.5	10.5	
Non., wet	13.9	20.2	17.0	28.1	31.6	29.8	19.9	17.5	18.7	20.6	23.1	21.8
Non., dry	7.8	8.5	8.2	16.0	23.1	19.6	12.8	14.3	13.6	12.2	15.3	13.8
Avg.	10.8	14.4		22.0	27.4		16.4	15.9		16.4	19.2	
	LSD (0.05) or level of significance											
Between NEM	**			**			**			**		
Between SW	**			**			**			**		
Between ST	*			**			NS			**		
SW × NEM	2.4*			1.8*			NS			1.8*		
SW × ST	NS			NS			NS			NS		
NEM × ST	2.4*			1.8*			4.8*			1.8*		
NEM × SW × ST	3.4*			2.5*			NS			NS		

*,** Significant differences at the 0.05 or 0.01 levels of probability, respectively. NS = no significant differences or interactions at $P = 0.05$.

† Nematode level was either infested with soybean cyst nematode (Inf.) or noninfested (Non.); soil water content was wet (soil water potential average of -30 kPa) or dry (pots received half the water of wet pots).

‡ Soil type was either Dubbs (Typic Hapludalf) silt loam surface soil or Sharkey (Vertic Haplaquept) clay surface soil.

on yield in the wet silt loam soil, where the difference was 25.7 g pot⁻¹. Yield from the wet soil was greater than from the dry soil except in the infested silt loam soil, where soil water content did not significantly affect yield. Nematode infestation and dry soil apparently had a more significant effect on soybean yield in the silt loam soil in 1988, but nematode infestation was the dominant factor.

In 1989, only the NEM × ST interaction was significant. Soil water content did not interact with either NEM or ST to influence seed yield, but the wet treatment always produced the highest seed yield at both NEM levels and in both soils. In the nematode-infested treatment, yield from clay soil averaged across SW was 5.6 g pot⁻¹ greater than average yield from silt loam soil, but average yields from the two soils

were nearly equal in the noninfested treatment. Average difference in yield between silt loam noninfested and infested treatments was 9.6 g pot⁻¹, while average difference between noninfested and infested clay treatments was only 3.5 g pot⁻¹. This again indicates that SCN infestation was more detrimental to seed yield in the silt loam soil than in the clay soil.

In the combined analysis, both the SW × NEM and NEM × ST interactions were significant for seed yield. In both the infested and noninfested treatments, seed yield was greater from the wet soil than from the dry soil, but the difference was greater in the noninfested treatment. Yield from clay soil exceeded that from silt loam in all cases, but the difference between the two soils was more pronounced in nematode-infested soils. Difference in yield between nematode-in-

Table 4. Number of seed of soybean grown with and without soybean cyst nematode at two soil water contents in loam and clay soil in a greenhouse at Stoneville, MS, in 1987, 1988, and 1989.

Nematode (NEM) and soil water (SW) levels†	1987			1988			1989			Combined		
	Soil type (ST)‡			Soil type			Soil type			Soil type		
	Loam	Clay	Avg.	Loam	Clay	Avg.	Loam	Clay	Avg.	Loam	Clay	Avg.
	no. pot ⁻¹											
Inf., wet	59	44	52	23	106	64	80	103	92	54	84	69
Inf., dry	23	27	25	7	56	32	15	70	42	15	51	34
Avg.	41	36		15	81		48	86		34	68	
Non., wet	93	123	108	185	199	192	146	132	139	141	152	146
Non., dry	54	57	56	100	144	122	75	93	84	76	98	87
Avg.	74	90		142	172		110	112		108	125	
	LSD (0.05) or level of significance											
Between NEM	**			**			**			**		
Between SW	**			**			**			**		
Between ST	NS			**			NS			**		
SW × NEM	13*			11*			NS			13*		
SW × ST	NS			NS			NS			NS		
NEM × ST	13*			11*			NS			13*		
NEM × SW × ST	19*			15*			NS			NS		

*,** Significant differences at the 0.05 or 0.01 levels of probability, respectively. NS = no significant differences or interactions at $P = 0.05$.

† Nematode level was either infested with soybean cyst nematode (Inf.) or noninfested (Non.); soil water content was wet (soil water potential average of -30 kPa) or dry (pots received half the water of wet pots).

‡ Soil type was either Dubbs (Typic Hapludalf) silt loam surface soil or Sharkey (Vertic Haplaquept) clay surface soil.

Table 5. Simple correlation coefficients expressing association between soybean seed yield and yield components in a greenhouse study with two soil types, two soil water contents, and two levels of soybean cyst nematode† infestation at Stoneville, MS.

Yield component‡	1987		1988		1989		Combined	
	Yield	No. of seed	Yield	No. of seed	Yield	No. of seed	Yield	No. of seed
1-seed pod	0.81***	0.81***	0.54***	0.54***	0.74***	0.70***	0.29**	0.32**
2-seed pod	0.84***	0.88***	0.93***	0.93***	0.93***	0.96***	0.82***	0.87***
3-seed pod	0.82***	0.85***	0.96***	0.97***	0.85***	0.85***	0.87***	0.84***
No. of pods	0.95***	0.98***	0.98***	0.99***	0.98***	0.99***	0.96***	0.98***
No. of seed	0.98***	—	0.99***	—	0.98***	—	0.99***	—
Avg. seed pod ⁻¹	0.37*	0.36*	0.56**	0.54**	0.52**	0.54**	0.59***	0.57***
Avg. seed weight	0.48**	0.33	0.65***	0.59***	-0.15	-0.29	0.43***	0.32**

*, **, *** Significant correlation at the 0.05, 0.01, and 0.001 levels of probability, respectively. $N = 32$ for individual years, and $N = 96$ for combined analysis.

† Two soil types were Dubbs (Typic Hapludalf) silt loam surface soil and Sharkey (Vertic Haplaquept) clay surface soil; two soil water contents were -30 kPa intended average soil water potential and half the available water; two levels of cyst nematode were infested and noninfested.

‡ Either total for each pot, or average per pot.

infested and noninfested treatments was greater in silt loam soil, again indicating that nematode infestation of silt loam was more detrimental to seed yield. Koenning et al. (1988) found that plants in more coarsely textured soils in the same field were damaged more by SCN.

The pattern of differences measured in number of seed per pot (Table 4) between levels of each treatment and their interactions are nearly identical to those determined for seed yield. In fact, seed yield was highly correlated ($P = 0.01$) with number of seed in each year of the study, as well as in the combined analysis (Table 5). In contrast to this, relatively few and inconsistent differences in average weight of seed between levels of factors or among factors were measured (Table 6), and these few differences were not highly correlated with seed yield (Table 5). Thus, the yield-reducing effect of SCN, dry soil, and the combination of the two was manifested almost totally in the effect on number of seed produced. Both seed yield and number of seed were highly correlated with number of pods, but not with number of seed per pod. Therefore, the stress imposed by both SCN and dry soil, plus the apparent synergism of the two, appears

to be manifested in fewer pods per plant and fewer seed produced.

The wet, nematode-infested silt loam soil always contained the most cysts of SCN at the second sampling (Table 2), while the clay soil (both soil water contents) always contained the fewest. Number of cysts in the wet silt loam soil increased between the initial and second samplings, number of cysts remained essentially the same in the dry silt loam soil, and number of cysts declined in the clay soil regardless of soil water content. However, seed yield was not significantly correlated with the number of cysts ($r = -0.18$) at the second sampling in the combined analysis, or with the change in number of cysts ($r = -0.14$). The dry silt loam soil had the lowest average seed yield, but the number of cysts was fewer than in the wet silt loam soil. Koenning et al. (1988) found that SCN density was lowest in sandier plots, but still caused significantly greater yield depression than similar SCN populations in plots with more clay. In our clay soil, SCN infestation at the second sampling was not different between soil water contents, but the wet soil still produced a higher average yield. This indicates that soil water content in each soil interacted

Table 6. Average weight of seed of soybean grown with and without soybean cyst nematode at two soil water contents in loam and clay soil in a greenhouse at Stoneville, MS, in 1987, 1988, and 1989.

Nematode (NEM) and soil water (SW) levels†	1987			1988			1989			Combined		
	Soil type (ST)‡			Soil type			Soil type			Soil type		
	Loam	Clay	Avg.	Loam	Clay	Avg.	Loam	Clay	Avg.	Loam	Clay	Avg.
mg seed ⁻¹												
Inf., wet	131	155	143	98	168	133	144	144	144	124	156	140
Inf., dry	120	155	138	89	166	128	139	147	143	116	156	136
Avg.	126	155		94	167		142	146		120	156	
Non., wet	150	162	156	152	158	155	139	134	136	147	151	149
Non., dry	145	148	146	160	160	160	170	155	162	158	154	156
Avg.	148	155		156	159		154	144		152	152	
LSD (0.05) or level of significance												
Between NEM	NS			**			NS			**		
Between SW	NS			NS			*			NS		
Between ST	**			**			NS			**		
SW × NEM	NS			NS			15*			NS		
SW × ST	NS			NS			NS			NS		
NEM × ST	NS			20*			NS			12*		
NEM × SW × ST	NS			NS			NS			NS		

*, ** Significant differences at the 0.05 or 0.01 levels of probability, respectively. NS = no significant differences or interactions at $P = 0.05$.

† Nematode level was either infested with soybean cyst nematode (Inf.) or noninfested (Non.); soil water content was set (soil water potential average of -30 kPa) or dry (pots received half the water of wet pots).

‡ Soil type was either Dubbs (Typic Hapludalf) silt loam surface soil or Sharkey (Vertic Haplaquept) clay surface soil.

with level of SCN infestation to influence soybean yield, but the interaction was dependent on neither similar SCN infestation levels between soils, nor similar differences in SCN infestations in wet and dry treatments within soil.

Since pots were sampled only at 60 d in this study, it can be projected that the yield reductions that occurred in the infested clay pots were the result of irreparable nematode-induced stress that occurred between transplanting and the 60-d sample date. This is consistent with results reported by Wrather and Anand (1988), who found that soybean seedling growth was inhibited by SCN infection at 2 or 4 wk after planting but not at 6 wk after planting. If the pots had not been reinfested at the beginning of each year, and if the pots had been stored to preserve the nematode population that was present at the end of the experiment, the yield reduction in the infested clay pots might have disappeared after the initial year's infestation. This should be investigated further to determine if a clay soil environment will in fact result in permanent reductions or eventual disappearance of populations of SCN regardless of soil water content.

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REFERENCES

- Brown, D.A., V.E. Nash, and A.G. Caldwell. 1970. A monograph of the soils of the southern Mississippi River valley alluvium. South. Coop. Ser. Bull. 178.
- Couch, H.B., and J.R. Bloom. 1960. Influence of soil moisture stresses on the development of the root knot nematode. *Phytopathology* 50:319-321.
- Danielson, R.E., and P.L. Sutherland. 1986. Porosity. p. 443-461. In A. Klute (ed.) *Methods of soil analysis*. Part 1. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.
- Dropkin, V.H., C.H. Baldwin, T. Gaither, and W. Nace. 1976. Growth of *Heterodera glycines* in soybeans in the field. *Plant Dis. Rep.* 60:977-980.
- Ferris, V.R., and R.L. Bernard. 1971. Effect of soil type on population densities of nematodes in soybean rotation fields. *J. Nematol.* 3:123-128.
- Heatherly, L.G., and W.J. Russell. 1979. Effect of soil water potential of two soils on soybean emergence. *Agron. J.* 71:980-982.
- Heatherly, L.G., L.D. Young, J.M. Epps, and E.E. Hartwig. 1982. Effect of upper-profile soil water potential on numbers of cysts of *Heterodera glycines* on soybeans. *Crop Sci.* 22:833-835.
- Kable, P.F., and W.F. Mai. 1968. Influence of soil moisture on *Pratylenchus penetrans*. *Nematologica* 14:101-122.
- Kerry, B.R., D.H. Crump, and L.A. Mullen. 1980. Parasitic fungi, soil moisture and multiplication of cereal cyst nematode, *Heterodera avenae*. *Nematologica* 26:57-68.
- Koenning, S.R., S.C. Anand, and J.A. Wrather. 1988. Effect of within-field variation in soil texture on *Heterodera glycines* and soybean yield. *J. Nematol.* 20:373-380.
- Lownsberry, B.F., and A.R. Maggenti. 1963. Some effects of soil temperature and soil moisture on population levels of *Xiphinema americanum*. *Phytopathology* 53:667-668.
- 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.
- Norton, D.C., L.R. Frederick, P.E. Ponchillia, and J.W. Nyhan. 1971. Correlations of nematodes and soil properties in soybean fields. *J. Nematol.* 3:154-163.
- Prot, J.-C., and S.D. Van Gundy. 1981. Effect of soil texture and the clay component on migration of *Meloidogyne incognita* second-stage juveniles. *J. Nematol.* 13:213-217.
- Rebois, R.V. 1973. Effect of soil water on infectivity and development of *Rotylenchulus reniformis* on soybean, *Glycine max.* *J. Nematol.* 5:246-249.
- Riggs, R.D., and D.P. Schmitt. 1987. Nematodes. p. 757-778. In J.R. Wilcox (ed.) *Soybeans: Improvement, production, and uses*. 2nd ed. Agron. Monogr. 16. ASA, CSSA, and SSSA, Madison, WI.
- Robbins, R.T., and K.R. Barker. 1974. The effects of soil type, particle size, temperature, and moisture on reproduction of *Belonolaimus longicaudatus*. *J. Nematol.* 6:1-6.
- Schmitt, D.P., and K.R. Barker. 1981. Damage and reproductive potential of *Pratylenchus brachyurus* and *P. penetrans* on soybean. *J. Nematol.* 13:327-332.
- Schmitt, D.P., H. Ferris, and K.R. Barker. 1987. Response of soybean to *Heterodera glycines* Races 1 and 2 in different soil types. *J. Nematol.* 19:240-250.
- Slack, D.A., and M.L. Hamblen. 1961. The effect of various factors on larval emergence from cysts of *Heterodera glycines*. *Phytopathology* 51:350-355.
- Slack, D.A., R.D. Riggs, and M.L. Hamblen. 1972. The effect of temperature and moisture on the survival of *Heterodera glycines* in the absence of a host. *J. Nematol.* 4:263-266.
- Sleeth, B., and H.W. Reynolds. 1955. Root-knot nematode infestation as influenced by soil texture. *Soil Sci.* 80:459-461.
- Todd, T.C., and C.A.S. Pearson. 1988. Establishment of *Heterodera glycines* in three soil types. *Ann. Appl. Nematol. (J. Nematol. 20, Supplement)* 2:57-60.
- Wallace, H.R. 1955. The influence of soil moisture on the emergence of larvae from cysts of the beet eelworm, *Heterodera schachtii*. *Ann. Appl. Biol.* 43:477-484.
- Wallace, H.R. 1958a. Movement of eelworms. I. The influence of pore size and moisture content of the soil on the migration of larvae of the beet eelworm, *Heterodera schachtii* Schmidt. *Ann. Appl. Biol.* 46:74-85.
- Wallace, H.R. 1958b. Movement of eelworms: II. A comparative study of the movement in soil of *Heterodera schachtii* Schmidt and of *Ditylenchus dipsaci* (Kühn) Filipjev. *Ann. Appl. Biol.* 46:86-94.
- Willis, C.B., and L.S. Thompson. 1969. The influence of soil moisture and cutting management on *Pratylenchus penetrans*: Reproduction in birdsfoot trefoil and the relationship of inoculum levels on yields. *Phytopathology* 59:1872-1875.
- Windham, G.L., and K.R. Barker. 1986. Effects of soil type on the damage potential of *Meloidogyne incognita* on soybean. *J. Nematol.* 18:331-338.
- Wrather, J.A., and S.C. Anand. 1988. Relationship between time of infection with *Heterodera glycines* and soybean yield. *J. Nematol.* 20:439-442.
- Young, L.D., and L.G. Heatherly. 1988. Soybean cyst nematode effect on soybean grown at controlled soil water potentials. *Crop Sci.* 28:543-545.
- Young, L.D., and L.G. Heatherly. 1990. *Heterodera glycines* invasion and reproduction on soybean grown in clay and silt loam soils. *J. Nematol.* 22:618-619.