Effects and Dynamics of a Nematode Community on Soybean[1]

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Abstract: The relationships between densities of all members of a plant-parasitic nematode community and yield of 'Davis' soybean and between final and preplant population levels were examined in small plots on sandy soils in north-central Florida. Plant-parasitic nematodes present in the community included *Belonolaimus longicaudatus, Criconemella sphaerocephala, Meloidogyne incognita, Paratrichodorus minor, Pratylenchus brachyurus,* and *Xiphinema* sp. Plant growth, including stand count, soybean yield (kg/ha), and size of young plants, was occasionally inversely correlated ($P \leq 0.05$) with densities of *B. longicaudatus* or *P. brachyurus,* but not with densities of other species or with a range of soil variables. The nature of this relationship varied with season, with more severe stand losses noted during 1987 than in 1988. Final population densities (Pf) of most nematode species showed significant ($P \leq 0.05$) linear relationships to densities measured at planting or earlier (Pi). These relationships were stronger (higher r^2) with the ectoparasite *B. longicaudatus* than with the endoparasites *M. incognita* and *P. brachyurus. Criconemella sphaerocephala* declined under soybean cultivation, reaching levels near zero after two seasons. A quadratic model showed an improvement ($P \leq 0.05$) over the linear model in describing the relationship between Pf and Pi measured at planting for *B. longicaudatus,* and gave a better indication of the leveling off of Pf at high values of Pi.

Key words: Belonolaimus longicaudatus, corn, Criconemella sphaerocephala, damage function, *Glycine max*, lesion nematode, *Meloidogyne incognita*, nematode community, population dynamics, *Pratylenchus brachyurus*, ring nematode, root-knot nematode, soybean, sting nematode.

Soybean (*Glycine max* (L.) Merr.) fields in the southeastern United States usually contain a polyspecific community of plant-parasitic nematodes (2,21). Several members of this community damage soybean (21,25), and damage functions for a few species are available (1,17,20). Expression of nematode damage to soybean may change with many factors, however, including cultivar (20), temperature (17), and soil texture (12). In some instances, the combined influence of two species on this host was investigated (10,19), resulting in a multivariate function expressing soybean yield in terms of densities of *Meloidogyne arenaria* (Neal) Chitwood and *Heterodera glycines* Ichinohe (19). The relatively little research done with polyspecific nematode communities allows us to draw few conclusions about their combined effects on soybean production.

The objectives of this study were to determine the effect of each member of a nematode community on soybean yield and to describe the dynamics and rate of growth of each species on the crop. These factors were evaluated in a series of small plots established across nematode population gradients occurring naturally in the field.

MATERIALS AND METHODS

In October 1986, following cultivation of a maize (*Zea mays* L.) crop, 16 permanent 3-m × 3-m plots were established in two adjacent 0.5-ha sites (eight plots per site) with similar cropping histories at the University of Florida Agronomy Farm near Jonesville in Alachua County. When considered together, these plots provided a range in naturally occurring populations of *Belonolaimus longicaudatus* Rau, *Meloidogyne incognita* (Kofoid & White) Chitwood, *Pratylenchus brachyurus* (Godfrey) Filipjev & Stekhoven, *Criconemella sphaerocephala* (Taylor) Luc & Raski, *Paratrichodorus minor* (Colbran) Siddiqi, and *Xiphinema* sp. (close to *X. floridae* Lamberti & Bleve-Zacheo).

In early November, half of each 0.5-ha site (four plots) was sown in hairy vetch

TABLE 1. Yield and other plant data from soybean plots over two seasons.

	Mean (range) of measurements	
	1987	1988
Harvest yield (kg/ha)	1,845 (594–2,626)	2,992 (2,062–3,812)
Stand count at harvest (plants/6 m)	39.9 (10–59)	82.2 (48–113)
Dry root weight, July (g/plant)	0.34 (0.1–0.7)	1.89 (0.4–5.0)
Dry top weight, July (g/plant)	1.00 (0.1–2.2)	8.33 (0.4–20.6)

Data are means (ranges) over 16 plots in each season.

(*Vicia villosa* Roth) or rye (*Secale cereale* L. cv. Wrens Abruzzi). Hairy vetch and rye were sown in rows 15 cm apart at rates of 68 and 50 kg/ha, respectively. Cover crops were mowed and disked in April 1987, and the field was plowed on 11 May. On 27 May, 56 kg/ha of K_2SO_4 and the herbicides trifluralin (0.56 kg a.i./ha) and metribuzin (0.56 kg a.i./ha) were applied and incorporated.

The soybean cultivar Davis was seeded at a rate of 67 kg/ha in rows 0.76 m apart on 2 June. Individual plots were planted along with the surrounding 0.5-ha site, so that all plots were contained within a large soybean field, eliminating any border effects to individual plots or alleyways near plots. Plots were cultivated in early July and were irrigated during the season as needed. Soon after pods were formed, all plots were sprayed with acephate (1.12 kg a.i./ha) for control of stinkbugs (*Nezara viridula* L.). Plots were harvested on 13 October.

Planting practices during the 1987–88 season were similar except that all cover crops were planted 12 November 1987 and plowed under in April, and soybean was planted 10 May 1988 and harvested 26 October. Herbicide rates in 1988 were 0.75 kg a.i./ha of trifluralin and 0.37 kg a.i./ha of metribuzin.

Soil samples were collected from each plot seven times each year: 1) early November (at planting of winter cover crop), 2) late March or early April (before disking under cover crops), 3) early May or June (just before planting of the soybean crop), 4) early July, 5) early August, 6) early September, and 7) October (at harvest). Individual samples consisted of 12 cores collected in a stratified random pattern with a sampling cone (6) 20 cm deep. Three replicate samples were collected from each plot for the November, March (April), soybean planting, and harvest samples. The July, August, and September samples consisted of single samples collected in the rhizosphere of the plants in each plot. The 12 rhizosphere cores were taken only from the outside two rows in each plot to minimize disturbance of the inside two rows. The nematodes were extracted from each sample with a modified sieving-centrifugation technique (11), using a 38-μm-pore sieve. Nematodes were extracted from a 100-cm³ subsample from each sample and counted.

Sand, silt, and clay content of soil samples collected at planting were determined using the Bouyoucos (3) hydrometer method. Organic matter and a range of fertility analyses were performed on these samples with standard methods (18) by the University of Florida Extension Soil Testing Laboratory.

Harvest data were collected from the inside two rows of each plot. Soybean seed yield is reported at 13% moisture. Stand counts were determined for the 6 m of row harvested in each plot. At the July sampling, four whole plants were collected per plot from 3 m of row adjacent to each plot. Three of these were used for weight measurements and extraction of nematodes from the roots and for visual examination of any root damage. Nematodes were extracted from root samples by chopping roots in a blender followed by incubation on Baermann trays for 48 hours. One plant

was dried to constant weight in an oven at 80 C for fresh to dry weight conversions.

Before analysis, all nematode data were transformed by $\log_2$ (nematode density + 1). For each season, Pearson product-moment correlation coefficients (26) were computed between all plant data and all nematode and soil data. Correlation coefficients also were calculated between final population densities (Pf) of each nematode species and its population density in earlier samples, as well as between population densities of one species with those of other species. Significant correlations ($P \leq 0.05$) were further examined by linear, quadratic, and (or) multiple regression analyses on preplant nematode density. All data analyses were performed using the SAS system (9).

RESULTS AND DISCUSSION

Effects on soybean yields: A considerable range in yield and other plant data was obtained from the 16 soybean plots in each season (Table 1). A preliminary analysis of variance of these plant measurements revealed no effects ($P \leq 0.05$) from cover crops. Mean plant size in July and yields were lower in 1987 than in 1988, possibly a result of the later planting date (2 June 1987 vs. 10 May 1988).

Over all plots, soil pH averaged 6.0 (range: 5.7–6.4); soil organic matter, 1.1% (0.9–1.4); sand, 96.0% (95.0–97.0); silt, 1.5% (0.4–2.4); clay, 2.5% (1.5–3.5); P, 76 ppm (42–97); K, 52 ppm (27–86); Mg, 52 ppm (38–85); Ca, 367 ppm (249–668); NO_3, 6.2 ppm (1.6–16.6); NH_4, 1.4 ppm (0.8–2.8). None of these factors were correlated ($P \leq 0.05$) with yield or other plant data. Such factors are known to influence plant yield and expression of nematode damage (8). A recent example demonstrates the effect of a range of sand content on the expression of *Heterodera glycines* damage to soybean (12). Ranges of these factors here, however, were probably too narrow to show much effect across the 16 test plots.

Relatively wide ranges in nematode population densities occurred in the plots during each season (Table 2). A few individ-

uals of a *Hoplolaimus* sp. also were found during the study.

In each season, plant data were correlated ($P \leq 0.05$) with $\log_2$-transformed *B. longicaudatus* or *P. brachyurus* densities at various times during the season (Table 3). No correlations ($P \leq 0.05$) were found between plant data and densities of other nematodes, except in 1988 when yield (kg/ha) was negatively correlated with *P. minor* density at harvest ($r = -0.519$). Although a number of negative correlations ($P \leq 0.05$) between *B. longicaudatus* or *P. brachyurus* density and soybean stand or yield were observed during the 1986–87 season, fewer relationships were evident the following season. On the other hand, little relationship between nematode density and size of young plants was observed in 1986–87, but numerous negative correlations ($P \leq 0.05$) were found in 1987–88 between size of young plants and density of nematodes, particularly *B. longicaudatus*. These relationships between density and early season growth were more apparent with top weight than with root weight. A possible explanation is that measuring top weight is relatively easier than measuring root weight because a complete root system is difficult to obtain. Early season plant size, particularly top weight, gave some indication of final yield, although there was inconsistency from season to season (Table 4). Even stand counts measured at harvest were not consistent indicators of yield (Table 4), possibly because of soybean's ability to compensate for low plant populations (22).

Although correlations between harvest yield and densities of *B. longicaudatus* throughout the season were observed here, and densities measured later in the growing season may show greater correlation with yield than densities measured earlier (15,16), densities measured at or before planting are still the most useful for predictive purposes because of the opportunity to plan control strategies (7,23). Relationships between stand count at harvest and $\log_2$-transformed nematode densities measured at planting (June) or before

TABLE 2.   Nematode population densities in soybean plots over two seasons.

	Nematodes/100 cm³ soil						
	Nov.	Mar. (Apr.)	Planting†	July	Aug.	Sept.	Harvest‡
Belonolaimus longicaudatus	0.7 (0–4)	6.2 (0–33)	4.5 (0–32)	1.9 (0–9)	2.2 (0–9)	9.1 (0–55)	3.7 (0–19)
Criconemella sphaerocephala	45.6 (2–152)	57.2 (0.3–201)	47.9 (2–159)	59.3 (0–228)	13.9 (0–66)	23.6 (0–76)	24.0 (1–118)
Meloidogyne incognita	17.6 (0–148)	0.3 (0–3)	37.0 (0–514)	22.9 (0–277)	0	1.1 (0–12)	2.9 (0–15)
Paratrichodorus minor	2.0 (0–8)	0	1.3 (0–5)	1.7 (0–7)	2.4 (0–9)	5.0 (0–17)	0.8 (0–3)
Pratylenchus brachyurus	66.3 (11–143)	26.4 (0.3–77)	9.6 (1–39)	4.0 (0–13)	4.8 (0–18)	35.9 (2–109)	67.0 (5–243)
P. brachyurus§	—	—	—	10.4 (0–26)	6.5 (0.6–20)	45.7 (0–417)	56.8 (6–356)
Xiphinema sp.	0	0	1.8 (0–14)	0.5 (0–2)	0.6 (0–5)	0	0.3 (0–2)
			1987–88				
Belonolaimus longicaudatus	1.8 (0–7)	4.8 (0–32)	5.4 (0–34)	17.8 (0–83)	10.6 (0–41)	19.1 (0–73)	10.2 (0–33)
Criconemella sphaerocephala	25.7 (1–135)	25.4 (1–125)	4.0 (1–16)	11.2 (0–85)	9.3 (1–45)	4.4 (0–38)	0.5 (0–2)
Meloidogyne incognita	15.6 (0–102)	0.9 (0–5)	15.2 (0–199)	6.4 (0–37)	6.6 (0–39)	16.2 (0–89)	49.4 (1–227)
Paratrichodorus minor	0.4 (0–2)	0.3 (0–2)	2.3 (0–18)	0	0	0	3.2 (0–11)
Pratylenchus brachyurus	75.3 (4–173)	18.6 (4–60)	19.9 (0–69)	1.8 (0–7)	6.3 (0–23)	17.4 (4–35)	24.3 (3–73)
P. brachyurus§	—	—	—	9.3 (1–42)	15.8 (0–60)	94.3 (28–378)	151.4 (29–319)
Xiphinema sp.	0.4 (0–1)	1.8 (0–9)	0	0.6 (0–3)	0.7 (0–5)	0	0.2 (0–1)

Data are means and ranges (in parentheses) from 16 plots on each sampling date.
† Planting dates: 2 June 1987, 10 May 1988.
‡ Harvest dates: 13 October 1987, 26 October 1988.
§ Population density per gram dry weight of root. Dashes indicate root populations not measured.

planting (November or April) are summarized for the 1986–87 season (Table 5). In addition, soybean yield in 1987 was negatively correlated ($P \leq 0.10$) with the $\log_2$ of *P. brachyurus* density measured in November 1986 ($r = -0.489$). Other relationships between yield and nematode densities in November, April, or June of the 1986–87 season were not significant even at $P \leq 0.10$, nor were any relationships between stand count or yield and preplant nematode densities during the 1987–88 season. Where significant correlations existed, relationships could be described by linear models (Table 5), but in one case a quadratic model resulted in an improved

fit over the linear model (i.e., significant increase in r^2 at $P \leq 0.05$). Attempts to relate yield data to multiple regression functions of *B. longicaudatus* and *P. brachyurus* densities or to *B. longicaudatus, P. brachyurus,* and other nematodes did not improve correlations over the linear regression models.

Linear relationships ($P \leq 0.05$) occurred between preplant nematode densities and stand count in the 1986–87 season but not in 1987–88. Overall, plant growth in the first season was much poorer, resulting in mean yields of 1,845 kg/ha, compared with 2,992 kg/ha in 1988 (Table 1). Means and ranges in population densities of the more

TABLE 3. Correlation coefficients between plant data for a given season and log$_2$-transformed densities of *Belonolaimus longicaudatus* or *Pratylenchus brachyurus* measured at selected times during that season.

Time of measurement	Belonolaimus longicaudatus				Pratylenchus brachyurus			
	Stand count	Yield (kg/ha)	Dry top wt (July)	Dry root wt (July)	Stand count	Yield (kg/ha)	Dry top wt (July)	Dry root wt (July)
				1986–87				
Nov.	NS	NS	NS	NS	−0.620*	−0.489	NS	NS
Apr.	−0.624**	NS	NS	NS	−0.532*	NS	NS	NS
June (planting)	−0.548*	NS	NS	NS	NS	NS	NS	NS
July	−0.791**	−0.637**	NS	−0.538*	NS	−0.447	NS	−0.623*
July†	—	—	—	—	NS	NS	NS	NS
Aug.	NS	NS	NS	NS	−0.466	NS	NS	NS
Aug.†	—	—	—	—	NS	NS	NS	NS
Sept.	−0.623**	−0.517*	NS	NS	−0.488	NS	NS	NS
Sept.†	—	—	—	—	−0.588*	NS	NS	NS
Oct.	−0.477	NS	NS	NS	NS	NS	NS	NS
Oct.†	—	—	—	—	NS	NS	NS	NS
				1987–88				
Oct. (1987)	NS	NS	−0.607*	−0.478	NS	NS	NS	NS
Nov.	NS	NS	−0.621*	−0.454	NS	NS	NS	NS
Mar.	NS	NS	−0.526*	NS	NS	NS	NS	NS
May (planting)	−0.472	NS	NS	NS	NS	NS	NS	NS
July	NS	NS	−0.466	NS	NS	NS	NS	NS
July†	NS	−0.456	−0.639**	−0.509*	NS	−0.493	NS	NS
Aug.	NS	NS	−0.517*	NS	NS	NS	−0.564*	−0.536*
Aug.†	—	—	—	—	−0.556*	−0.556*	−0.508*	NS
Sept.	NS	NS	−0.514*	NS	NS	NS	NS	NS
Sept.†	—	—	—	—	NS	−0.544*	NS	NS
Oct. (1988)	NS	NS	−0.499*	NS	NS	NS	−0.514*	−0.653**
Oct. (1988)†	—	—	—	—	NS	NS	NS	NS

Correlation coefficients for 16 observations. *, ** denote significance at $P \leq 0.05$, and $P \leq 0.01$, respectively. Coefficients significant at $P \leq 0.10$ are unmarked. NS = not significant. Dashes indicate correlation not evaluated.
† Nematode density per gram dry weight of root.

TABLE 4. Correlation coefficients between plant data from soybean plots for two seasons.

	Stand count	Yield (kg/ha)	Dry top weight (July)
		1986–87	
Dry root weight (July)	0.693**	0.884**	0.863**
Dry top weight (July)	0.576*	0.745**	
Yield (kg/ha)	0.781**		
		1987–88	
Dry root weight (July)	NS	NS	0.938**
Dry top weight (July)	NS	0.510*	
Yield (kg/ha)	NS		

Correlation coefficients for 16 observations. *, ** denote significance at $P \leq 0.05$ and $P \leq 0.01$ respectively. NS = not significant.

damaging nematode species such as *B. longicaudatus* and *P. brachyurus*, however, were similar at and before planting in both seasons (Table 2). It is possible that the later planting date (2 June 1987 vs. 10 May 1988) could be responsible at least in part for the poor growth of Davis soybean during the first season. In addition, rainfall, which was similar during May, June, and July in both years, was greater in 1988 during August (38 vs. 14 cm) and September (28 vs. 9 cm).

Nematode population dynamics: In each season numerous positive correlations ($P \leq 0.05$) were found between pairs of log$_2$-transformed *B. longicaudatus* densities measured at different times of the year (Table 6). Positive correlations ($P \leq 0.05$) also were found frequently between *C. sphaeroceph-*

TABLE 5. Summary of regression equations for relationships between stand count at harvest and nematode densities at or before planting for the 1986–87 season.

Dependent variable (y)	Independent variable (x)[†]	Coefficient of determination (r^2)[‡]	Regression equation[§]
Stand count (plants/6 m)	BL, Nov.	NS	
Stand count (plants/6 m)	BL, Apr.	0.389**	y = 49.2 − 5.23x
Stand count (plants/6 m)	BL, June	0.300*	y = 48.5 − 5.68x
Stand count (plants/6 m)	PB, Nov.	0.384*	y = 113.2 − 12.47x
Stand count (plants/6 m)	PB, Nov.	0.681**	y = 112.2 + 72.41x − 7.77x²
Stand count (plants/6 m)	PB, Apr.	0.283*	y = 60.7 − 5.11x
Stand count (plants/6 m)	PB, June	NS	

† Log_2 of (population density + 1)/100 cm³ soil of *Belonolaimus longicaudatus* (BL) or *Pratylenchus brachyurus* (PB).
‡ Coefficients based on 16 observations. *, ** denote significance at $P \le 0.05$, and $P \le 0.01$, respectively. NS = not significant.
§ Regression equations were computed only for relationships having significant ($P \le 0.05$) correlation coefficients. Quadratic regression equation shown only for case in which a significant ($P \le 0.05$) increase in r^2 was provided over the linear model.

ala densities, between *M. incognita* densities, and occasionally between *P. brachyurus* densities, but never between *P. minor* densities (data not shown). Negative correlations ($P \le 0.05$) were not found between density of one species and that of another species, and positive correlations ($P \le 0.05$) between species were rare.

For predictive purposes in planning cropping sequences, knowledge of the relationship between final (Pf) and initial (Pi) population densities on the crop is essential (7). The opportunity existed here to relate Pf (October) to each of several choices of Pi measured at or before planting: Pi at planting (May or June), preplant Pi in March or April (end of cover crop) or the previous November (at planting of cover crop), or in the case of the 1988 season, Pi in October at the end of the previous (1987) crop. A summary of these relationships for the most common nematode species present in the plots (Table 7) revealed stronger and more consistent relationships between Pf and Pi for the ectoparasites *B. longicaudatus* and *C. sphaerocephala* than for the endoparasites *P. brachyurus* and *M. incognita*. Relationships between Pf and Pi were more consistent for *B. longicaudatus* than for *C. sphaerocephala*, which declined under

TABLE 6. Correlation coefficients between log_2-transformed *Belonolaimus longicaudatus* densities measured at selected times during each of two seasons.

Time of measurement	Nov.	Mar. (Apr.)	May (June)	July	Aug.	Sept.
			1986–87			
Apr.	0.736**					
June	0.797**	0.851**				
July	0.564*	0.856**	0.800**			
Aug.	NS	0.550*	NS	0.532*		
Sept.	0.561*	0.835**	0.866**	0.862**	0.546*	
Oct.	0.654**	0.833**	0.867**	0.830**	0.629**	0.959**
			1987–88			
Mar.	0.852**					
May	0.805**	0.920**				
July	0.803**	0.793**	0.774**			
Aug.	0.858**	0.886**	0.899**	0.918**		
Sept.	0.817**	0.899**	0.908**	0.893**	0.974**	
Oct.	0.859**	0.915**	0.904**	0.904**	0.971**	0.973**

*, ** denote significance at $P \le 0.05$ and $P \le 0.01$, respectively. NS = not significant.

TABLE 7. Summary of regression equations for relationships between final nematode densities at harvest (October) and densities measured at or before planting for two growing seasons.

Dependent variable (y)† (October)	Independent variable (x)†	Coefficient of determination (r²)‡		Linear regression equation‡	
		1986–87	1987–88	1986–87	1987–88
BL	BL, previous Oct.	—	0.736**		y = 0.82 + 1.12 x
BL	BL, Nov.	0.427**	0.738**	y = 0.66 + 1.30 x	y = 0.79 + 1.49 x
BL	BL, Mar. (Apr.)	0.695**	0.838**	y = 0.12 + 0.71 x	y = 0.67 + 1.12 x
BL	BL, planting§	0.751**	0.816**	y = 0.006 + 0.87 x	y = 0.62 + 1.06 x
PB	PB, previous Oct.	—	NS		
PB	PB, Nov.	0.375*	NS	y = −0.43 + 1.02 x	
PB	PB, Mar. (Apr.)	0.375*	NS	y = 3.57 + 0.49 x	
PB	PB, planting§	NS	0.311*		y = 2.60 + 0.42 x
CS	CS, previous Oct.	—	0.211		
CS	CS, Nov.	0.456**	0.302*	y = 1.20 + 0.57 x	y = 1.11 − 0.18 x
CS	CS, Mar. (Apr.)	0.470**	0.339*	y = 1.49 + 0.49 x	y = 1.19 − 0.20 x
CS	CS, planting§	0.605**	NS	y = 0.74 + 0.66 x	
MI	MI, previous Oct.	—	0.226		
MI	MI, Nov.	NS	0.707**		y = 1.70 + 0.96 x
MI	MI, Mar. (Apr.)	NS	NS		
MI	MI, planting§	0.195	0.296*		y = 2.94 + 0.63 x

† Log_2 of (population density + 1)/100 cm³ soil of *Belonolaimus longicaudatus* (BL), *Pratylenchus brachyurus* (PB), *Criconemella sphaerocephala* (CS), or *Meloidogyne incognita* (MI).
‡ *, ** denote significance at $P \leq 0.05$, and $P \leq 0.01$, respectively. Coefficients significant at $P \leq 0.10$ are unmarked. NS = not significant. Dashes indicate not evaluated. Linear regression equations derived only for cases significant at $P \leq 0.05$.
§ Planting dates: 2 June 1987, 10 May 1988.

soybean cultivation and reached near zero levels after two seasons (Table 2).

Where relationships ($P \leq 0.05$) existed between Pi and Pf (Table 7), they were roughly linear. When there were linear relationships between Pf and each of several different Pi measurements for a particular nematode species within a season, these relationships often had fairly similar slopes and intercepts (Table 7). The linear equations for *C. sphaerocephala* obtained in 1987–88 are unusual in that the slopes are negative, reflecting the decline to near zero levels in most plots during that season.

In several instances, quadratic relationships provided significant ($P \leq 0.05$) increases in r^2 over linear models (Table 8). This was true for the relationship between Pf of *B. longicaudatus* and Pi measured at planting in each season. Although there is typically much variability in population densities measured in field plots, the improved fits of quadratic over linear models for *B. longicaudatus* over the range of Pi examined (Fig. 1) suggest the tendency for Pf to level off at an equilibrium density, as described by theoretical models (24) for density-dependent population growth. Linear models, observed with most nematodes here (Table 7), could arise when the range of densities observed in the field does not include the relatively high Pi values needed for density-dependent intraspecific competition and the resultant leveling off of Pf at an equilibrium density (14). The leveling off of *B. longicaudatus* Pf at high Pi values, as indicated in this study, was not observed on maize, on which density-independent population growth was observed (14). Because mature maize plants and root systems are much larger than those of soybean, a given *B. longicaudatus* population would take a higher proportion of the resources from a soybean root system, and thus resource limitation would occur first on the smaller plant.

Perhaps the relative lack of severe crop damage allowed us to observe only a few hints of intraspecific competition and no evidence of interspecific competition.
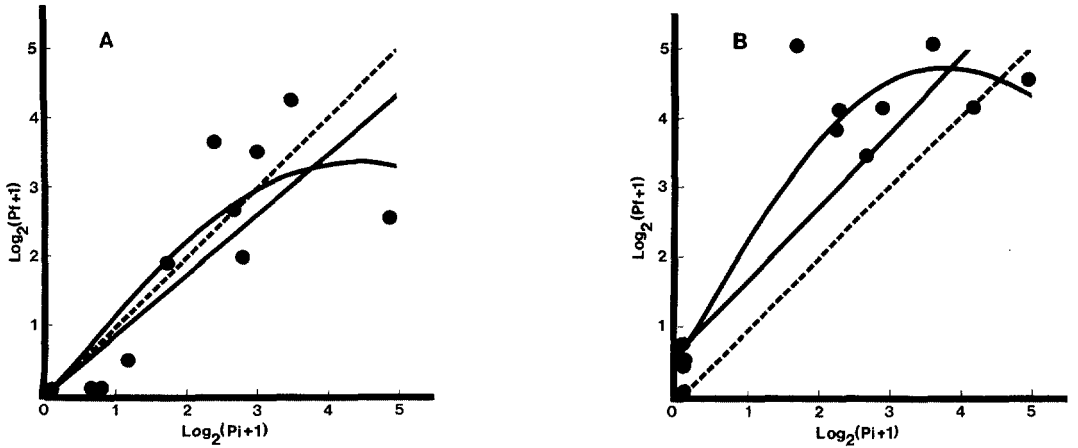
FIG. 1. Relationship between *Belonolaimus longicaudatus* density at harvest (y = log$_2$ [Pf + 1]) and initial density at planting (x = log$_2$ [Pi + 1]). Dashed line is maintenance line, with y = x. A) 1987. Linear regression equation: y = 0.006 + 0.87x, r^2 = 0.751; quadratic regression equation: y = −0.26 + 1.61x − 0.18x^2, r^2 = 0.822. B) 1988. Linear regression equation: y = 0.62 + 1.06x, r^2 = 0.816; quadratic regression equation: y = 0.34 + 2.28x − 0.30x^2, r^2 = 0.937.

Thus, critical point models (7) of nematode population multiplication could be developed independently for each species under these conditions. Final densities and population growth rates of *B. longicaudatus* were greater in 1988 than in 1987 (Fig. 1). This difference may have been the result of the longer time from planting to harvest (5½ months in 1988 vs. 4½ months in 1987).

Although the experimental design used provided substantial ranges in Pi for several species (Table 2) and the opportunity to observe plant response to these ranges in the field, relatively little severe plant damage was observed. Occasional negative correlations ($P \leq 0.05$) occurred between yield and densities of *B. longicaudatus* or *P. brachyurus* measured during the growing season. Expression of damage to soybean by *P. brachyurus* may be strongly influenced by cultivar (20), and possibly the differences in planting date with the same cultivar (Davis) also could have had an important influence, as shown elsewhere with 'Forrest' soybean (13). The maximum Pi of *P. brachyurus* observed here (up to 173/ 100 cm^3 soil), however, was still lower than the 200–2,000/100 cm^3 for which yield losses to soybean in microplots are predicted by a quadratic model (20). *Belono-*

TABLE 8. Quadratic relationships between initial (x) and final (y) nematode densities that provide significant ($P \leq 0.05$) increase in r^2 over corresponding linear models.

Dependent variable (y)† (October)	Independent variable (x)†	r^2 for linear model‡	r^2 for quadratic model‡	Quadratic regression equation
		1986–87		
BL	BL, planting§	0.751**	0.822**	y = −0.26 + 1.61 x − 0.18 x^2
		1987–88		
BL	BL, Mar.	0.838**	0.948**	y = 0.36 + 2.27 x − 0.28 x^2
BL	BL, planting§	0.816**	0.937**	y = 0.34 + 2.28 x − 0.30 x^2
MI	MI, Mar.	NS	0.501*	y = 4.18 − 5.31 x + 2.61 x^2

† Log$_2$ of (population density + 1)/100 cm^3 soil of *Belonolaimus longicaudatus* (BL) or *Meloidogyne incognita* (MI).
‡ *, ** denote significance at $P \leq 0.05$ and $P \leq 0.01$, respectively. NS = not significant.
§ Planting dates: 2 June 1987, 10 May 1988.

laimus longicaudatus Pi of up to 34/100 cm³ were associated with some stand reduction, but not with consistent yield reductions, yet similar population densities in an adjacent field caused severe damage to maize (14). The severe damage of *B. longicaudatus* to maize seedlings is well documented (4). Stand reduction (from optimum row spacings) in maize results in fewer ears produced and lower yield (5), but in many cases the soybean plant can compensate for stand reduction by producing large plants, resulting in little or no reduction in yield (22). Thus, it is not particularly surprising that thresholds of a stand-reducing pest like *B. longicaudatus* should be higher on a host that can compensate for stand reduction than on a host that cannot.

Plots with a range of nematode densities within a field provide an opportunity for deriving plant damage functions under more realistic growing conditions, relative to microplots. However, since Pi is arbitrary and controlled in microplot studies, a much wider range of densities can be used. Thus, in designing field plots over infield density gradients, the main emphasis must be on maximizing the range of Pi available; consequently, only some fields will be suitable for such studies. The 16 plots used here provided a considerable range in nematode densities (Table 2), but an even wider range in Pi would have been desirable and may have shown more effects on yield. We chose to minimize variation in Pi by taking three replicate samples from each plot when determining Pi. Although this approach was helpful in reducing the scatter of points around regression lines, perhaps a preferable allocation of sampling effort would have been to establish more plots, taking only single samples from each. Although more variability in counts would be expected, more opportunity for a greater range of Pi also would be available, permitting the development of more detailed critical point models of the relationship between plant damage and Pi. However, the triplicate sampling scheme used and the resultant stabilization of density estimates probably accounts for our success in developing numerous critical point models relating Pf to Pi, and it may be the preferable approach in population dynamics studies.

LITERATURE CITED

1. Appel, J. A., and S. A. Lewis. 1984. Pathogenicity and reproduction of *Hoplolaimus columbus* and *Meloidogyne incognita* on 'Davis' soybean. Journal of Nematology 16:349–355.

2. Baird, S. M., and E. C. Bernard. 1984. Nematode population and community dynamics in soybean–wheat cropping and tillage regimes. Journal of Nematology 16:379–386.

3. Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Science 42:225–229.

4. Christie, J. R. 1959. Plant nematodes. Their bionomics and control. Agricultural Experiment Station, University of Florida, Gainesville.

5. Dickson, D. W., and T. E. Hewlett. 1987. Effect of two nonfumigant nematicides on corn grown in two adjacent fields infested with different nematodes. Annals of Applied Nematology (Journal of Nematology 19, Supplement) 1:89–93.

6. Esser, R. P., J. B. MacGowan, and H. M. Van Pelt. 1965. Two new nematode subsampling tools. Plant Disease Reporter 49:265–267.

7. Ferris, H. 1985. Density-dependent nematode seasonal multiplication rates and overwinter survivorship: A critical point model. Journal of Nematology 17:93–100.

8. Ferris, H. 1978. Nematode economic thresholds: Derivations, requirements, and theoretical considerations. Journal of Nematology 10:341–350.

9. Freund, R. J., and R. C. Littell. 1981. SAS for linear models. A guide to the ANOVA and GLM procedures. SAS Institute, Cary, NC.

10. Ibrahim, K. A., and S. A. Lewis. 1985. Host-parasite relationships of *Meloidogyne arenaria* and *M. incognita* on susceptible soybean. Journal of Nematology 17:381–385.

11. Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease Reporter 48:692.

12. 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. Journal of Nematology 20:373–380.

13. Koenning, S. R., D. P. Schmitt, and K. R. Barker. 1985. Influence of planting data on population dynamics and damage potential of *Pratylenchus brachyurus* on soybean. Journal of Nematology 17:428–434.

14. McSorley, R., and D. W. Dickson. 1989. Effects and dynamics of a nematode community on maize. Journal of Nematology 21, in press.

15. McSorley, R., and J. L. Parrado. 1985. Relative performance of two cassava cultivars in a field infested with *Meloidogyne incognita*. Soil and Crop Science Society of Florida Proceedings 44:180–183.

16. McSorley, R., and J. L. Parrado. 1986. Rela-

tionship between height of kenaf and root galling by *Meloidogyne incognita.* Nematropica 16:205–211.

17. Nardacci, J. F., and K. R. Barker. 1979. The influence of temperature on *Meloidogyne incognita* on soybean. Journal of Nematology 11:62–70.

18. Rhue, R. D., and G. Kidder. 1983. Procedures used by the IFAS Extension Soil Testing Laboratory and interpretation of results. Circular 596, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

19. Rodríguez-Kábana, R., and J. C. Williams. 1981. Determination of soybean yield losses caused by *Meloidogyne arenaria* and *Heterodera glycines* in a field infested with the two parasites. Nematropica 11:93–104.

20. 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.

21. Schmitt, D. P., and G. R. Noel. 1984. Nematode parasites of soybeans. Pp. 13–59 *in* W. R. Nickle, ed. Plant and insect nematodes. New York: Marcel Dekker.

22. Scott, W. O., and S. R. Aldrich. 1970. Modern soybean production. Champaign, IL: S & A Publications.

23. Seinhorst, J. W. 1965. The relation between nematode density and damage to plants. Nematologica 11:137–154.

24. Seinhorst, J. W. 1966. The relation between population increase and population density in plant parasitic nematodes. I. Introduction and migratory nematodes. Nematologica 12:157–169.

25. Sinclair, J. B., ed. 1982. Compendium of soybean diseases. St. Paul: The American Phytopathological Society Press.

26. Sokal, R. R., and F. J. Rohlf. 1969. Biometry. San Francisco: W. H. Freeman and Company.