The Influence of Temperature on *Meloidogyne incognita* on Soybean[1]

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Abstract: The effects of temperature and initial inoculum density of *Meloidogyne incognita* on soybean growth and nematode reproduction were investigated in greenhouse temperature tanks and in controlled-growth chambers. The interactions of initial inoculum density (P_i) and soil temperature in effects on shoot growth were adequately described by multiple-regression models. At the highest temperatures (30 or 32/28 C), moderate to high inoculum killed many plants. A P_i of 27,000 eggs/15-cm-diam pot retarded shoot growth at 26 C. Only the greatest P_i (81,000 eggs/15-cm pot) suppressed shoot growth at 18, 22, or 20/16 C. Inoculation with 3,000 or 9,000 eggs/plant resulted in heavier root systems at all temperatures except 30 C. At that temperature, 9,000 eggs suppressed root growth. At 18 and 26 C, a P_i of 81,000 eggs was required to retard root growth. Nematode reproduction was related directly to temperature and P_i except at a density of 81,000 eggs/15-cm pot. *Key Words: Glycine max*, root-knot, population dynamics.

Meloidogyne incognita (Kofoid and White) Chitwood poses a serious problem in the production of soybean, *Glycine max* (L.) Merr., in the coastal-plain area of the southern United States (24). Most research on this problem has involved rating cultivars for disease resistance (6), reporting of disease incidence (9, 16, 17), and evaluating nematicides (15). Kinloch (15) found that about 40% of soybean fields sampled in Florida were infested with *M. incognita*. Soybean yields of susceptible and resistant cultivars were respectively suppressed by 53–90% and 32–40%.

Relatively little has been done to determine the relationship between soybean yield and initial population density (P_i) of *M. incognita* (18). In a greenhouse experiment, Ibrahim et al. (13) found that 2,000 larvae/15-cm-diam pot resulted in shoot dry weights of 'Lee 68' soybeans that were slightly less than in healthy plants. Field plots with P_i of 15 larvae/100 cm^3 of soil treated with 1,3-dibromo-3-chloropropane (DBCP) yielded 840 kg/ha more than controls on root-knot-susceptible 'Pickett 71' (15).

These studies did not include any measure of the influence of temperature on this host-parasite relationship. The general ef-

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fects of temperature on the reproduction of *Meloidogyne* spp. have been demonstrated (3, 23, 25). Godfrey (10) determined the critical temperature for reproduction of an unknown *Meloidogyne* species on soybeans to be 28 C. Dropkin (8) suggested that *M. incognita acrita* reproduces well on soybeans at temperatures between 24 and 35 C, depending on host cultivar.

Temperature may affect nematode reproduction directly, although it also acts indirectly by influencing plant growth (22). Since larger vigorously growing plants can support greater nematode populations (1, 22), temperature can modify the relationship between P_i and P_f (final nematode population density). The influence of environment on the relationship between tomato growth and P_i of *M. incognita* has been documented (2).

Although field experimentation is necessary to establish realistic threshold densities, greenhouse and growth-chamber studies are useful for indicating basic nematode-host interactions. The experiments reported herein were designed to determine the effects of temperature on the reproduction of *M. incognita* on soybeans, and to ascertain the effect of temperature on the relationship between soybean growth and initial nematode inoculum level.

MATERIALS AND METHODS

Preparation of Inoculum and Culture of Plants: Inoculum for the greenhouse temperature-tank experiment was obtained from tobacco roots grown in microplots at the Central Crops Research Station in Clayton, North Carolina. For the phytotron experiment, 3-week-old 'Manapal' tomato (*Lycopersicum esculentum* Mill.) seedlings were transplanted to 15-cm-diam clay pots containing a 1:1 mixture of methyl-bromide-treated Norfolk sandy-loam and 65-mesh silica sand with a greatest mean diam of 245 μm. Plants were inoculated by dispensing a suspension of about 20,000 eggs of *M. incognita* around the roots. A solution of VHPF (Miller Chemical and Fertilizer Corp., Hanover, PA) supplemented with 1.2×10^{-3} mM of KNO_3, 1.9×10^{-3} mM of $MgSO_4$, and 1.6×10^{-5} mM of H_3BO_3 was supplied semiweekly or as needed. Eggs were extracted from roots of tobacco or 75-to-90-day-old tomato by a NaOCl technique (12). Eggs were counted with a stereoscopic microscope, and desired inoculum densities were prepared.

Unless stated otherwise, soybean [*Glycine max* (L.) Merr.] cv 'Lee 68' seedlings were transplanted singly to 15-cm-diam pots containing 1,500 cm^3 of the potting mixture. At transplanting, 200 mg of a commercial preparation of *Rhizobium japonicum* (Kirch.) Buchanan (Nitragin: Nitragin Co., Milwaukee, WI) were added around the roots. Modified VHPF was added to each pot 1 or 2 days after transplanting. Plants were watered as needed with half-strength Hoagland's solution (11) minus nitrogen, or with tap water. Water was added daily to bring the soil moisture to about 8% by weight as determined with an Agtronic soil moisture meter (Agtronics Co., Barstow, CA).

Experimental design and statistical analysis: A complete random block design was used in both experiments with six replicates per treatment. At the end of each experiment, the plants were harvested and data recorded as: 1) shoot dry weight (105 C for 3 days); 2) root fresh weight; and 3) final nematode numbers. The final population densities of larvae and males (P_f) in the soil were determined by thoroughly mixing the soil from each pot, taking a 500-cm^3 subsample, and processing with a combination of elutriation (4) and centrifugal flotation (14). Eggs were extracted from roots by the method of Byrd et al. (5).

Analyses of variance were used to test the significance of P_i or temperature and the interaction of these variables in effects on plant growth and final nematode densities. Regression analyses were used to determine relationships when P_i and temperature interacted to influence plant growth. These relationships were fitted to linear or quadratic models, and the choice of best fit was based on tests of significance. A $\log_{10}(X + 1)$ transformation of nematode numbers was used in these analyses to stabilize variance and to facilitate handling of nematode data.

Temperature-tank experiment: Seed were germinated in vermiculite for 5 days, at which time the seedlings were transplanted into 15-cm-diam plastic pots containing 1,500 cm^3 of the potting mixture.

Various densities of *M. incognita* were established by dispensing a 50-ml egg suspension or water into 10 holes around the base of the plant to give 0, 3,000, 9,000, 27,000, or 81,000 eggs/pot.

Pots were placed in Wisconsin-type temperature tanks maintained at 18, 22, 26, and 30 C with ambient temperature ranging from 20 to 35 C. Each pot was equipped with a drainage system consisting of a plastic fitting in the bottom of the pot attached to Tygon tubing (0.64 cm I.D.) connected to a central drain in the tank. Each tank had a heating and cooling system, and a pump for water circulation. Multi-vapor lamps (225 hlx) provided long-day (14 h) illumination for the first 28 days, and supplemental lighting for the remainder of the experiment. The experiment was terminated at 90 days. At 30 C, however, some of the plants died before that time, so data were collected upon plant death.

Phytotron experiment: In a growth-chamber experiment, 2-day-old seedlings, germinated in vermiculite in a 27.5 C incubator, were transplanted to 90-cm^3 Dixie paper cups containing 75 cm^3 of the soil mixture. Seedlings were maintained in the greenhouse at 26/22 C (alternating day/night temperature). At 7 days, the seedlings with root balls intact were transferred to 15-cm-diam clay pots with 1,500 cm^3 of the potting mixture. Immediately before transplanting, the soil in each pot had been infested with 0, 9,000, 27,000, 54,000, or 81,000 eggs of *M. incognita*.

The pots were placed in "C-type" growth chambers (7) and were maintained at alternating day/night ambient temperatures of 32/28, 28/24, 24/20, or 20/16 C. Soil temperatures closely paralleled those ambient temperatures. A combination of T-12 1,500-ma cool white fluorescent and Krypton-filled incandescent filament lamps provided an illuminance of 430 to 480 (hlx). The plants were grown under long-day (14 h) conditions for 28 days, and then maintained at short days (10 h) for 54 days (harvest). Many plants died under the two highest temperature regimes before the 82nd day, and data were collected upon plant death.

RESULTS

Temperature-tank experiment: Soil temperature and initial inoculum density (P_i) greatly affected the growth of shoots and roots. Dry weight of shoots was related inversely to temperature and P_i (Fig. 1). The interaction between P_i and soil temperature on shoot growth ($P = 0.01$) was adequately described by a multiple-regression model (Fig. 1). At 30 C, 100, 100, 67, and 33% of plants respectively inoculated with 81,000, 27,000, 9,000, and 3,000 eggs of *M. incognita* died before the experiment was terminated. All control plants survived. Shoot dry weights of plants grown at 26 C respectively inoculated with 27,000 or 81,000 eggs were 34 and 72% less than those of controls. At 22 and 18 C, a P_i of 81,000 eggs was required to suppress shoot growth.

Root weights increased with temperature from 18 to 26 C, but were lowest at 30 C. Root weights were greater than those of controls at P_i's of 3,000, 9,000, and 27,000 (Table 1). A P_i of 81,000 suppressed root growth. There was also an interaction of P_i and soil temperature with root growth (Table 1). Root fresh weights were greater ($P = 0.05$) than those of controls at a P_i of 9,000 eggs at all temperatures except 30 C. At 30 C, a P_i of 9,000, 27,000, or 81,000 eggs resulted in root weights that were respectively 36, 39, and 77% less than those of controls. A P_i of 3,000 eggs generally stimulated root growth. Initial densities of 81,000 eggs were required to suppress root growth at 18 and 26 C. On the basis of fresh weight, however, *M. incognita* did not depress root growth at 22 C.

Reproduction of *M. incognita* at 30 C was greatest when P_i was 3,000 (Table 2). Nematode reproduction was depressed at 18 C, and was insufficient to maintain ($P_i = P_f$) the population at the highest density. P_i was highly correlated with the P_f of larvae plus eggs. At harvest, larvae and adult males were few in numbers compared with egg populations (Table 3). The highest temperature yielded the greatest number of all stages counted. The relationship of P_i and P_f (for eggs and larvae) for each temperature was reasonably described by a quadratic model (Fig. 2-A). On the basis of these models, equilibrium densities ["E"

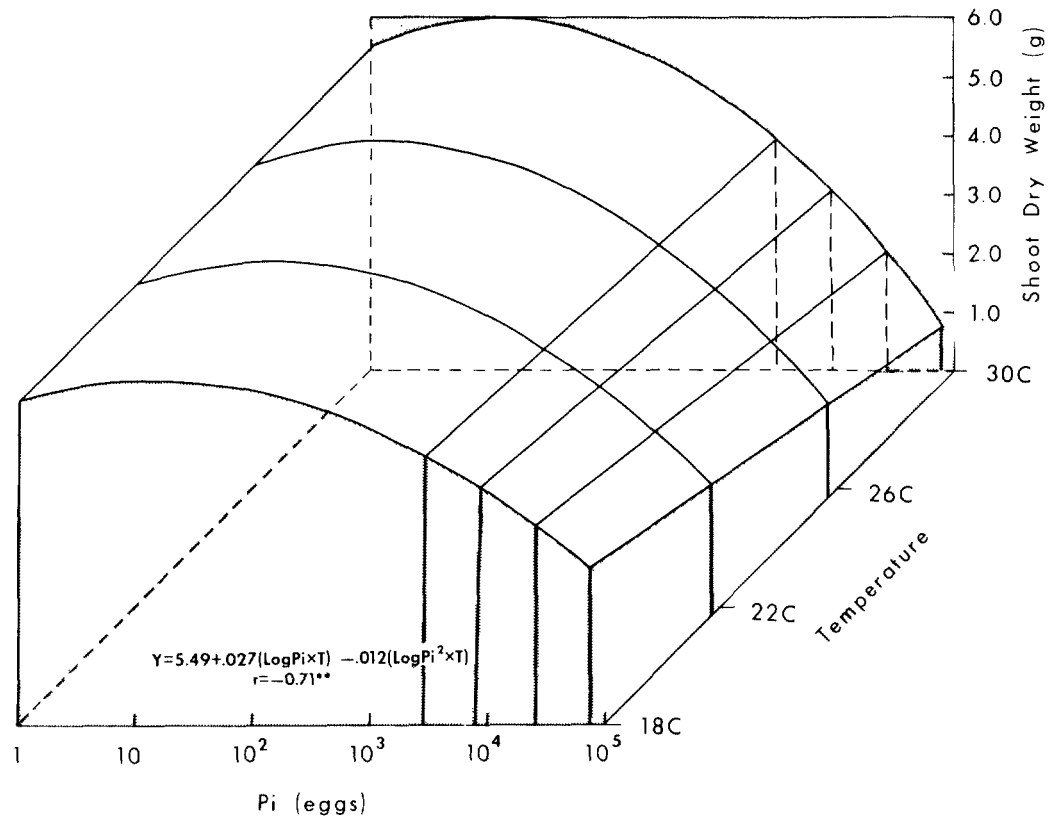

FIG. 1. Relationship of initial inoculum density (P_i) of *Meloidogyne incognita* and temperature to growth of soybean in the greenhouse.

TABLE 1. Influence of inoculum density and temperature on root growth of soybean.

Inoculum density (eggs in 1,000's/pot)	Root fresh wt. (g) per temperature				
Temperature tank:	18 C	22 C	26 C	30 C	Mean
0	5.9	6.8	8.4	7.7	7.2
3	6.8	9.5	8.5	11.2	9.0
9	10.0	10.5	14.3	4.9	9.9
27	8.4	10.2	14.2	4.7	9.4
81	3.9	6.8	7.4	1.8	5.0
Mean	7.0	8.8	10.5	6.1	8.1
LSD:				P = 0.05	P = 0.01
Temperature				2.1	2.9
P_i				1.5	2.0
Interaction (Temp × P_i)				3.0	4.0
Phytotron expt.:	20/16[a]	24/20	28/24	32/28	Mean
0	5.9	5.4	6.8	6.4	6.1
9	7.3	7.6	8.6	10.2	8.4
27	7.4	8.0	9.6	9.8	8.7
54	8.9	8.2	9.6	10.7	9.3
81	5.5	9.0	7.6	7.7	7.4
Mean	7.0	7.6	8.4	9.0	8.0
LSD:				P = 0.05	P = 0.01
Temperature				1.3	NS
P_i				1.6	2.1
Interaction (Temp × P_i)				NS	—

[a]Temperatures alternate day/night. Data are means of six replicates.

TABLE 2. Reproductive factors (R) of *Meloidogyne incognita* on soybean as affected by inoculum density and temperature.

Inoculum density (eggs in 1,000's/pot)	$R(P_f/P_i)$ per temperature			
Temperature tank:	18 C	22 C	26 C	30 C
0	0	0	0	0
3	2.9	9.7	17.7	83.7
9	2.7	11.0	17.5	16.8
27	1.0	8.7	12.9	10.7
81	0.2	2.6	3.4	2.9
LSD:			P = 0.05	P = 0.01
Temperature			4.6	6.1
P_i			5.2	6.9
Interaction (Temp × P_i)			10.4	13.7
Phytotron expt.:	20/16 C[a]	24/20 C	28/24 C	32/28 C
0	0	0	0	0
9	0.8	9.1	20.0	33.7
27	0.9	7.5	12.7	18.9
54	0.8	5.0	7.9	12.7
81	0.5	2.8	4.7	7.7
LSD:			P = 0.05	P = 0.01
Temperature			1.4	1.8
P_i			1.5	2.0
Interaction (Temp × P_i)			3.1	4.0

[a]Temperatures alternate day/night. Data are means of six replicates. P_f include eggs and larvae.

(death rate = birth rate) is the point where the curve crosses the maintenance line] for this nematode at 18, 22, 26, and 30 C were respectively about 20,000, 320,000, 650,000, and 180,000.

There was a significant (P = 0.01) interaction between P_i and temperature in effects on nematode reproduction. The P_f of larvae plus eggs increased with P_i, except for 3,000 at 30 C and 81,000 at all temperatures. Reproduction was greatest at 30 C, but that reflects the high reproductive rate at that temperature at a P_i of 3,000.

TABLE 3. Relative numbers of larvae, eggs, and males of *Meloidogyne incognita* on soybean as affected by temperature.

Experiment & temperature	P_f in 1,000's/1,500 cm³ soil (pot)		
	Larvae	Larvae + eggs	Males
Temperature tank:			
18 C	0.2	19	0.1
22	1.1	144	0.1
26	3.2	209	0.4
30	5.9	232	0.4
LSD @ $P=0.01$	1.7	80	0.1
Phytotron expt.:			
20/16 C[a]	0.1	29	0.2
24/20 C	0.3	196	0.3
28/24 C	1.4	333	0.9
32/28 C	2.8	532	1.3
LSD @ $P=0.01$	0.8	79	0.7

[a]Temperatures alternate day/night.

Phytotron experiment: Temperature and initial inoculum density (P_i) affected plant growth (Fig. 3). Dry weights of shoots were greater at 28/24 and 24/20 C than at the two temperature extremes, and were inversely related to P_i. The interaction of P_i and temperature with shoot growth (P = 0.01) was adequately described by a multiple-regression model (Fig. 3). All nematode-infected plants grown in the 32/28 C temperature regime died before the end of the experiment. At 28/24 C, respectively 33, 67, and 67% of plants died when inoculated with 81,000, 54,000, and 27,000 eggs. All control plants survived at both of those temperatures. A P_i of 9,000 eggs was sufficient to suppress shoot weight by 44% at 28/24 C. At 24/20 C a P_i of 54,000 eggs suppressed shoot weight by 42%, whereas at 20/16 C a P_i of 81,000 eggs caused an 82% suppression.

Root fresh weights were positively re-

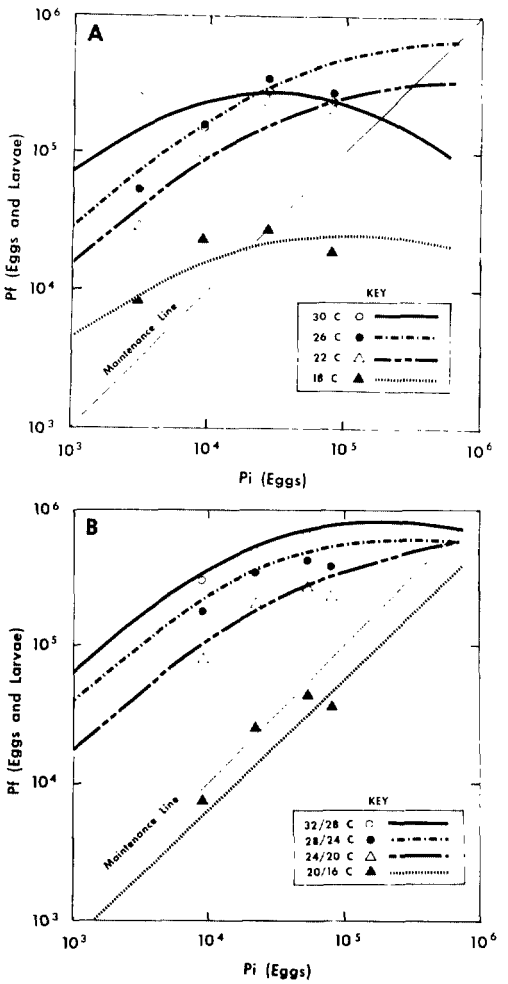

FIG. 2. (A-B). Effects of initial inoculum density (P_i) on the reproduction of *Meloidogyne incognita* at four temperatures. (Maintenance line: $P_i = P_f$). *A*) Greenhouse temperature-tank experiment. Respective quadratic regression models are:

30 C $P_f = -0.007 + 2.42(\text{Log}P_i) - 0.27(\text{Log}P_i)^2$ $r = 0.99^{**}$

26 C $P_f = -0.005 + 1.99(\text{Log}P_i) - 0.17(\text{Log}P_i)^2$ $r = 0.99^{**}$

22 C $P_f = -0.008 + 1.88(\text{Log}P_i) - 0.16(\text{Log}P_i)^2$ $r = 0.99^{**}$

18 C $P_f = -0.007 + 1.73(\text{Log}P_i) - 0.17(\text{Log}P_i)^2$ $r = 0.97^{**}$

B) Phytotron experiment. Respective quadratic regression models are:

32/28 C $P_f = -0.0003 + 2.23(\text{Log}P_i) - 0.21(\text{Log}P_i)^2$ $r = 0.99^{**}$

28/24 C $P_f = -0.0007 + 2.10(\text{Log}P_i) - 0.19(\text{Log}P_i)^2$ $r = 0.99^{**}$

24/20 C $P_f = -0.001 + 1.86(\text{Log}P_i) - 0.15(\text{Log}P_i)^2$ $r = 0.99^{**}$

20/16 C $P_f = 0.01 + 0.95(\text{Log}P_i)^2$ $r = 0.98^{**}$

lated to temperature, and increased with P_i except at the highest P_i (Table 1).

Final densities and reproductive rates of *M. incognita* increased with temperature increments (P = 0.01) (Fig. 2-B, Table 2). Those relationships were adequately described by quadratic models for temperature regimes of 32/28, 28/24, and 24/20 C. A linear regression equation characterized the relationship best at 20/16 C, but that temperature regime allowed the maintenance of the initial population only at a P_i of 27,000. Few males and larvae were recovered as compared with eggs (Table 3). On the basis of the quadratic models, the equilibrium densities on a total plant basis were similar: 24/20 = 550,000; 28/24 = 600,000; 32/28 = 725,000. Final densities increased with P_i except at the highest density (81,000 eggs).

Nematode reproduction interacted significantly with P_i and temperature. For larvae plus eggs, P_f increased with P_i for all temperatures except at densities of 81,000 eggs of *M. incognita*. Again, the reproductive factor was greatest at the highest temperature and lowest P_i.

DISCUSSION

A recent review (1) offers a thorough discussion of the terminology and schemes used to designate a host as good or poor for a given nematode species. Oostenbrink's (19) reproductive factor (R) provides a basic measurement of the nematode's reproductive capabilities. Seinhorst (21) used the equilibrium density (E) and maximum rate of reproduction (a) to determine host status. Quantitative characterization of relationships in this manner provides fundamental models for predicting nematode reproduction. Most studies involving environmental factors add to knowledge of the requirements for nematode species, although many fail to characterize the relationship between P_i and P_f.

In the present study, the equilibrium density and the reproductive factor for *M. incognita* on soybean were greatly influenced by temperature. At the lowest temperatures (18 and 20/16 C) both E and R were low, probably the result of poor growth of the host plant, although the direct effect of temperature on nematode infection and development should also be

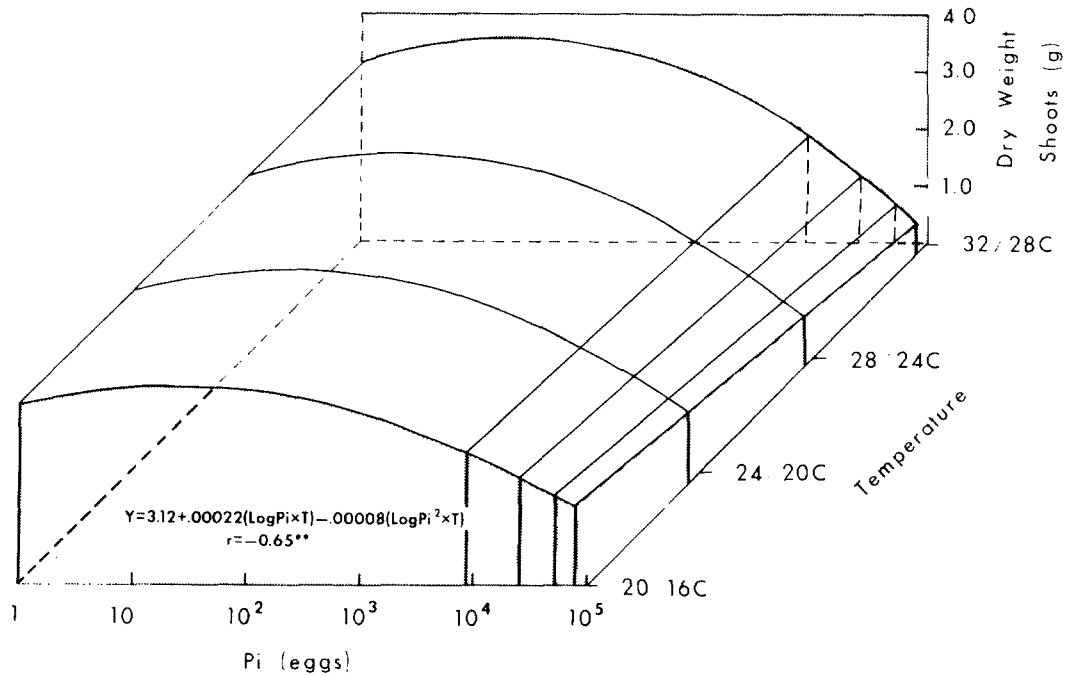

FIG. 3. Relationship of initial inoculum density (P_i) of *Meloidogyne incognita* and temperature to soybean growth in a Phytotron.

recognized. Under conditions optimum for plant growth, both E and R were high. Optimum temperatures seem to signify an overlap in the requirements of both host and parasite for growth and development (10). These results are consistent with other reports. Rates of reproduction for different populations of four *Meloidogyne* spp. on tomato were greater at 25–32 C than 20–21 or 15–16 C (23). Godfrey (10) suggested the optimum temperature for an unknown *Meloidogyne* sp. on soybean to be 28 C.

Meloidogyne incognita acrita has been shown to reproduce well at temperatures as high as 35 C (8). The present results, however, suggest this to be possible only at low initial nematode densities. Since R was so great at the highest temperatures (30 and 32/28 C), one would expect extensive root damage to have limited nematode feeding sites, causing a subsequent drop in E. That situation developed in the temperature tanks but not in the growth chambers. In the phytotron experiment, soybean seedlings had been held in the greenhouse for 7 days before transplanting to nematode-infested soil. Those plants with additional feeding sites were more tolerant of initial nematode infection, resulting in a higher E than for the younger plants in the temperature tanks. This result supports the suggestion (22) that plant size or age is more important than temperature.

R decreased as P_i increased at the highest temperatures, indicating that competition for feeding sites was a limiting factor. At low temperatures, the change in R with increasing P_i was slight, signifying poor nematode infection and/or development. On the basis of equilibrium density and the reproductive factor, soybean would be considered a good host at all temperatures studied above 18 or 20/16 C. External factors, such as temperature, influence the relationship between P_i and P_f directly and also by their action on the host, as suggested by Seinhorst (21).

The close correlation between P_i and crop response or yield has been established (1, 2, 19, 20, 26). The environment has a strong influence on this relationship. According to Wallace (27), crop failures are often most serious when some environmental stress coincides with nematode infection. Barker et al. (2) demonstrated that fact in determining the relations between P_i and damage to tomato at two locations in North Carolina. Under condi-

tions favorable for plant growth, losses to *M. incognita* were slight. In contrast, when temperatures were high, rainfall moderate, and soil coarse-textured, nematode damage was severe. Although controlled-environment experiments may not be directly related to field tests, the present results point toward a similar relationship for *M. incognita* on soybeans. Negative correlations of P_i and temperature versus shoot growth were highly significant ($P = 0.01$) as shown by multiple-regression analyses. The tolerance level of soybean appears to be low (1,000 eggs/500 cm^3 of soil) at high temperatures, but extremely high at low temperatures. [Previous studies indicate that only about 20% of larvae are infective when hatched from eggs extracted in NaOCl (12)]. Ibrahim et al. (13) demonstrated that 2,000 larvae of *M. incognita*/pot were required to cause a slight loss of shoot dry weight of 'Lee 68' soybean. Stress conditions were not provided in that study, so a higher tolerance level would be expected.

The multiple-regression models developed for P_i and temperature have only a limited potential. Soybeans do not normally die from root-knot nematode infection. Some of the initial densities and temperatures used in these tests are probably higher than a young plant encounters in the field. Nevertheless, it is evident that the effect of initial density on final density or crop response is modified by temperature. Further, these parameters are interrelated in such a way that the precise effect of each on the other must be carefully determined. Additional information from field and/or microplots is needed before the effects of P_i, temperature, and rainfall can be integrated into a useful model for predicting soybean yield.

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