Factors Affecting the Biology and Pathogenicity of *Heterodera schachtii* on Sugarbeet[1]

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Abstract: A direct relationship exists between soil temperature and *Heterodera schachtii* development. The average developmental period of two nematode populations from Lewiston, Utah, and Rupert, Idaho, from J2 to J3, J4, adult, and the next generation J2 at soil temperatures of 18–28 C were 100, 140, 225, and 399 degree-days (base 8 C), respectively. There was a positive relationship ($P < 0.05$) between nematode Pi, nematode generations, and sugarbeet yields. The greatest sugarbeet growth inhibition (87%) occurred when sugarbeets were exposed to a Pi of 12 eggs/cm³ soil for five generations (1,995 degree-days), compared with a 47% inhibition when plants were exposed to the same Pi for two generations. There was a negative correlation ($P < 0.05$) between the Pi, Pf, and sugarbeet yield for each population threshold. The smaller the Pi, the greater the sugarbeet yields and the greater the Pf. Root yields were 80 and 29 t/ha and Pf were 8.4 and 3.6 eggs/cm³ soil when sugarbeet seeds were planted at Pi of 0.4 and 7.9 eggs/cm³, respectively, at a soil temperature of 8 C. The number of years rotation with a nonhost crop required to reduce the nematode population density below a damage threshold level of 2 eggs/cm³ depends on the Pi. A Pi of 33.8 eggs/cm³ soil required a 5-year crop rotation, whereas a Pi of 8.4 eggs/cm³ soil required a 2-year crop rotation.

Key words: basal thermal temperature, *Beta vulgaris*, damage threshold population, degree-day, final population density, *Heterodera schachtii*, initial population density, nematode generation, reproduction, soil temperature, sugarbeet cyst nematode, yield.

The sugarbeet cyst nematode, *Heterodera schachtii* Schmidt, found in most sugarbeet producing areas of the world, is one of the most damaging pathogens on sugarbeet (19,23). Climatic conditions vary considerably between sugarbeet growing regions of the world, from hot desert areas to coastal regions and high mountain regions. Sugarbeets are planted from late fall to early spring, depending on the growing area. This variability in climatic conditions results in differences in the damage threshold levels of *H. schachtii*. Cooke and Thomason (5) found the "tolerance limit" in the Imperial Valley of California to be 1 egg/g soil. The threshold levels in south central Idaho and eastern Oregon were 2.0 and 3.5 eggs/g soil, respectively (11). The threshold level in Holland was 3–8 eggs/g soil (14). In England, where monthly temperatures never exceeded 17 C, the threshold level was 10–20 eggs/g soil (15). Steudel and Thielmann (24) reported that the critical economic population density in

Germany was 20 eggs and juveniles/cm³ soil when sugarbeets were planted the first of April, but dropped to 2.5 eggs and juveniles/cm³ soil when plantings were delayed until the middle of May.

Several studies have shown a direct relationship between soil temperature at time of planting, *H. schachtii* soil population density, and sugarbeet yields (5,11,18,21). Tyler (26) studied the effect of soil temperature on nematode development and equated nematode development with heat units. Other studies have used degree-days as a basis for computing heat units (1,6,7,29).

Since temperature appears to affect the relationship of *H. schachtii* to the growth of sugarbeet, studies were made to determine 1) the temperature requirement for nematode development in degree-days, and if the required degree-days are consistent over a given range of temperatures; 2) how sugarbeet production is affected by differences in nematode development and reproduction (generations per year); and 3) the relationship between initial nematode inoculum (Pi), sugarbeet yields, and final nematode populations (Pf), and how Pf may affect crop rotation.

MATERIALS AND METHODS

Soil temperature and H. schachtii development: Nematode inoculum (population 1) was collected originally from a nematode-infested field at Lewiston, Utah, and cultured on sugarbeet under controlled greenhouse conditions. Inoculum was obtained by extracting cysts with an elutriator (2) and hatching juveniles (J2) in a sugarbeet root diffusate at 25 C. Nematodes were decanted daily, rinsed, and maintained at 5 C in distilled water. Inoculum was never held longer than 5 days before use.

Germinated sugarbeet (*Beta vulgaris* cv. Tasco AH-3) seeds were planted into methyl bromide-sterilized sandy loam soil (91% sand, 5% silt, 4% clay; pH 8.4) in 10-cm-d plastic containers (four seeds per container). Fourteen-day-old transplants were inoculated with 200 *H. schachtii* J2 per seedling and grown in temperature-controlled growth chambers at 2-C increments from 16 to 30 C. Twenty-four hours after inoculation, seedlings were carefully removed from the containers, washed free of soil, transplanted into methyl bromide-treated soil in a similar container, and returned to the chambers.

Starting 24 hours after transplanting, four plants were harvested from each temperature at 12-hour intervals and stained in hot lactoglycerol (1:1:1: lactic acid : glycerol : distilled water) and acid fuchsin, and the nematode developmental stage was determined (17,25). This procedure was continued until egg production was observed at all soil temperatures. Eggs were placed in sugarbeet root diffusate, and the time to hatch was recorded.

Data was analyzed by ANOVA and a linear regression analysis. The reciprocal of the number of days required for development of each life stage was plotted against the temperature for each population, and the basal threshold for development and its relationship to the basal temperature for hatch and invasion (3,11,27) were determined. Data were converted to degree-days (1,6,7,29) for each temperature. Since pathological and race differences in nema-

tode populations of cyst nematodes have been observed (9,20), the experiment was repeated using similar experimental methods and analysis with a collection (population 2) from Rupert, Idaho.

Nematode inoculum and reproduction and sugarbeet yields: To determine the relationship between nematode Pi and reproduction (generations per year) and the growth of sugarbeet, 14-day-old Tasco AH-3 sugarbeet seedlings in 15-cm-d plastic containers filled with sandy loam soil (one plant per container, replicated six times) were inoculated with 0, 4, 8, and 12 eggs/cm³ soil and grown in temperature-controlled water baths. Using data obtained from the nematode development study, the periods of growth were adjusted to obtain two, three, four, and five nematode generations before harvest: 17 C for 88.7 days = two generations; 21 C for 92.1 days = three generations; 25 C for 93.9 days = four generations; and 28 C for 99.8 days = five generations. These temperatures were chosen to eliminate disparity in growth time between treatments. After completion of each nematode generation, plants were harvested, root yields obtained, and the data analyzed with a two-way ANOVA (Pi × D-D) and a linear regression analysis.

Because environmental conditions vary from year to year within a given geographical area, the relationship of sugarbeet yield to different nematode Pi were studied over a 3-year period (1979–81) in nontreated control microplots at Logan, Utah. The number of accumulated degree-days per growing season was used as an indicator of climatic differences. Degree-days (1,7,29) were obtained from data collected with temperature-recording thermographs at a depth of 15 cm. Microplots were 3.0 × 4.3 m, with a sandy loam soil (73% sand, 17% silt, 10% clay; pH 7.8–8.4) with different 3-year Pi ranges of 2.1–3.2 (mean = 2.5) and 6.9–8.3 (mean = 7.7) eggs/cm³ soil.

Microplot Pi were determined by collecting soil samples on 30-cm centers to a depth of 30 cm with a 1.75-cm-d Oakfield probe. Cysts were extracted with an elutriator (2), separated from soil debris by

alcohol flotation (22), and crushed in water in a Potter Elvehjem Type tissue grinder to facilitate the egg counts. Microplot fertility was determined by the Utah State Testing Laboratory in Logan, and fertilizer was added as recommended for commercial production (110 ppm potash, 60 ppm nitrates, 20 ppm phosphates) immediately before planting. Sugarbeets were planted on 56-cm row spacings, and thinned to 25-cm plant spacings after 28 days. No herbicides were used, and the plots were hand weeded. Plots were irrigated with a sprinkler irrigation system, 2.5–3.0 cm water immediately after planting, and subsequently as needed. Treatments were replicated six times. Harvest root weights were converted to metric tons per hectare. Data were analyzed with a two-way ANOVA (Pi × D-D), and multiple comparisons were made.

Relationships between Pi, Pf, and sugarbeet yields: Tasco AH-3 sugarbeet seeds were planted into *H. schachtii*-infested microplots (3.05 × 4.27 m) with nematode Pi of 0.0, 1.2, 2.4, 4.3, 6.4, and 7.9 eggs/cm^3 soil at planting soil temperatures of 8, 12, 16, and 20 C at a depth of 15 cm. Nematode-infested soil was added to noninfested plots or plots were fallow cultivated to obtain the desired initial population densities. Each treatment was replicated six times, and agronomic practices used were similar to those previously described for other microplot studies. Plants were grown for 143, 131, 118, and 107 days when seeds were planted at 8, 12, 16, and 20 C, respectively. At harvest, root weights were converted to metric tons per hectare, microplots were rototilled to evenly disperse nematode cysts, and soil samples were collected to determine Pf values. Data were analyzed using a linear regression analysis.

Nematode population densities and required length of crop rotation: Field studies were conducted over a 5-year period. Four fields previously planted to sugarbeet or a nonhost crop in Lewiston, where the damage threshold level is approximately 2 eggs/cm^3 soil (11), were chosen for study. Spring sampling showed Pi of 8.4, 15.7, 22.3, and

33.8 eggs/cm^3 soil in the different fields. Replicated plots, 15 × 60 m, were marked off in each field and replicated six times. The 5-year cropping system for each field consisted of barley, alfalfa, wheat, corn, and barley. Standard agronomic practices were used and fields were furrow irrigated. Following harvest, the plots were plowed. Soil Pf determinations were made on soil samples as described for microplots immediately before spring plantings. Data were analyzed using ANOVA and mean separation with LSD ($P < 0.05$) over the 5-year period.

RESULTS

Soil temperature and H. schachtii development: There was a direct relationship between soil temperature and the number of days required for nematode development. Degree-days required for development of populations 1 and 2 were not significantly different ($P < 0.05$) at soil temperatures of 18–28 C, which differed significantly ($P < 0.05$) from degree-days at 16 and 30 C. There were no consistent differences in the basal thermal threshold (base) for either population 1 or 2. The base for development was 6.62 ± 0.48 for population 1 and 6.00 ± 0.64 for population 2, with an average of 6.3 ± 0.65 for the two populations. The minimum soil temperature for hatch and invasion is greater than 6.3 C (3,11,27) and must be considered in choosing a base temperature for the overall nematode life cycle. Hence a base of 8 C was chosen to determine the number of degree-days required for nematode development from J2 to J2. Respective degree-day requirements from J2 to J3, J4, adult, and the next J2 generation at 18–28 C were 94, 133, 219, and 390 for population 1 from Lewiston and 105, 147, 231, and 408 for population 2 from Rupert (Fig. 1). At the same temperatures, the average degree-days requirements for both populations from J2 to J3, J4, adult, and the new J2 were 100, 140, 224, and 399 degree-days, respectively. Maximum variation in degree-days for development of J2 to J3, J4, adult, and new J2 for population 1 was
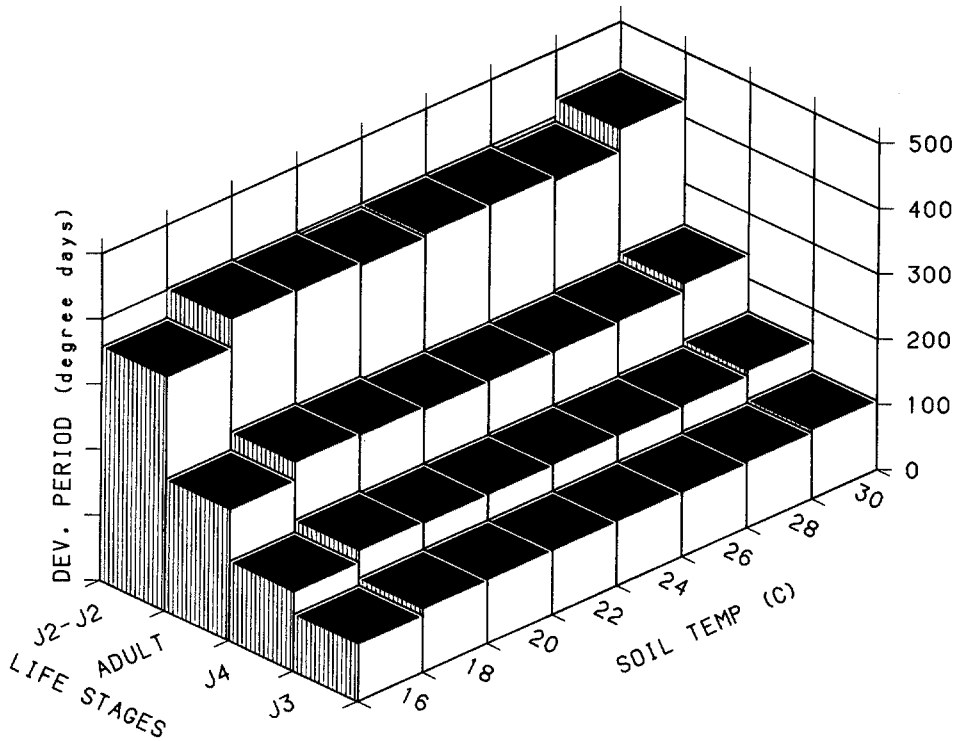
FIG. 1.   Average length of life cycle in degree-days (D-D) of two *Heterodera schachtii* populations at different soil temperatures (no significant difference among soil temperatures). ANOVA LSD ($P < 0.05$) soil temperature × developmental stages = 12.75; developmental stage × soil temperature = 9.01.

4, 7, 14, and 14 degree-days, respectively at 18–28 C. This increased to 13, 29, 34, and 61 degree-days, respectively, at 16–30 C. The average length of time required of combined populations 1 and 2 to a complete nematode generation differed from 45.2 days at 16 C to 18.9 days at 30 C (Fig. 2). Linear regression R^2 for the different live stages were 0.956, 0.954, 0.979, and 0.983 for J3, J4, adult, J2/J2, respectively.

Nematode inoculum density, nematode reproduction, and sugarbeet root yields—greenhouse: There was a significant relationship ($P < 0.05$) between nematode Pi, nematode generations per year, and sugarbeet yields. The greater the Pi and nematode generation, the greater the reduction in sugarbeet root yields (Fig. 3). The greatest significant ($P < 0.05$) reduction in sugarbeet growth (percentage of noninoculated controls) occurred when the seedlings were exposed to *H. schachtii* Pi of 12 eggs/cm³ soil for five nematode generations (1,995 degree-days). There were reduc-

tions in root growth of 60, 76, and 87% at inoculum levels of 4, 8, and 12 eggs/cm³ soil, respectively, after the five generations. At Pi of 4, 8, and 12 eggs/cm³ soil, respective growth reductions were 49, 65, and 76% for four generations (1,596 degree-days); 38, 52, and 63% for three generations (1,197 degree-days); 22, 32, and 47% for two generations (798 degree-days).

Field: Data similar to that found in the greenhouse study were found under field conditions (Fig. 4). There was a direct relationship ($P < 0.05$) between inoculum densities, degree-days, and sugarbeet root yields; the greater the nematode inoculum densities and the greater number of degree-days, the greater the reduction in root yields.

Relationships between Pi, Pf, and sugarbeet yields: Nematode Pi and planting soil temperature were negatively correlated ($P < 0.05$) with sugarbeet yields. The greatest root yields occurred in early planted plots (8 C) with the lowest Pi, poorest root yields
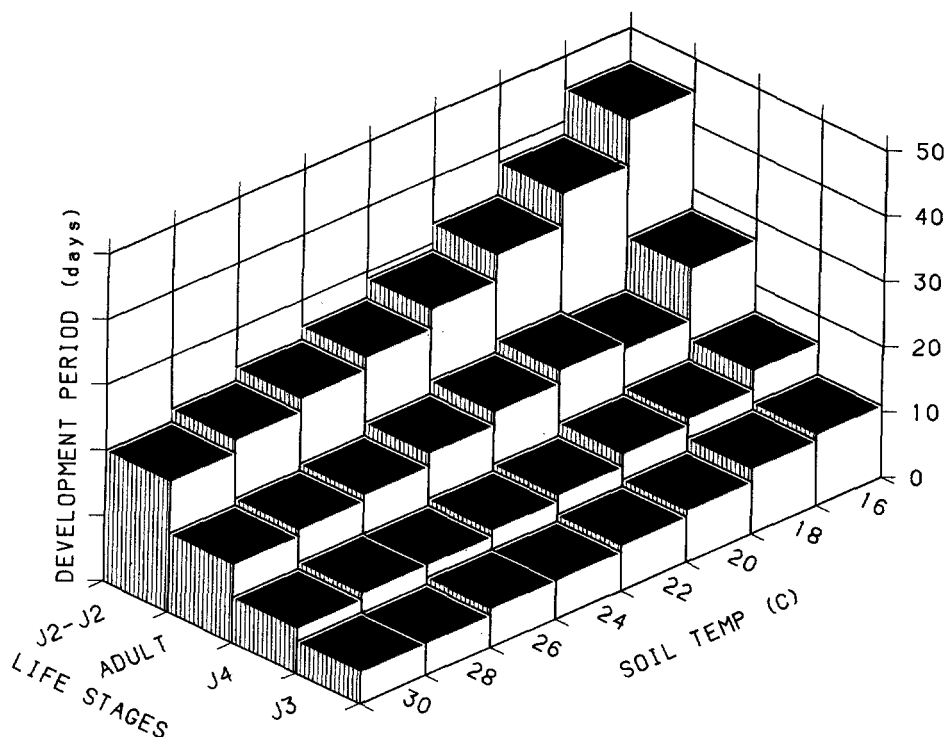
FIG. 2. Number of days required for life cycle development of *Heterodera schachtii* at different soil temperatures. Linear regression R^2 (developmental period × soil temperature) J3 = 0.956; J4 = 0.954; adult = 0.979; J2/J2 = 0.983.

occurred in late planted plots (20 C) with the greatest Pi (Fig. 5), and sugarbeet yields were positively correlated ($P < 0.05$) to Pf. There was also a negative correlation ($P < 0.05$) between Pi and Pf (Fig. 6).

Nematode population densities and required length of crop rotation: The annual reduction in the nematode Pi under the croppings of nonhosts was ca. 50–60% under barley, wheat, and corn and 40–50% under alfalfa. However, the period of rotation required to reduce the nematode population below the threshold level differed for each Pi. Two, three, four, and five years were required to reduce population densities below 2.0 eggs/cm³ soil at initial Pi of 8.4, 15.7, 23.3, and 33.8 eggs/cm³ soil, respectively (Table 1).

DISCUSSION

Several studies have shown that *H. schachtii* Pi and soil planting temperature affect sugarbeet yields (5,10,11,14,15,24) and that the damage threshold level is affected by soil temperature at time of planting. Steudel and Thielmann (24) stated that the critical economic population density changed from 20 eggs and juveniles/cm³ soil in April to 2.5 in May because of differences in soil temperature at planting. The simulation model of the effect of *H. schachtii* on sugarbeet yields developed by Caswell et al. (4) encompasses these factors. However, expressing the degree-day length of development of *H. schachtii* from J2 to J2 at a temperature range of 18–28 C also makes it possible to differentiate the ef-

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FIG. 3. Relationship of nematode inoculum density and number of nematode generations to sugarbeet yields under greenhouse conditions. ANOVA LSD ($P < 0.05$) Pi × degree-days (D-D) = 2.8; Pi × nematode generations = 3.3.

FIG. 4. Relationship of nematode inoculum density (Pi) and degree-days (D-D) to sugarbeet yields under field conditions. ANOVA ($P < 0.05$) Pi × D-D (years) = 2.4.
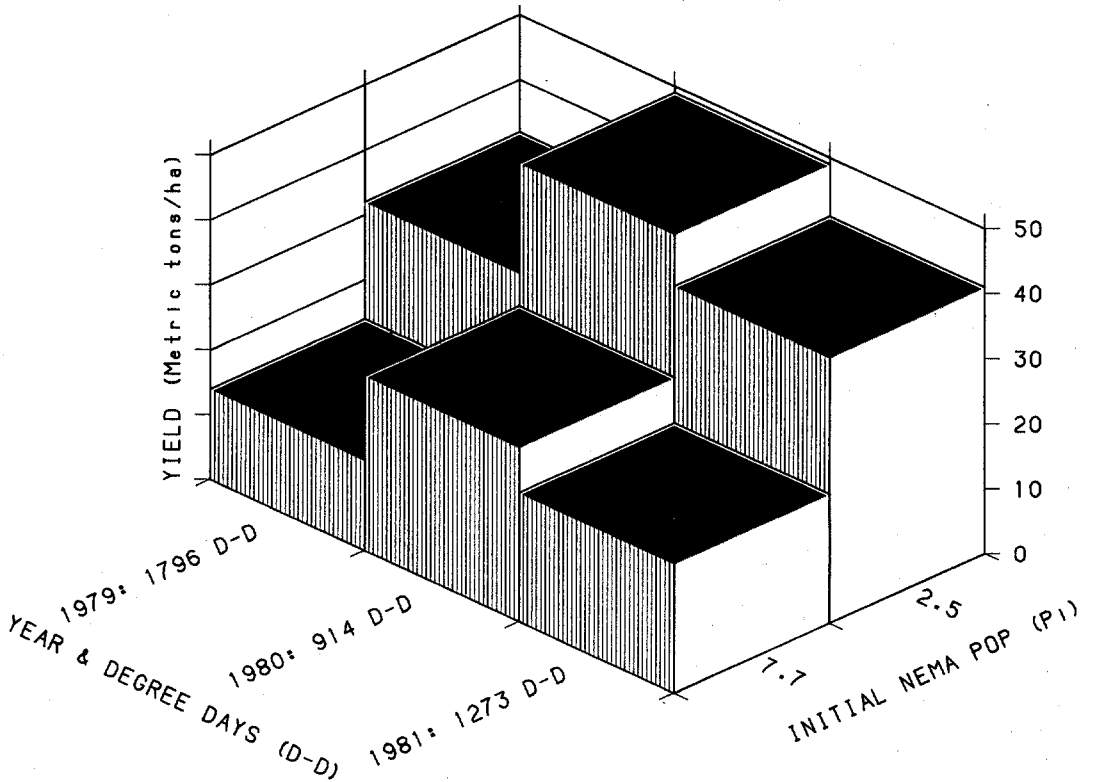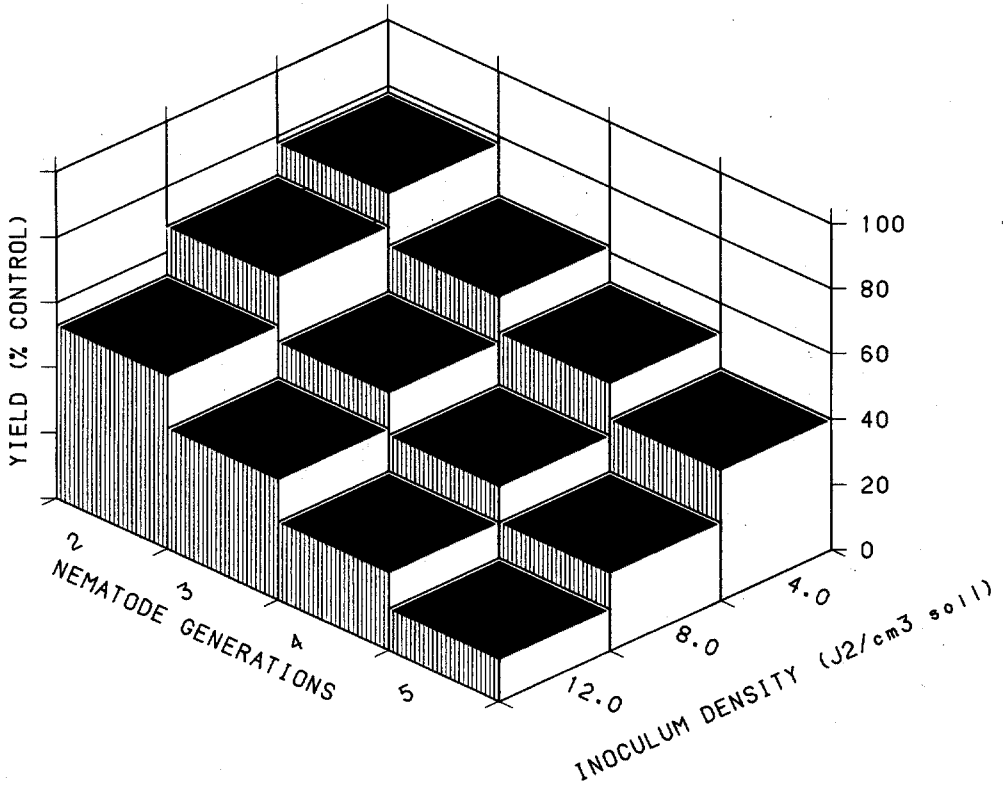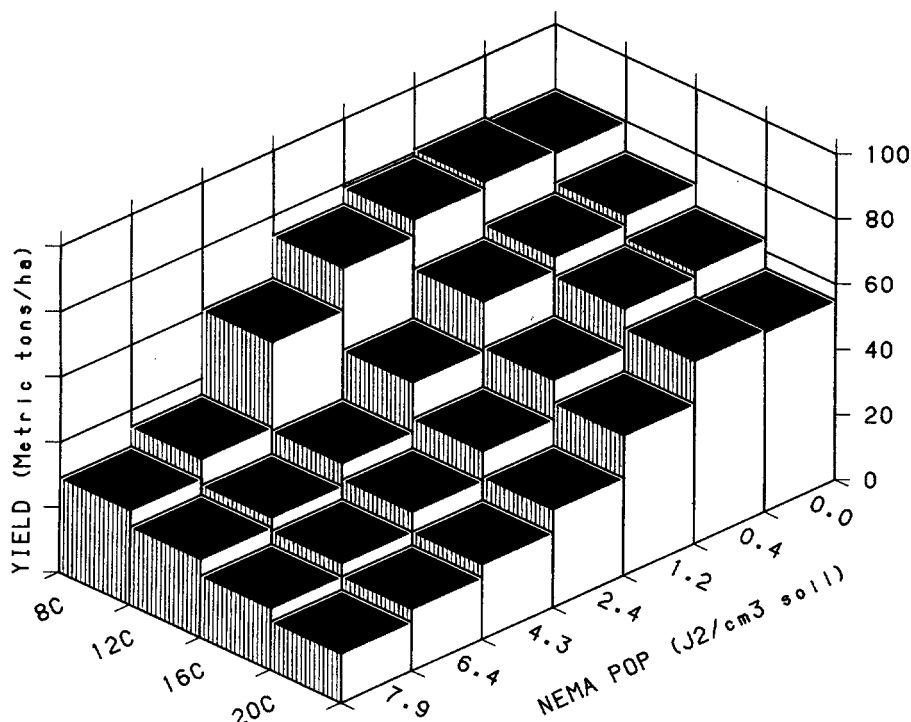
FIG. 5. Relationship of initial nematode soil populations (Pi) to sugarbeet yields as affected by soil planting temperature. Linear regression for 8 C intercept = 85.20, R^2 = 0.927; 12 C intercept = 68.49, R^2 = 0.993; 16 C intercept = 59.13, R^2 = 0.904; 20 C intercept = 51.11, R^2 = 0.863.

fect(s) of seasonal soil temperatures on the nematode–plant relationship.

Previous studies have shown that longer exposure to the nematode results in greater inhibition of root growth (5,11). Greenhouse and field experiments in this study verify these findings and explain why this occurs. Five generations of *H. schachtii* at a Pi of 12 eggs/cm³ soil resulted in a 40% greater crop loss than did two generations of nematodes at the same Pi.

Differences in the basal thermal thresholds for *H. schachtii* egg hatch and invasion of sugarbeet seedlings (11,27) and nematode development can be expected. There are several reports showing differences in the temperature requirements for hatch, activity, development, and reproduction within a given species (28). The use of a base of 8 C fit the model for nematode development, including hatch and invasion, and was consistent through a tem-

TABLE 1. Effect of nonhost cropping systems on the population decline of *Heterodera schachtii*.

Nematode Pi (eggs/cm soil)	Population decline (eggs/cm³ soil)					LSD (P < 0.05) Pf
	Year 1 barley	Year 2 alfalfa	Year 3 wheat	Year 4 corn	Year 5 barley	
8.4	3.6†	1.9	1.1	0.6	0.4	0.6
15.7	6.9†	3.7†	1.7	0.9	0.6	1.1
23.3	10.5†	5.6†	2.6†	1.3	0.8	1.7
33.8	15.9†	9.2†	4.5†	2.3†	1.1	2.3
LSD (P < 0.05)	2.9	1.5	1.0	0.7	0.4	

Figures are means of six field plots (15 × 60 m) in each of four fields of different Pi at Lewiston, Utah. Spring samples were collected immediately before field was prepared for planting.

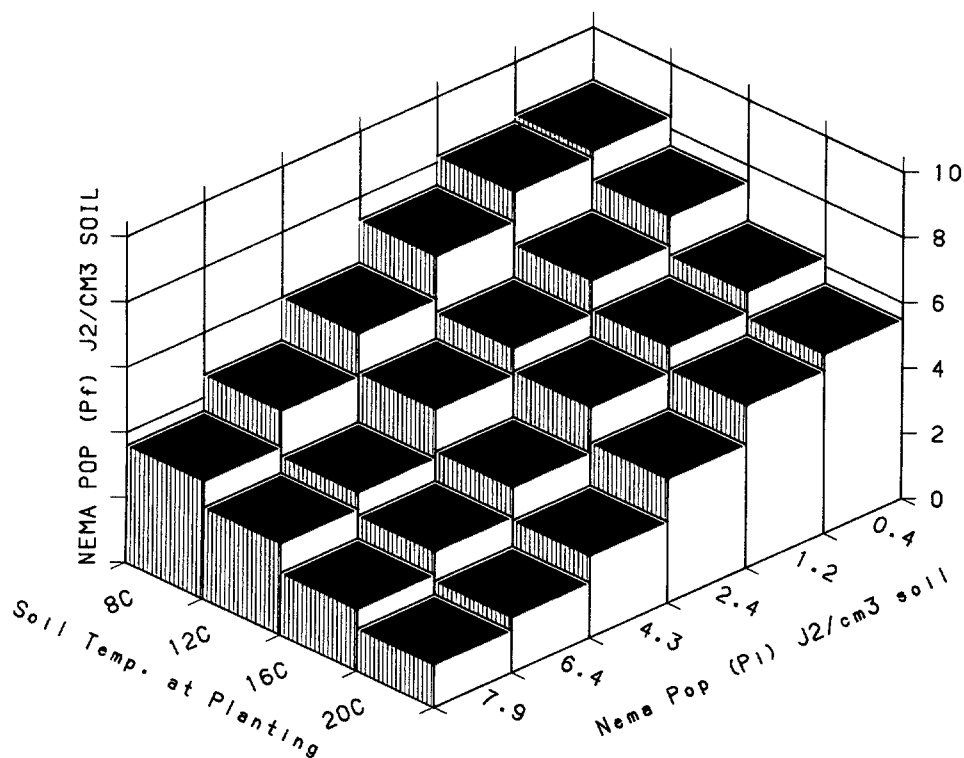† Pi exceeding damage threshold level of 2 eggs/cm³ soil.

FIG. 6. Relationship of initial nematode soil populations (Pi) to final nematode soil populations (Pf) as affected by soil temperature. Linear regression for 8 C intercept = 8.86, R^2 = 0.909; 12 C intercept = 7.36, R^2 = 0.927; 16 C intercept = 6.29, R^2 = 0.939; 20 C intercept = 5.50, R^2 = 0.923.

perature range of 18–28 C, although the thermal base temperature for development was plotted at 6.3 C.

The relationship between sugarbeet yields and Pf shows the importance of the relationship between sugarbeet growth and nematode reproduction (3,12). The positive correlation between the higher sugarbeet yield and increased nematode Pf is probably due to the effect of the reduced initial nematode Pi on sugarbeet root growth. A low degree of parasitism, resulting from a low Pi inoculum, provides for vigorous root growth on which subsequent generations can develop. This resulted in a greater overall increase in the nematode population. This hypothesis is consistent with results of a study (Griffin, unpubl.) in which soil fumigation in year 1 (Pi of 8.7 eggs/cm³ soil) resulted in a yield of 58 t/ha compared with 29 t/ha in nontreated control plots. In year 2, yields in previously nontreated plots increased to

32 t/ha compared with 23 t/ha on previously fumigated plots. The yield difference was attributed to higher Pf in treated plots in year 1. Understanding this relationship will help growers improve nematode-control methods and result in more effective crop rotations and(or) chemical control. Knowing how sugarbeet yields affect nematode population densities helps determine the length of rotation required and whether crop rotation or chemical treatment is the best control. This is, however, subject to proper cultural practices, including weed control (8).

The reduction in *H. schachtii* under nonhost crops is consistent with previous findings (13,19). This study, however, emphasizes the importance of the Pf following sugarbeet production, which determines the Pi the following year. At a constant rate of decline, the higher the nematode Pf following sugarbeet, the longer the rotation period necessary to decrease the Pi below

the tolerance level. Therefore, if the Pf is known, predictions of the rotation length needed to reduce the nematode population to the desired Pi level can be reasonably accurate. Growers can then decide whether to use crop rotation or nematicide to control *H. schachtii.* Growers should be made aware of the relationships between plants and their pathogens. The data presented here can also be used to demonstrate to growers how *H. schachtii* is related to the growth of sugarbeet and provide data useful in developing simulation models (4,16).

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