The Relationship of Plant Age, Soil Temperature, and Population Density of *Heterodera schachtii* on the Growth of Sugarbeet[1]

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Abstract: There were direct relationships between inoculum density of *Heterodera schachtii* Schm. (nematode population density), initial soil temperature, the growth of sugarbeets in the greenhouse under controlled temperatures, and nematode populations. *Heterodera schachtii* was least pathogenic on plants inoculated at 6 wk of age and most pathogenic on plants grown from inoculated germinated seed (0 wk of age). In the field, *H. schachtii* was least pathogenic on sugarbeets grown at an initial soil temperature of 6 C and most pathogenic on those grown at an initial soil temperature of 24 C. The growth period for sugarbeets at the different soil temperatures was determined by heat units; since penetration of sugarbeet roots by *H. schachtii* larvae is accelerated at soil temperatures above 10 C, each hour-degree above 10 C was counted as one effective heat unit (HU). Using this guideline it was determined that root weight depressions in the greenhouse, for each degree-unit population (HU-UP) where unit population = one larvae/g soil, were 0.052, 0.09, 0.12, and 0.17 mg at initial soil temperatures of 6, 12, 18, and 24 C, respectively. Root weight depressions were 0.28, 0.23, 0.15, and 0.086 mg when plants were inoculated at 0, 2, 4, and 6 wk of age. *Key words:* sugarbeet cyst nematode, heat units, unit populations, root weight depression, geographical differences, sugarbeet yields.

Sugarbeets are grown in the United States in wide ranges of soils and climatic conditions. Growing areas may vary from short-season continental climates with severe winters to intermediate climates in high mountain valleys to hot desert and mild coastal climates. Sugarbeets may be seeded in late winter, early spring, or early fall, depending on the geographical area.

The sugarbeet cyst nematode, *Heterodera schachtii* Schm., is the most important plant-parasitic nematode and one of the important plant pathogens affecting sugarbeet. Because of the great variation in climatic and environmental conditions under which sugarbeets are grown, there is considerable variation in the degree of pathogenicity of *H. schachtii* on sugarbeet (1,4,5,6,7,8,9,10, 12, 13, 14).

Variation in climatic and environmental conditions in geographically separated sugarbeet growing areas of the intermountain region of the western U.S. can affect the susceptibility of sugarbeet to *H. schachtii.* Therefore, a study was initiated to determine the effect of plant age, soil temperature, and initial *H. schachtii* inoculum population densities on the growth of sugarbeet.

Received for publication 14 March 1980.

[1]Cooperative investigation by USDA, SEA, AR and Utah State Agricultural Experiment Station. Journal Paper No. 2535.

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MATERIALS AND METHODS

Greenhouse studies: The effects of soil temperature and the initial *H. schachtii* inoculum density on the growth of sugarbeet were studied under controlled temperatures. Cysts of *H. schachtii* from an Idaho collection, cultured on sugarbeet in the greenhouse, were surface sterilized with 0.5% sodium hypochlorite solution, rinsed in distilled water, and hatched in a $ZnCl_2$ solution. Newly hatched larvae (2) were added to previously sterilized (bromomethane) soil which was then thoroughly mixed and diluted with sterilized soil to give initial nematode infestations of 2.5, 5.0, and 7.5 larvae/g of soil. Seven-day-old sugarbeet seedlings (Tasco AH3) were transplanted into 12.5-cm plastic containers of nematode-infested or uninfested soil and placed in temperature controlled water baths at 6, 12, 18, and 24 C. Each treatment was replicated 10 times. The plants were grown under a 19-h day with high-output fluorescent lamps.

To simulate field conditions, water bath temperatures were raised 2 C every 7 d until a maximum soil temperature of 30 C was reached; plants were maintained at 30 C until the end of the experiment. The growth period at each temperature was determined by calculating heat units. A preliminary temperature-gradient study to determine the effect of soil temperature on infection of sugarbeet seedlings by *H. schachtii* larvae showed that penetration is accelerated above 10 C. The numbers of *H. schachtii* larvae invading sugarbeet seedlings were 2, 20, 81, and 155 per plant at 6, 12, 18, and 24 C, respectively (Fig. 1). Therefore, each hour-degree above 10 C was counted as one effective heat unit (15). Plants at each temperature received 55,584 heat units which was 168.3, 147.3, 130.5, and 120 days for plants grown at initial soil temperatures of 6, 12, 18, and 24 C, respectively. Top and root weights were recorded.

To determine the relationship of plant age and initial *H. schachtii* inoculum density on the growth of sugarbeet, germinated seed and 2-, 4-, and 6-wk-old sugarbeets were transplanted into previously sterilized soil containing 2, 4, and 6 *H. schachtii* larvae/g in 15-cm plastic containers of methyl bromide-fumigated soil. Treatments, including uninoculated controls, were replicated 10 times. Plants were grown under a 19-h day at a greenhouse temperature of 22 ± 4 C. Treatments were harvested 105 d after germination, after plants had received about 30,000 heat units, and the roots and tops weighed.

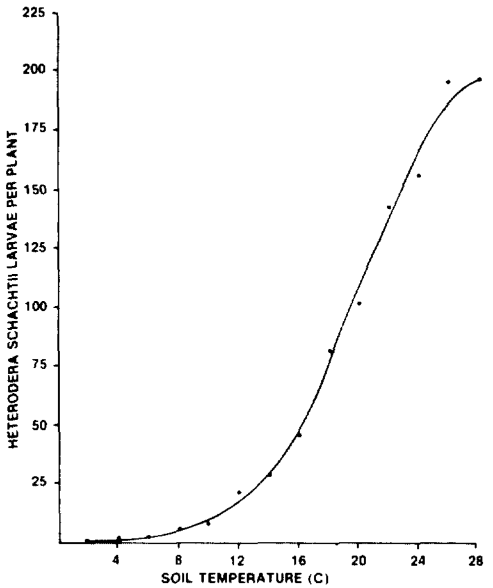

Fig. 1. Effect of soil temperature on infection of 14-d-old sugarbeet seedlings by *Heterodera schachtii* larvae.

Field studies: A study similar to that conducted in the greenhouse was undertaken in microplots, 3.0 × 4.0 m of sandy loam soil. The plots, infested with 0, 2.5, 4.3, 5.5, and 6.6 *H. schachtii* larvae/g of soil, were planted with 'Tasco AH3' sugarbeet seed on 6 March at 6 C, 6 April at 12 C, and 26 April at 18 C. Selected nematode popultion densities were obtained by adding various amounts of uninfested soil of the same type to the microplots and mixing until sampling showed that infestation was uniform ($P = 0.05$). Each treatment was replicated six times. Standard fertilizer and irrigation practices were followed; sugarbeets were thinned in the four-leaf stage, and all weeding was done by hand. All plants were harvested on 23 September, 150 days after the final planting on 26 April, and root weights converted to metric tons/ha were determined.

A final study was conducted in widely separated areas of the intermountain region of the western U.S. to determine the effect of soil temperatures at planting on the pathogenicity of *H. schachtii* to sugarbeet. The areas were Parma, Idaho—88 km northwest of Boise; Rupert, Idaho—456 km southeast of Boise; and Tremonton, Utah—189 km north of Salt Lake City. The February-March rainfall was about 2.5 cm at Parma and 5.7 cm at Rupert and Tremonton. The lesser amount of rainfall facilitated an earlier planting of sugarbeets in the Parma area.

Four sandy loam fields with different nematode population densities (larvae/g of soil) were chosen for study in each area. The population densities were 2.9, 4.2, 5.9, and 6.8 larvae/g soil at Parma; 1.6, 2.9, 4.0, and 5.3 larvae/g of soil at Rupert; and 1.8, 2.9, 4.1, and 5.1 larvae/g of soil at Tremonton. Six-row plots (3.35 × 61 m), including 1-3, dichloropropene treated and untreated control plots (six replicates/treatment) were established. Soil temperatures at planting were 5.0-7.5 C at Parma on 10 and 11 March; 10.0-13.5 C at Rupert on 10 April; and 17.5-20 C at Tremonton on 9 and 10 May. Standard fertilization, weeding, and irrigation practices were followed on all three locations. Sugarbeets in all plantings were harvested after 202, 174, and 152 days growth at Parma, Rupert, and Tremonton, respectively, and yields converted to metric tons/ha were determined.

RESULTS

Greenhouse studies: Growth of sugarbeets was inversely related to both *Heterodera schachtii* inoculum density and initial soil temperature. Significant decreases in root weights were observed as soil temperature and nematode inoculum were increased (Fig. 2). *H. schachtii* was least virulent on sugarbeets grown at an initial soil temperature of 6 C and most virulent on those grown at an initial soil temperature of 24 C; plant growth was affected more by an increase in nematode inoculum at 24 C than at 6 C. Differences in top growth of inoculated and uninoculated control plants (Fig. 3) were less than comparable differences in root growth. The root weights, as affected by inoculum densities at each soil temperature were 89, 74, 62, and 40% of those of uninoculated controls at 6, 12, 18, and 24 C, respectively, with an inoculum

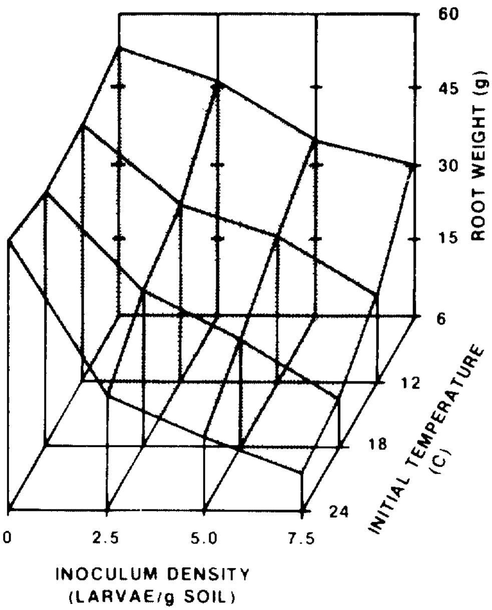

Fig. 2. Effects of initial soil temperature at planting and *Heterodera schachtii* inoculum density on the root weight of sugarbeets. Soil temperature was raised 2 C weekly until a maximum of 30 C was reached. All plants received 55,584 heat units (HU) during growth (1 h at 1 degree above 10 C = one HU; *P*, 0.05 = 1.31).

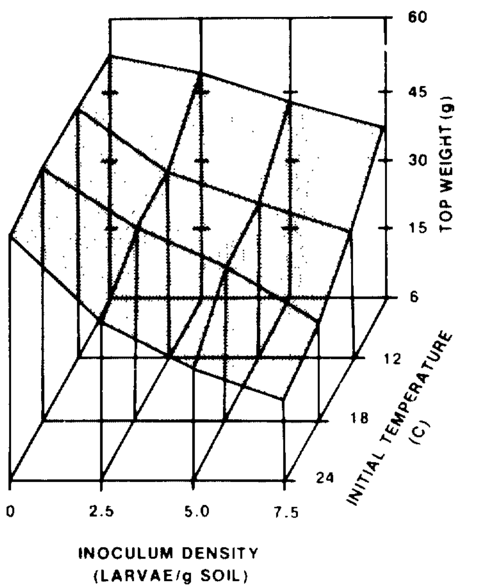

Fig. 3. Effects of initial soil temperature at planting and *Heterodera schachtii* inoculum density on the top growth of sugarbeets. Soil temperature was raised 2 C weekly until a maximum of 30 C was reached. All plants received 55,584 heat units (HU) during growth (1 h at 1 degree above 10 C = one HU; *P*, 0.05 = 3.74).

density of 2.5 larvae/g of soil; 70, 57, 44, and 25% at an inoculum density of 5.0 larvae/g of soil; and 56, 34, 19, and 13% at an inoculum density of 7.5 larvae/g of soil. Data on top weights were similar but more erratic. Top weights were 94, 75, 86, and 63% of those of uninoculated controls at 6, 12, 18, and 24 C, respectively, with 2.5 larvae/g soil; 82, 62, 69, and 46% with 5.0 larvae/g of soil; and 71, 53, 41, and 33% with 7.5 larvae/g of soil.

Plant age at time of root exposure to *H. schachtii* also affected sugarbeet growth (Fig. 4), but this was a direct relationship. *Heterodera schachtii* was most virulent on plants inoculated at germination, and least virulent on plants inoculated at 6 wk of age. Nematode inoculum density was inversely related to root-growth regardless of age of the plant at inoculation. However, seedlings inoculated at germination were affected more and had greater reductions in growth with increased inoculum density than seedlings inoculated at 6 wk of age. Root weights were 37, 21, and 8% of those of uninoculated controls when inoculated at germination with 2, 4, and 6 larvae/g of soil, respectively; 54, 32, and 16% when 2-wk-old plants were inoculated; 70, 49, and 32% when 4-wk-old plants were inoculated; and 92, 68, and 50% when 6-wk-old plants were inoculated.

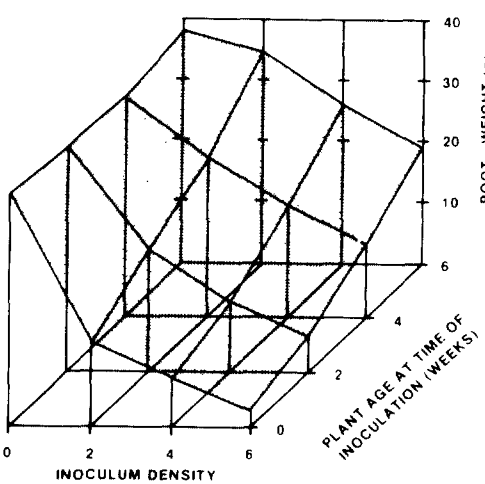

Fig. 4. Effects of plant age at time of inoculation and *Heterodera schachtii* inoculum density on the root growth of sugarbeets. Plants were grown at 22 ± 4 C and received about 30,000 heat units (HU) during growth (1 h at 1 degree above 10 C = one HU; *P*, 0.05 = 2.06).

Differences in top growth of inoculated and uninoculated control plants (Fig. 5) were less than those in root growth. Top growth was 58, 34, and 20% of that of uninoculated controls when germinated seeds were inoculated at 2, 4, and 6 larvae/g of soil, respectively; 66, 48, and 36% when 2-wk-old plants were inoculated; 84, 81, and 71% when 4-wk-old plants were inoculated; and 90, 84, and 68% when 6-wk-old plants were inoculated. Reductions in sugarbeet weights were closely related to unit-population (UP) increases (one UP = one larva/g soil) in the nematode population density. Root weights were reduced 2.9, 5.0, 6.5, and 9.3 g with every UP increase when plantings were made at 6, 12, 18, and 24 C, respectively. This compared to root weight reductions of 8.4, 7.0, 4.5, and 2.6 g with every UP increase when plantings were made at 0, 2, 4, and 6 wk of age.

Field studies: Results for microplots were comparable to those for greenhouse studies, but treatment effects were not as marked. An inverse relationship was found between sugarbeet yields (metric tons/ha) and both soil temperature at time of planting and nematode populations (Fig. 6). The

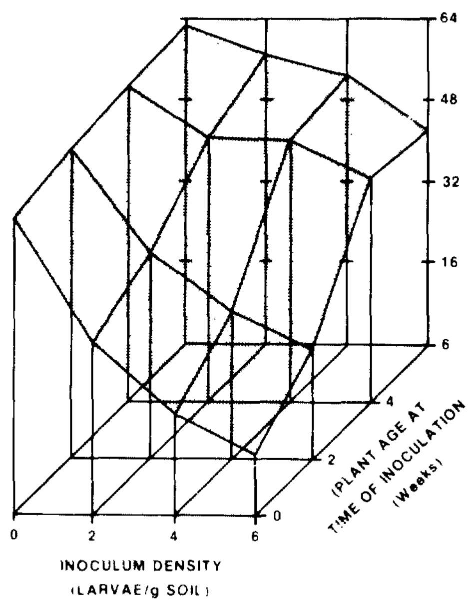

Fig. 5. Effects of plant age at time of inoculation and *Heterodera schachtii* inoculum density on the top growth of sugarbeets. Plants were grown at 22 ± 4 C and received about 30,000 heat units (HU) during growth (1 h at 1 degree above 10 C = one HU; *P*, 0.05 = 4.86).

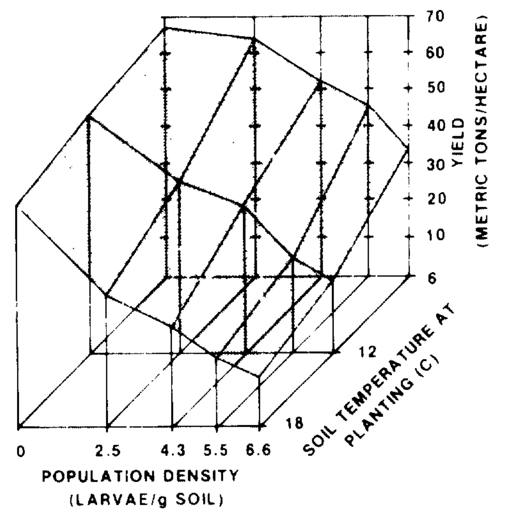

Fig. 6. The effect of initial soil temperature at planting and *Heterodera schachtii* population density on yield of sugarbeets after 150 d of growth in microplots (*P*, 0.05 = 5.83).

greatest yields in nematode-infested plots were in those of plots planted at a soil temperature of 6 C, while the smallest yields were from those planted at 18 C. Yields were 90, 72, and 57% of those of uninfested controls at 6, 12, and 18 C, respectively, at a population density of 2.5 larvae/g soil; 78, 61, and 45% at a population density of 4.3 larvae/g of soil; 69, 42, and 30% at a population density of 5.5 larvae/g of soil; and 49, 30, and 22% at a population density of 6.6 larvae/g of soil. Reductions in sugarbeet yields were also closely related to UP increases in the nematode population density. Sugarbeet yields were reduced 3–5, 6–7, and 7–10 metric tons/ha with every UP increase when plantings were made at 6, 12, and 18 C, respectively.

Results of the field study were similar to those of the greenhouse and microplot studies; yield was inversely related to soil temperature (Fig. 7). The highest yields (metric tons/ha) were from early-planted plots at Parma and the lowest from the late-planted plots at Tremonton. The yield losses due to *H. schachtii* were 7, 22, 43, and 47% at nematode population densities of 2.9, 4.2, 5.9, and 6.8 larvae/g of soil, respectively, at a planting soil temperature of 6 C (Parma); 10, 23, 41, and 55% at population densities of 1.6, 2.9, 4.0, and 5.3 larvae/g of soil, respectively, at a soil temperature planting of 12 C (Rupert); 12, 32, 53, and 70%

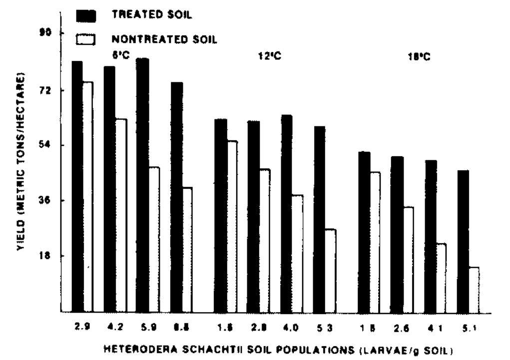

Fig. 7. Effects of initial soil temperature at planting and *Heterodera schachtii* inoculum density on yield of sugarbeets. Sugarbeets planted at 6 C and grown for 202 d at Parma, at 12 C and grown for 175 d at Rupert, and at 18 C and grown for 154 d at Tremonton (*P*, 0.05 = Parma—7.92; Rupert—6.27; Tremonton—5.31).

at population densities of 1.8, 2.6, 4.1, and 5.1 larvae/g of soil, respectively, at a soil temperature of 18 C (Tremonton). The soil temperature at planting plus the longer growing season combined to give increased plant growth and yield at Parma when compared to Rupert and Tremonton. Reductions in sugarbeet yields, as related to nematode populations were 2–6, 4–7, and 3–7 metric tons/ha with every unit-population increase when plantings were made at 5.0–7.5 C, 10.0–13.5 C and 17.5–20 C, respectively.

DISCUSSION

This study shows the importance of the combined effects of soil temperature and *H. schachtii* population densities on the growth of sugarbeets. Soil temperature has a double influence on the relationship of *H. schachtii* and sugarbeet; at the higher initial soil temperature (24 C), there is increased penetration by *H. schachtii* larvae. There is also an increase in nematode metabolism (10,11,14) with a corresponding increase in soil temperature; this results in reduced plant growth. The percentage reduction in top growth, especially at the higher soil temperatures and with the higher inocula, were less than those for root growth in the greenhouse, apparently because of adequate soil moisture-nutrient relations. Field observations suggest that sugarbeet top growth is not always an indicator of root growth.

A close relationship between root weight depression and both soil temperature and nematode population density was observed in greenhouse, microplot, and field studies. Increasing soil temperatures 2 C weekly until a maximum temperature of 30 C was reached resulted in average root weight depressions of 2.9, 5.0, 6.5, and 9.3 g for every UP at initial greenhouse soil temperatures of 6, 12, 18, and 24 C. When expressed as depression per HU-UP the depression was greatest at an initial soil planting temperature of 24 C and smallest at an initial soil planting temperature of 6 C (Fig. 8). On the basis of the age of the plant at inoculation, the greatest root weight depression per HU-UP unit occurred when plants were inoculated at germination, and the smallest root weight depression occurred when plants were inoculated at 6 wk of age (Fig. 8).

From the temperature infection relationship (Fig. 1), one might assume that it would be more realistic to calculate heat units at a temperature below 10 C. This study was established with 10 C as a base, and any calculations made, regardless of the base temperature, would show a similar relationship between soil temperature, nematode population density, and sugarbeet growth as is shown in this study.

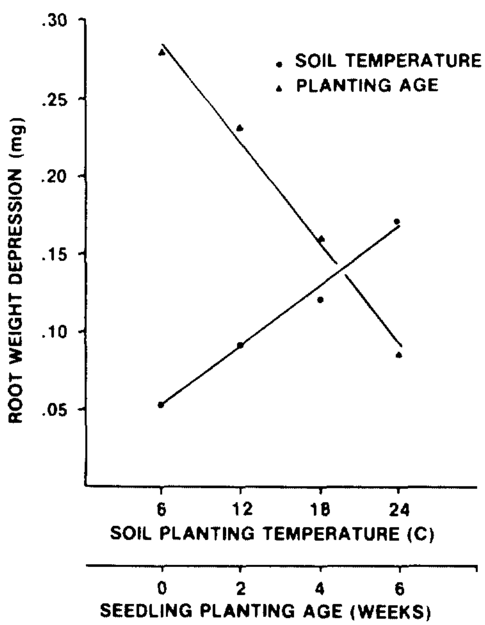

Fig. 8. Effect of soil temperature and plant age at time of inoculation on the virulence of *Heterodera schachtii* on sugarbeet. Data expressed in terms of plant weight loss per heat unit-unit population (1 h at 1 degree above 10 C = one heat unit; 1 unit population = 1 larvae/g soil).

No attempt was made to determine the root weight depression (HU-UP) in the microplot and field studies. However, from these data it appears that sugarbeet losses may be determined fairly accurately when soil temperatures, initial population densities, and length of growing season are considered.

It should be noted that the reason for similar reductions in sugarbeet yields per UP at soil planting temperatures of 12 C (Rupert) and 18 C (Tremonton) is apparently the differences in the growing season. A similar growing period would produce a greater reduction in yields from untreated plots at Tremonton, since it has been shown that there was a greater percentage loss from nematodes when plantings were made at the higher temperatures.

Soil temperatures at time of planting were more important than maximum summer temperatures. Maximum summer temperatures in sugarbeet plantings were 27 C at Parma and 23–24 C at Rupert and Tremonton. However, because of the lower planting temperatures, the economic population threshold at Parma is about 175% of that at Rupert and Tremonton. Seinhorst (12) states that we cannot assume that sugarbeet yields at high nematode densities will be very low, since plants may reach a certain size before being parasitized and this dramatically affects damage threshold levels. Sugarbeet losses of 22 and 43% from nematode population densities of 4.2 and 5.9 larvae/g of soil, respectively, occurred at Parma. This compared to sugarbeet losses of 23 and 41% from nematode populations of 2.9 and 4.0 larvae/g soil at Rupert. Sugarbeet losses of 55% from 5.3 larvae/g soil was similar to that (53%) from 4.1 larvae/g of soil at Tremonton. The damage population threshold varied with location; they were 2.9–4.2 at Parma, 1.6–2.9 at Rupert, and 1.8–2.6 at Tremonton. One may wish to consider the damage threshold level in terms of economic response. The economic population threshold is a fluctuating entity; it refers to the nematode population at which the value of the damage caused is equal to the cost of the control. When sugarbeet losses were correlated to reproductive costs and sugarbeet prices during 1978–79, the threshold levels were about 3.5 at Parma and 2.0 at Rupert and Tremonton. This agrees with the findings of Steudel and Thielman (13) who reported that the critical economic population density was 20 eggs and larvae/cm^3 when sugarbeets were planted the first of April, but dropped to 2.5 viable eggs and larvae/cm^3 when plantings were not made until the middle of May.

Cook and Thomason (1), referring to "the tolerance limit," found the threshold level in the Imperial Valley to be 100 eggs/100 g of soil when sugarbeets were planted in soil at about 32 C and grown at soil temperatures that never dropped below an average of 14.5 C, with an overall average of about 20 C or above. Jones (5) found threshold levels to be 10–20 eggs/g of soil in England where monthly average soil temperature never exceeded 17 C, and Heijbroek (4) found threshold levels to be 3–8 eggs/g of soil in Holland. Differences in threshold levels among different geographical areas are important in choosing the best control methods, thus emphasizing the importance of accurately determining populations (3).

The greatest variation in threshold levels in England and Holland is apparently due to uncontrolled variation in soil moisture. However, where soil moisture is controlled by irrigation, which also affects the growth of sugarbeets (1,2,3,4,5), relationships between population densities and yields are closer and yearly pattern of yield in relation to soil temperature is more predictable. Cook and Thomason (1) state the seasonal variations in the threshold levels are likely to be small in the Imperial Valley of California because of controlled soil moisture and predictable soil temperatures. Conditions are similar in the intermountain region of the western United States. Thus, it seems possible to predict with some reliability some characteristics of the host-parasite relationship, including the sugarbeet yields that can be obtained with given temperatures and nematode population densities.

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