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POPULATION STUDIES OF THE CEREAL CYST NEMATODE (*Heterodera avenae* WOLLENWEBER)

The populations of *Heterodera avenae*, large enough to injure cereal crops, are often slow in building up, but the nematodes are capable of surviving in soil for long periods of time. The distribution of the cereal cyst nematode is wider than indicated by crop injury: the pest has been observed in agricultural areas all over the territory of the Estonian SSR, mostly in fields of oats and barley on sandy soil.

Many workers have dealt with the initial and final populations of plant parasitic nematodes in soil and reported a need for a detailed study of the population dynamics. B. G. Chitwood and J. Feldmesser (1948), M. Oostenbrink (1950), D. W. Fenwick and E. Reid (1953), J. Schmidt (1954), N. G. Hague and J. J. Hesling (1958) have studied the reproduction rate of *Globodera rostochiensis* (in pots). All agree that the multiplication at low inoculum levels decreases simultaneously with the density of the nematodes rising to a maximum. In addition, the negative density factor works for higher population levels (Kort, 1962).

The relationships between the population increase and population density, the population density and the damage caused by the nematodes to plants, the concept of tolerance level in developing mathematical models and population curves have been described by numerous authors (Jones, 1955, 1957; Seinhorst, 1965, 1966, 1967, 1981; Wallace, 1971; Seinhorst, den Ouden, 1971; Jones, Kempton, 1978 et al.).

The purpose of this study is to give preliminary information on the multiplication rate of the cereal cyst nematode in permanent cereal growing areas under field conditions of the Estonian SSR. The need for this study became acute when the cereal cyst nematode was discovered on large territories of collective farms in the most important cereal producing areas of southern and central Estonia.

Material and methods

The investigations on population dynamics of *Heterodera avenae* were carried out in the years 1978—1981 on the territory of the collective farm Paistu in Viljandi District. The soil samples containing cereal cyst nematodes were taken from infested fields of barley 'Otra' and rye 'Vambo'. 20—40 microplots per field, each 1 m^2 in size, were laid out every year in spring after sowing. The samples were taken twice a season: in spring after establishing the plots, and in summer before harvesting. From the ploughed layer of each plot, about 1 kg of infested soil was collected. At the same time the crop weight was estimated and the mean length of the stems measured in each plot. After logarithmic transformation, the data of the yield were analyzed statistically.

After drying, the soil samples were stored until the following winter, when all cysts were washed out of the soil and crushed under a binocular microscope. The content of cysts, all eggs and larvae, were counted. The smallest sampling error in the study of the population, the Poisson error, was calculated within 95 per cent of probability limits.

The relationships between the initial and pre-harvest populations, as well as the relationships between the number of eggs and the amount of the yield are plotted on logarithmic scales.

Results

Tables 1 and 2 contain the results of the analyses of some soil samples from a field where the barley 'Otra' was grown in 3 successive seasons, followed by the rye variety 'Vambo' in the last year. The densities of the nematodes on the sample plots range from 106 to 19631 eggs per kg of soil.

The multiplication rate per 4 years is shown in Fig. 1, where P_i is the population density after sowing and P_f — before harvesting. P_i and P_f are plotted on logarithmic scales in order to avoid slight fluctuations of results. The straight line E_q, the logistic equilibrium level, is drawn at an angle of 45°, showing neither an increase nor decrease in population; the points on the line indicate the multiplication rate throughout the year, which is ×1. The results in Fig. 1 show that the increase in the values of P_i is accompanied by an increase of P_f to a maximum. In the years of 1978 and 1979, at the initial nematode density of 100—200 eggs per kg of

Table 1

Effect of different infestation levels of *Heterodera avenae* on reproduction rate in 1978 and 1979

Years and crop	P_i, eggs/kg of soil	log P_i	P_f, eggs/kg of soil	log P_f	P_f/P_i
1978 (barley)	106± 20.6	2.025	1198± 69.2	3.075	11.30
	371± 38.6	2.569	1268± 71.2	3.100	3.41
	861± 58.6	2.935	2288± 95.4	3.358	2.65
	1036± 62.4	3.012	2992±109.4	3.475	2.88
	1790± 84.6	3.252	3540±119.0	3.549	1.97
	1873± 86.6	3.271	3222±113.6	3.507	1.72
	2440± 98.8	3.387	4257±130.4	3.628	1.74
	2579±101.1	3.411	4095±128.0	3.611	1.58
	2663±103.2	3.424	3532±118.8	3.547	1.32
	2865±107.0	3.456	3290±114.8	3.517	1.14
	2990±109.4	3.475	4044±127.2	3.606	1.35
	3144±111.6	3.492	4408±132.8	3.643	1.41
	4184±129.4	3.621	6899±166.2	3.838	1.44
	4577±135.4	3.659	6803±165.0	3.832	1.48
1979 (barley)	120± 22.0	2.079	524± 45.8	2.719	4.36
	212± 29.0	2.326	648± 51.0	2.812	3.06
	318± 35.6	2.502	675± 52.0	2.829	2.12
	731± 54.0	2.873	1273± 71.4	3.103	1.74
	886± 59.6	2.947	1624± 80.6	3.209	1.83
	1048± 64.8	3.017	1894± 86.4	3.276	1.80
	1661± 81.6	3.220	1552±101.0	3.406	1.53
	1944± 88.2	3.287	2646±102.8	3.421	1.36
	2120± 92.0	3.326	3046±110.4	3.482	1.43
	2517±100.4	3.399	3561±119.4	3.551	1.41
	3364±117.6	3.526	4986±141.2	3.697	1.48
	3564±119.4	3.551	5100±142.8	3.707	1.43
	3722±122.0	3.570	4658±136.4	3.667	1.25
	4776±138.2	3.678	5578±149.4	3.745	1.16

P_i — initial population, P_f — final population, P_f/P_i — reproduction rate (valid also for Table 2).

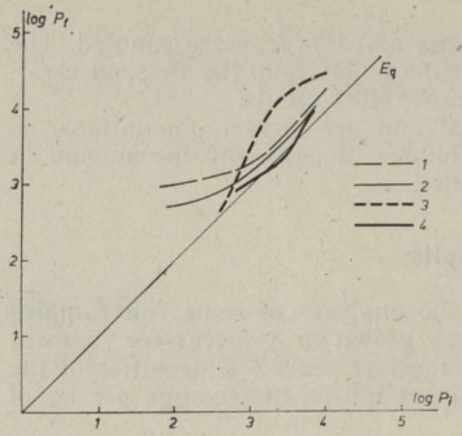

Fig. 1. The multiplication rate of *Heterodera avenae* in four successive years: *1* — in 1978, *2* — in 1979, *3* — in 1980, *4* — in 1981. P_i and P_f — eggs/kg of soil after sowing and before harvesting, respectively, E_q — logistic equilibrium density.

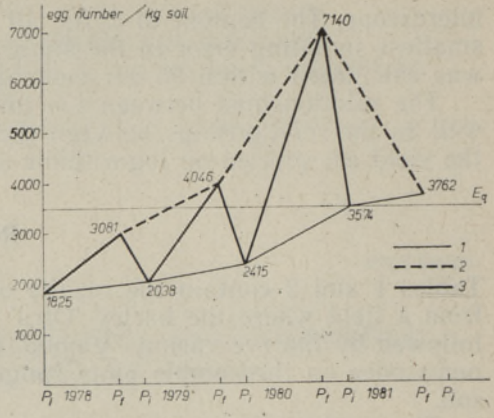

Fig. 2. Population increase of *Heterodera avenae* in four successive years after continuous cultivation of cereals: *1* — egg number/kg of soil after sowing (P_i), *2* — egg number/kg of soil before harvesting, *3* — fluctuations in the number of eggs per four seasons, E_q — observed equilibrium density.

soil, the multiplication rate was 3—11. With a further increase of P_i, the values of P_f did not rise at the former rate, but approached gradually the equilibrium level. In 1980, after cultivation of barley for 3 successive

Table 2

Effect of different infestation levels of *Heterodera avenae* on reproduction rate in 1980 and 1981

Years and crop	P_i, eggs/kg of soil	log P_i	P_f, eggs/kg of soil	log P_f	P_f/P_i
1980 (barley)	780± 55.8	2.892	1 133± 67.4	3.053	1.45
	804± 56.8	2.905	912± 60.4	2.960	1.13
	996± 63.2	2.998	3 076±110.0	3.487	3.08
	1070± 65.4	3.029	2 657±103.0	3.423	2.48
	1158± 68.0	3.060	4 875±139.6	3.687	4.22
	1256± 70.8	3.096	8 038±179.4	3.904	6.39
	1600± 80.1	3.204	5 221±144.6	3.717	3.26
	1656± 81.4	3.220	8 728±186.8	3.940	5.27
	2379± 97.6	3.374	8 176±180.8	3.912	3.43
	2393± 97.8	3.378	7 936±178.2	3.899	3.31
	2583±101.6	3.411	16 250±255.0	4.209	6.29
	2873±107.2	3.457	13 708±234.2	4.136	4.77
	2897±107.6	3.460	10 664±206.6	4.025	3.68
	3224±113.6	3.507	19 631±280.2	4.292	6.08
1981 (rye)	1848± 86.0	3.264	1 924± 87.6	3.283	1.04
	1854± 86.2	3.267	1 762± 84.0	3.245	0.95
	2270± 95.2	3.356	3 520±118.6	3.546	1.55
	2602±100.0	3.415	3 677±121.2	3.564	1.41
	2640±102.8	3.421	2 260± 95.0	3.354	0.85
	2901±107.8	3.462	2 806±106.0	3.447	0.96
	3138±110.0	3.495	2 824±106.2	3.450	0.89
	3938±125.6	3.594	4 068±127.6	3.608	1.03
	3995±126.4	3.601	4 738±137.6	3.674	1.18
	4124±128.4	3.614	3 498±118.2	3.542	0.84
	4427±133.0	3.645	5 004±141.4	3.699	1.13
	4705±137.2	3.672	3 157±112.4	3.498	0.67
	4788±138.4	3.679	4 338±131.8	3.636	0.90
	6565±162.0	3.816	6 583±162.2	3.818	1.00

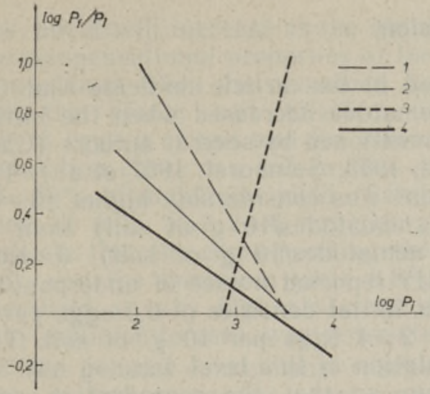

Fig. 3. Estimation of population fluctuations of *Heterodera avenae* after cultivation of cereals: *1* — data in 1978, *2* — in 1979, *3* — in 1980, *4* — in 1981. P_i — eggs/kg of soil after sowing, P_f/P_i — reproduction rate of nematodes.

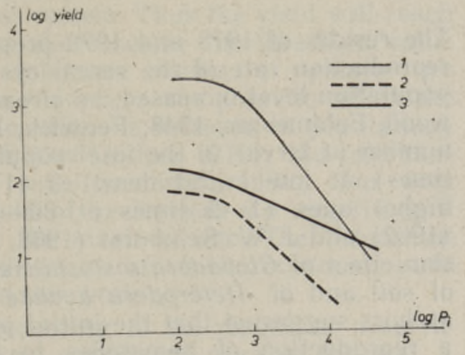

Fig. 4. Relationships between population density of *Heterodera avenae* and the yield (barley 'Otra'): *1* — weight of grain/m², *2* — mean length of plants/m², *3* — number of grains/m².

years, the final population density of the nematodes was relatively higher than in the previous seasons, but at low initial densities the population increased in number at a slower rate than 1—2 years before. After rising to a maximum graphical point, the final density decreased to a logistic equilibrium level.

The maximum multiplication rate (11.3 times) was observed in 1978 in barley, and the minimum multiplication rate in 1981 in rye (0.67 times).

In four subsequent years the mean initial density in the field increased continuously, as indicated by Fig. 2: 1825±85.4, 2038±90.2, 2415±98.2 and 3574±119.6 eggs/kg soil. The mean values of P_f were 3081±11.0, 4046±127.2, 7140±169.0 eggs/kg of soil; after cultivation of rye the number of the nematodes diminished to 3762±122.6 (50.3%). The equilibrium density was estimated at 3485 eggs/kg of soil.

For determining the population fluctuation type, the final population against the initial density, the ratio of P_f/P_i to P_i, was plotted on logarithmic scales as described by F. G. W. Jones and D. M. Parrott (1969). In Fig. 3, the sloping straight lines drawn through the points of data show the extent of fluctuations in respect to the equilibrium level. The tangent of the angle of the slopes less than −1 (in 1979 tan= −0.96 and in 1981 tan= −0.70) indicates a gradual approach to the equilibrium density. The slope of the angle tan= −1.60 in 1978 shows that equilibrium will be approached with slight fluctuations only, and in 1980, when there was a maximum population density in the field, tan=3.48 shows considerable fluctuations in comparison with the equilibrium level.

Relationships between different nematode densities and yield are plotted in Fig. 4. The weight of crop per m² and the number of corns per m² of field against the initial egg density give two parallel straight lines, the slope of which depends on the population number in soil. The negative nematode density factor affects the growth of plants to a lesser extent, as indicated by the median line. The tolerance level was reached at the initial density of 240±31.0 eggs/kg of soil. It was the value of P_i below which there occurred no losses in yield, and the growth of plants remained at a constant level. The observed minimum yield of plants constituted 8.8 per cent of the maximum yield.

Discussion

The results of 1978 and 1979 presented in this article indicate that the reproduction rate of the cereal cyst nematode decreased when the initial population level increased, as already mentioned by several authors (Chitwood, Feldmesser, 1948; Fenwick, Reid, 1953; Seinhorst, 1967 et al.). The number of larvae in the final populations was considerably higher (3—11 times) at low initial densities (1—2 nematodes/10 g of soil) than at higher ones (1—2 times at 30—50 nematodes/10 g of soil). J. Kort (1962) and J. W. Seinhorst (1968, 1981) reported a case of underpopulation effect of *Globodera rostochiensis* at initial densities of 0.5 eggs per g of soil and of *Heterodera avenae* at 2—4 eggs per 10 g of soil. The authors suggested that the initial population at this level was too low for a reproduction of nematodes to occur, so that the reproduction rate could diminish to zero. Our data, however, show that the initial density of 1 egg per 10 g of soil gave the maximum multiplication rate in 1978. According to J. Kort (1962), in the case of cyst nematodes it is doubtful whether such a low limit exists in practice, because the cyst normally ensures a local high density of eggs. Moreover, the nematodes in our plots may not have been equally distributed in the soil, and so the cysts may have occurred as small infestation foci. Furthermore, the larvae emerging in our plots could have spread easily in host roots and multiplied at an increased rate. As our results show, there was no indication of a lower multiplication rate at lowest initial densities, as compared to the higher ones.

The maximum population increase was observed after successive cultivation of barley in 1980. Our data suggest that in 1980 there occurred an optimal distribution of cysts in soil. The mean initial infestation value in plots was about 2500 eggs/kg of soil. The points indicating the relationships between the initial and final densities of nematodes in 1980 (Fig. 1) form a typical S-shaped curve (Seinhorst, 1966, 1967). Nevertheless, the decrease of the curve at the initial density of about 100 eggs/g of soil below the logistic equilibrium level on account of an increasing competition between individuals and due to decreasing food supplies was not stated in our work. The maximal density in our microplots was about 16—20 eggs/g of soil, and field observations indicate the existence of normal feeding and multiplying conditions for the nematodes at that level.

In case of a moderate increase of population and a slight damage to plants, a continuous cultivation of host plants in successive years will result in a gradual approach to an equilibrium density when $P_i = P_f$ and the rate of multiplication being 1—1.5 (Seinhorst, 1967). When the increase of population is as excessive as in 1980, the population will surpass the equilibrium rate, and a decrease will follow in the succeeding year. The low values of the population level in 1981 may have been influenced by the winter crop, on which the cereal root nematode had not been able to build up such great densities as on the roots of barley. Despite this suggestion, the delay in the multiplication rate may also have been influenced by normal fluctuations in population, at which a great increase in the egg numbers is followed by a diminished population level. Unfortunately, more information is needed before definite conclusions can be made concerning the great fluctuations in 1980—1981.

J. W. Seinhorst (1965), H. R. Wallace (1971), J. W. Seinhorst and H. den Ouden (1971) introduced the term tolerance level. According to the hypothesis, the growth of the plants remains at a constant level until a critical nematode density is reached. As described by H. R. Wallace (1971), with an increase of the nematode numbers, the decrease in the weight of the above-ground parts of the plant per nematode is initially low, but it will increase as the absolute numbers of the nematodes surpass the compensational properties of the root system. Thus the yield will reach a maximum when the nematode density decreases to the threshold value that the plants can tolerate. The tolerance limits of potato are 1.5—6 eggs/g of soil and the minimum yield (i. e. the point to which the population curve can fall in case of a continuous increase in population) 10—30% of maximum yield (Seinhorst, den Ouden, 1971); the tolerance level of oats was 2—6 eggs/10 g of soil (Seinhorst, 1981). Our data indicate that the corresponding threshold of barley was 2.4 eggs/10 g of soil, and the minimum yield 8.8% of the maximal one. The theoretical threshold at very high nematode densities, at which the minimum yield may diminish to zero, was not stated in our work.

The general conclusions, reached according to the results of observations in four successive years, under field conditions, were as follows:

1) The initial infection with the cereal cyst nematode after the sowing of the cereals for 4 successive years increases gradually, approaching the logistic equilibrium point in the last year.

2) Final density of the population before harvesting, in case of a continuous cultivation of the host plants, increases every season, reaching a maximum in the third year, and subsequently approaching the logistic equilibrium point once again.

3) In case of winter crop (rye) the reproduction rate of the cereal cyst nematode decreases to the equilibrium level.

4) Knowledge of the multiplication rate of *Heterodera avenae* and the establishment of the tolerance level of cereals in respect to that nematode under different field conditions may enable to predict yield losses caused by *H. avenae* Wollenweber.

REFERENCES

Chitwood, B. G., Feldmesser, J. Golden nematode population studies. — Proc. helm. Soc. Wash., 1948, **15**, 43—55.

Fenwick, D. W., Reid, E. Population studies on the potato root eelworm (*Heterodera rostochiensis* Woll.). — J. Helminthol., 1953, **27**, 119—128.

Hague, N. G., Hesling, J. J. Population studies on cyst-forming nematodes of the genus *Heterodera*. — Proc. Linn. Soc., London, 1958, **169**, 86—92.

Jones, F. G. W. Quantitative methods in nematology. — Ann. Appl. Biol., 1955, **42**, 372—381.

Jones, F. G. W. Soil population of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. III. Further experiments with microplots and with pots. — Nematologica, 1957, **4**, 257—282.

Jones, F. G. W., Kempton, R. A. Population dynamics, population models and integrated control. — In: Plant Nematology. London, 1978, 333—361.

Jones, F. G. W., Parrott, D. M. Population fluctuations of *Heterodera rostochiensis* Woll. when susceptible potato varieties are grown continuously. — Ann. Appl. Biol., 1969, **63**, 175—181.

Kort, J. Effect of population density on cyst production in *Heterodera rostochiensis* Woll. — Nematologica, 1962, **7**, 305—308.

Oostenbrink, M. Het aardappelaaltje (*Heterodera rostochiensis* Wollenweber), een gevaarlijke parasiet voor de eenzijdige aardappelcultuur. — Versl. Plziekt. Dienst., Wageningen, 1950, **115**, 1—230.

Schmidt, J. Zur Populationsdynamik des Kartoffelnematoden. — Wiss. Z. Univ. Rostock, 1954, **4**, 187—190.

Seinhorst, J. W. The relation between nematode density and damage to plants. — Nematologica, 1965, **11**, 137—154.

Seinhorst, J. W. The relationships between population increase and population density in plant parasitic nematodes. I. Introduction and migratory nematodes. — Nematologica, 1966, **12**, 157—169.

Seinhorst, J. W. The relationships between population increase and population density in plant parasitic nematodes. II. Sedentary nematodes. — Nematologica, 1967, **13**, 157—171.
Seinhorst, J. W. Underpopulation in plant parasitic nematodes. — Nematologica, 1968, **14**, 549—553.
Seinhorst, J. W. Growth and yield of oats at a range of *Heterodera avenae* densities and under different watering regimes. — Nematologica, 1981, **27**, 52—71.
Seinhorst, J. W., Ouden, H. den. The relation between density of *Heterodera rostochiensis* and growth and yield of two potato varieties. — Nematologica, 1971, **17**, 347—369.
Wallace, H. R. The influence of the density of nematode populations on plants. — Nematologica, 1971, **17**, 154—166.

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KAERA-KIDUUSSI (*HETERODERA AVENAE* WOLLENWEBER) POPULATSIOONIDÜNAAMIKA

Töö eesmärk oli kaera-kiduussi paljunemiskiiruse ja teraviljadele tekitatava kahju selgitamine. Mullaproovide analüüs näitas, et parasiidi peremeestaimede pideval kasvatamisel nelja aasta jooksul suurenes mulla keskmine algnakkus: 1978. a. 1825 muna 1 kg mulla kohta (peremeestaimeks oder), 1979. a. 2038 muna (oder), 1980. a. 2415 muna (oder) ja 1981. a. 3574 muna (rukis). Populatsiooni tihedus mullas suurenes maksimaalselt kolmandal odra kasvatamise aastal (7140 muna/kg). Pärast talivilja kultiveerimist neljandal vaatlusaastal lähenes kaera-kiduussi arvukus tasakaalupunktile, mis oli vaatlustingimuste põhjal 3762 muna/kg. Maksimaalne parasiidi arvukus 1 kg mullas, mille puhul veel ei täheldatud saagi langust, oli 240±31 muna, minimaalne saak nakatamata taimedega võrreldes 8,8%. Populatsiooni arvukuse kõikumine tasakaalutaseme suhtes oli otseses sõltuvuses kaera-kiduussi paljunemismäärast, kuigi nakatatud aladel nematoodi munade üldarv kasvas algnakkuse suurenedes.

Эрика МЯГИ

ИЗУЧЕНИЕ ДИНАМИКИ ПОПУЛЯЦИИ ОВСЯНОЙ ЦИСТООБРАЗУЮЩЕЙ НЕМАТОДЫ (*HETERODERA AVENAE* WOLLENWEBER)

Обсуждаются вопросы, связанные с динамикой популяции овсяной цистообразующей нематоды в естественных условиях с целью выявления закономерностей в скорости размножения этого паразита. Работа по изучению колебания численности популяции овсяной нематоды проводилась автором с 1978 по 1981 г. в Вильяндиском районе Эстонской ССР на полях ячменя 'Отра' и ржи 'Вамбо'. Результаты обработки почвенных проб показали, что средняя численность паразита в почве в результате ежегодного возделывания зерновых культур постепенно повышается; по годам она следующая: в 1978 г. (ячмень) 1825, в 1979 г. (ячмень) 2038, в 1980 г. (ячмень) 2415 и в 1981 г. (рожь) 3574 яиц/кг почвы. Плотность популяции нематоды перед уборкой урожая после трехкратного возделывания ячменя достигала максимума (7140 яиц/кг почвы). После посева ржи в четвертом году плотность популяции нематод приближалась к равновесному уровню инвазионной нагрузки и составляла 3762 яиц/кг почвы. Определили некоторые параметры, характеризующие динамику популяции. Степень устойчивости ячменя оказалось 240±31 яиц/кг почвы (т. е. максимальная степень плотности популяции, при которой потери урожая не наблюдалось). Максимальная плотность популяции (7140 яиц/кг почвы) обусловливала минимальный урожай (8,8% от урожая на незараженных участках поля). Равновесный уровень нагрузки составлял около 3485 яиц/кг. Установили, что колебания численности паразита в отношении равновесного уровня оказались в прямой зависимости от степени размножения, но абсолютная численность популяции возрастала с повышением исходной зараженности.