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Simulation of the host/parasite system Lolium perenne/ Tylenchorhynchus dubius. 1. Population dynamics of Tylenchorhynchus dubius

A.L. DEN TOOM

Department of Nematology, Wageningen Agricultural University, Binnenhaven 10, 6709 PD Wageningen, the Netherlands

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Abstract

An explanatory dynamic simulation model of the population dynamics of the ectoparasitic nematode *Tylenchorhynchus dubius* during the first month after the grass *Lolium perenne* was seeded has been developed, using published data.

Experimental results were simulated to estimate certain parameters and to test the model. The results of experiments at temperatures between 18 and 25 °C in which no moisture stress occurred, were described well by the model. However, the population increase was underestimated for low temperatures and overestimated at sub-optimal water supply for the host. To improve the explanatory value of the model, better data are needed on nematode fecundity and on the relation between temperature and nematode development.

To simulate population dynamics for periods exceeding a few weeks, the effect of root growth on nematode develoment and oviposition rate has to be incorporated. This is probably also needed to explain the effect of soil moisture on population increase.

Additional keywords: ectoparasitic nematodes, perennial ryegrass.

Introduction

Every year about 10% of the grassland in the Netherlands is reseeded. On 5 to 10% of the reseeded area problems are encountered during the establishment phase (De Jong and Boeken, 1985). Nematodes are assumed to be at least partly responsible for these problems (Van Bezooijen, 1984; Spaull et al., 1985). Ectoparasitic nematodes are always abundant in old pastures (Van Bezooijen, 1986). Whether they cause problems at reseeding depends on environmental conditions (Van Bezooijen, 1985).

To determine the effect of environmental conditions on the relation between ectoparasitic nematodes and grass hosts, the ectoparasitic nematode/grass system *Tylenchorhynchus dubius* (Bütschli, 1873) Filipjev, 1936/*Lolium perenne* L. was studied (Den Toom, 1988a) and an explanatory dynamic simulation model of these interactions is being developed. The model consists of submodels for the population dynamics of the nematode and the growth of the host. This paper describes a preliminary submodel for the population dynamics of *T. dubius.*

The model is based on published data and has been constructed according to the state variable approach (De Wit and Goudriaan, 1978).

The model

Description

The structure of the model is represented in a relational diagram in Fig. 1.

The life cycle of *T. dubius* is divided into five development classes: eggs (including the first juvenile stage which moults inside the egg), juveniles (J2 to J4), adult males, pre-oviposition females and reproductive females. Apart from the eggs, all stages are mobile and parasitic, even when moulting (Sharma, 1971). The model simulates the changing numbers of individual nematodes in each of the development classes, both in soil and on the roots, as a function of temperature and root growth. A direct effect of soil moisture on the nematodes is not included in the model.

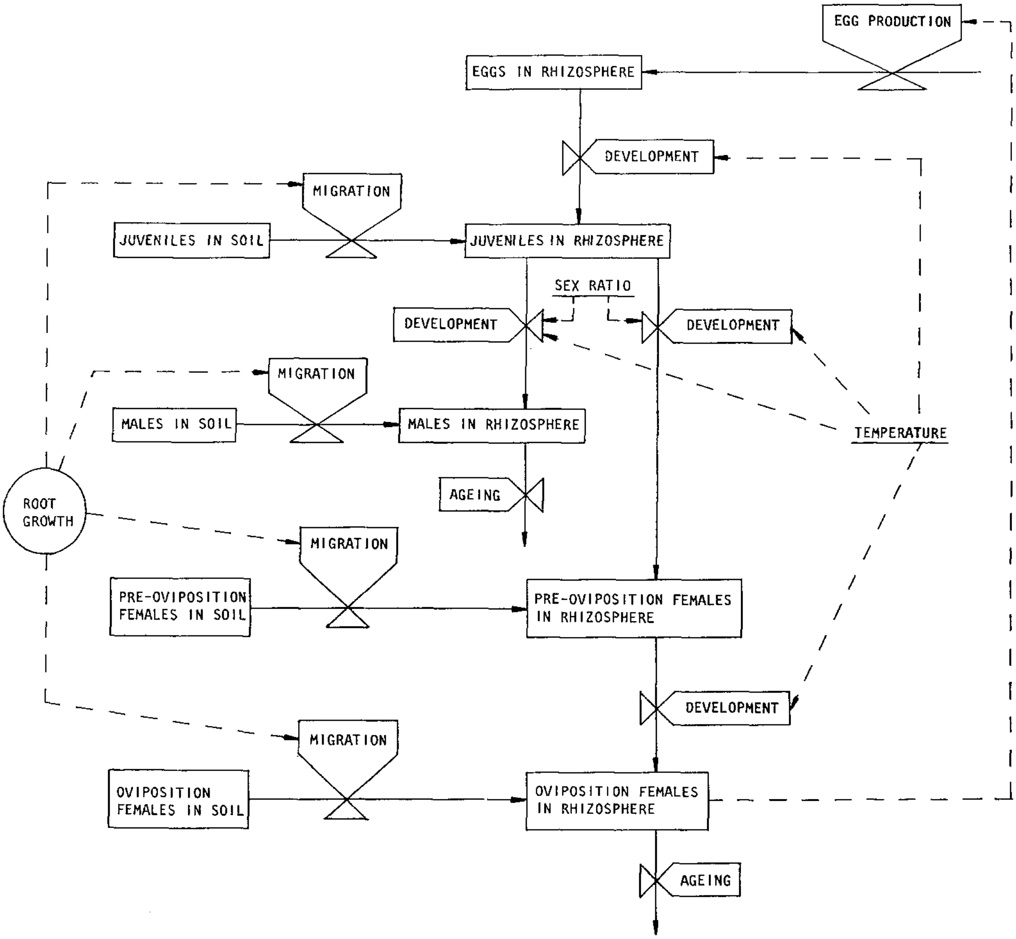

Fig. 1. Relational diagram for the population dynamics of *Tylenchorhynchus dubius*. Rectangles: state variables; Valve symbols: rate variables; Underlined: driving variables; → flow of material; - - → flow of information.

The nematode population in the soil outside the rhizosphere is assumed to be homogeneously distributed. These nematodes enter the rhizosphere as a result of rhizosphere expansion, which is calculated from the increase of root length and the rhizosphere radius. The rhizosphere radius is defined as the distance over which nematodes are attracted to the roots, plus the radius of the root. Nematodes in the rhizosphere are assumed to stay there. So, when the rhizosphere volume is equal to the pot-volume, the nematode population in the soil is assumed to be depleted and migration stops. In this preliminary model the population in the soil is assumed to consist of mobile stages only. So, eggs only occur in the rhizosphere as a result of oviposition and not as a result of migration. No quantitative data are available on the eggs of *T. dubius* in the soil, because the eggs are lost in the usual extraction procedures. Ignoring them is not a major shortcoming in the structure of the model, since the eggs of *T. dubius* do not function as a resting stage (Simons, 1973). Mortality of the nematodes in the soil is ignored. No data are available on the mortality of *T. dubius* during the first weeks after removal of a host, but it is expected to be limited during this period.

In the model, development and oviposition occur only on the roots. It is assumed that no overpopulation occurs on the roots during the first weeks of the growth of the host. Therefore, development and oviposition of nematodes in the rhizosphere are assumed to be independent of food supply.

To enable the introduction of age-dependent processes such as mortality in a later phase of model development, development of the nematode is simulated with an escalator boxcar train (Goudriaan and van Roermund, in press). Each stage is divided into a number of age classes of equal length. The content of each age class is transferred to the next class whenever the residence time in a class is exceeded. The residence time equals the average duration of the development stage, divided by the number of age classes. The duration of development depends on temperature. The outflow from the last age class of the eggs is quantitatively transferred to the first age class of the juveniles. The outflow from the juveniles is divided into males and pre-oviposition females, according to the sex-ratio. Since fertilization of *T. dubius* is not hampered by low densities (Seinhorst, 1966), all pre-oviposition females are assumed to develop into reproductive females, even at low population densities. The outflow from the last age class of adult males and reproductive females represents mortality by ageing. Mortality during development is ignored, because there are no published data on this. The juveniles and adults migrating into the rhizosphere are assumed to be equally distributed over their respective age classes.

Fecundity is assumed to be independent of temperature, as is the case for *Aphelenchus avenae*, (Fisher, 1969), *Tylenchus emarginatus* (Gowen, 1970) and *Pratylenchus penetrans* (Mamiya, 1971). The oviposition rate of *T. emarginatus* and *P. penetrans* at constant tempeatures is about constant during the first weeks of the oviposition period, and declines thereafter. Since the estimated length of the oviposition period of *T. dubius* is shorter than that of the above-mentioned species, the oviposition rate of *T. dubius* is assumed to be independent of the age of the female during the total oviposition period in this preliminary model.

Quantification

Conversion of root mass into root length. Root mass is introduced as a function of time. Root mass is converted into root length with a conversion factor of 6.67 cm root length per mg root mass on the basis of data on *Lolium perenne* cv. Pelo (J.G. Mulder, personal communication).

Rhizosphere radius. *T. dubius* is not specifically attracted to the roots of *L. perenne* (Sharma, 1971). The maximum distance over which non-specific attractants are assumed to act is 2 cm (Prot, 1980). Since the radius of the roots of *L. perenne* is negligible compared with this figure, a maximum rhizosphere radius of about 2 cm is realistic. To test the importance of this parameter, the effect of values of 2, 1, 0.5 and 0.1 cm on the simulated results will be evaluated.

Development and ageing. At 20 °C the duration of the development stages is 8 days for the egg, 26 days for the juveniles, 8 days for the males, 4 days for the pre-oviposition females and 14 days for the reproductive females (estimated from Sharma, 1971). The influence of temperature on the duration of the stages is derived from data on the life cycle of *Tylenchus emarginatus* (Gowen, 1970) and *Pratylenchus penetrans* (Mamiya, 1971). Because there are no reasons to assume that any of the stages of *T. dubius* is more sensitive to temperature than the others, it is assumed that the duration of each stage is influenced in the same way as the length of the total life cycle (Fig. 2).

Fecundity. Sharma (1971) found a maximum fecundity of 12 eggs for *T. dubius* and Bridge (1971) found an average fecundity of 6 eggs for *T. maximus*. These values are low compared with the averages of 180 and 50 found for *Tylenchus emarginatus* (Gowen, 1970) and *Pratylenchus penetrans* (Mamiya, 1971) respectively. The low values found for *Tylenchorhynchus* are probably due to experimental conditions. To estimate fecundity, experimental results will be simulated using values of 10, 20, 30 and 40 eggs per female. The value of 40 is derived from the average egg production of 3 eggs per female

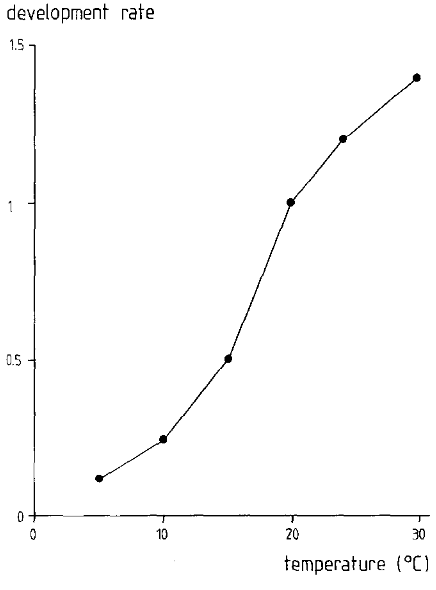

Fig. 2 Effect of temperature on the development rate of the nematode. The rate is expressed as a fraction of the development rate at 20 °C.

of *T. dubius* in 24 hours at 22 °C found by Brzeski and Dowe (1969), assuming a constant oviposition rate during two weeks.

Oviposition rate. The oviposition rate is calculated as the quotient of the fecundity and the temperature dependent duration of the reproductive stage.

Sex ratio. *T. dubius* is an obligatory amphimictic species. It is generally expected that such species have a strong genetic mechanism of sex determination that will insure the development of approximately equal numbers of males and females in each generation (Triantaphyllou, 1973). Sharma (1971) found no clear influence of environmental conditions on sex ratio, and intersexes are not known for this species. Therefore, a juvenile sex ratio of 50% is assumed.

The model is written in Fortran. It uses Euler's rectilinear integration method and a time step of integration of 0.05 day.

Simulations

The most uncertain parameters in the model are fecundity and rhizosphere radius. First, the fecundity was estimated by simulating an experiment in which migration could be ignored. Using the resulting value, other experiments were simulated to estimate the rhizosphere radius.

The ability of the model to explain the effects of moisture stress and host cultivar on the nematode population was then tested.

Initial nematode population. The initial numbers of juveniles, males and females in the simulated experiments were known. From these figures the initial concentration of the stages in soil was calculated. The females were divided over the pre-oviposition and the oviposition stage according to the estimated duration of these stages, so 23% in the pre-oviposition stage and 77% in the reproductive stage. The initial population in the rhizosphere was calculated from the nematode concentration in soil and the initial rhizosphere volume, assuming a homogeneous distribution over the age classes within each stage.

Fecundity. Data on the increase of *T. dubius* on *L. perenne* at 18 °C (J.G. Mulder, personal communication) were used to estimate the fecundity. The simulation was set to start about a month after the grass had been seeded. By this time migration has ended, so the total population was assumed to reside on the roots.

Population increase was simulated with values for fecundity of 10, 20, 30 and 40 eggs per female (Fig. 3). The total active population (juveniles and adults on the roots) was described reasonably well when values for fecundity were 30 and 40. The number of females was underestimated with both values, but the value of 30 gave a better prediction of the number of juveniles (Table 1). Therefore, the value of 30 was used for the rest of the simulations.

The initial decrease of the simulated population can be attributed to the assumed absence of eggs on the roots at the start of the simulation.

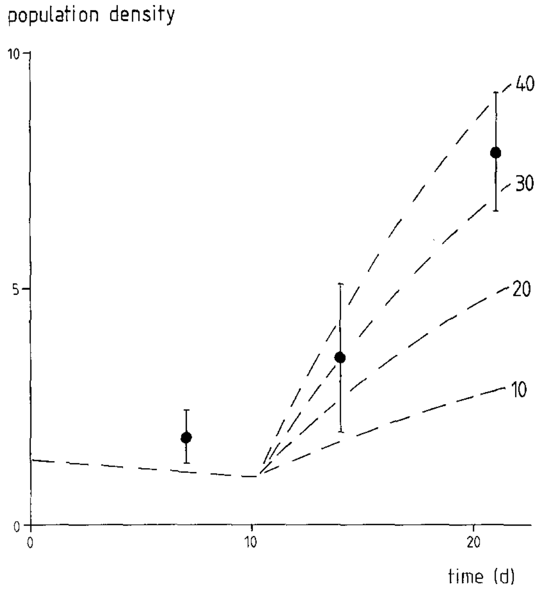

Fig. 3. Effect of various levels of fecundity (10 to 40 eggs per female) on population increase. ------ : Simulated; • : Observed by J.G. Mulder (unpublished results), vertical bars represent the standard deviations of the measurement.

Table 1. Effect of fecundity on the predicted composition of the population.

Stage	Code[1]	Time[2]					
		7		14		21	
Juveniles[3]	M	1294	(680)	2961	(1561)	6607	(846)
	S30	750		3262		6626	
	S40	750		4135		8696	
Females[3]	M	431	(89)	465	(182)	1146	(455)
	S30	258		160		191	
	S40	258		160		191	
Males[3]	M	105	(48)	86	(62)	137	(51)
	S30	97		74		137	
	S40	97		74		137	

[1] M: measured by J.G. Mulder (personal communication); S30: simulated with a fecundity of 30 eggs per female; S40: simulated with a fecundity of 40 eggs per female.

[2] Time in days from the start of the simulation (33 days after the host was sown).

[3] Numbers per 100 ml soil.

Rhizosphere radius. The population increase of *T. dubius* on *L. perenne* in moist soil in pot experiments at 10, 18 and 25 °C (Den Toom, 1988a) was simulated, to estimate the rhizosphere radius.

When the total initial population was assumed to reside on the roots (not realistic for these experiments), the active population was overestimated at 18 and 25 °C, but

Table 2. Effect of assumptions on nematode migration on the predicted active population on the roots of *L. perenne*.

Temperature	Code[1]	Intermediate population[2]	Final population[3]
10	M	5.7	12.6
	S no migration	5.1	8.4
18	M	11.1	31.7
	S no migration	18.3	61.9
	S radius 1 cm	11.9	50.5
25	M	18.6	35.1
	S no migration	23.7	38.6
	S radius 2 cm	21.2	35.9

[1] M measured by Den Toom (1988a), S simulated.

[2] Total number of juveniles and adults on the roots in thousands per pot 21 days after emergence of *L. perenne* at 10 and 18 °C, and 22 days after emergence at 25 °C.

[3] Total number of juveniles and adults on the roots in thousands per pot 43 days after emergence of *L. perenne* at 10 °C, 42 days after emergence at 18 °C and 30 days after emergence at 25 °C.

the active population at 10 °C was greatly underestimated (Table 2). There is no reason to expect a higher fecundity at low temperatures, therefore the development rate at 10 °C was probably underestimated.

When migration was not ignored, the population increase at 25 °C was best simulated with a rhizosphere radius of 2 cm, corresponding with a migration period of 4 days. The intermediate population density at 18 °C was best simulated with a rhizosphere radius of 1 cm, corresponding with a migration period of a week, but the final density was overestimated. This indicates that the assumption of non-limiting food supply might not hold for the total duration of the experiment.

Moisture stress. The population increase at 25 °C in soil with sub-optimal water supply was over-estimated when a rhizosphere radius of 2 cm was used (Table 3). When a rhizosphere radius of 1 cm was assumed, the prediction improved.

Effect of root growth on population increase. The population increase on the fast growing cultivar Pelo and the slow growing cultivar Idole in a pot experiment (Den Toom, 1988b) was simulated. The environmental conditions during this experiment were comparable with the dry treatment of the aforementioned experiment at 25 °C, therefore a rhizosphere radius of 1 cm was used.

The simulations show that differences in root growth during the migration period may cause large differences in population density (Fig. 4). However, the predicted final density was much too high for both cultivars. For 'Pelo' the difference between this prediction and the one for the moisture experiment can be explained from the higher initial nematode density and the higher number of plants in the cultivar experiment.

Tabel 3. Influence of moisture stress on increase of the active nematode population at 25 °C (in thousands per pot).

Moisture treatment	Code[1]	Time[2]	
		22	30
wet	M	18.6	35.1
	S radius 2 cm	21.2	35.9
dry	M	15.7	27.4
	S radius 2 cm	18.9	33.3
	S radius 1 cm	12.5	26.1

[1] M measured by Den Toom (1988a), S simulated.

[2] Time in days after emergence of *L. perenne*.

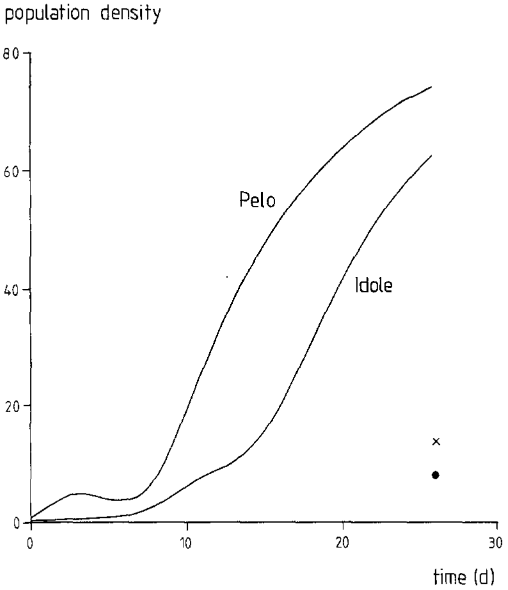

Fig. 4. Influence of the *Lolium perenne* cultivars Pelo (fast growth) and Idole (slow growth) on population increase of *T. dubius*. —— : Simulated; × : measured for 'Pelo'; • : measured for 'Idole'.

The higher number of plants initially caused a higher growth rate of the plant mass per pot, resulting in a higher migration rate. It also caused earlier and stronger competition between the plants, resulting in slower growth of the individual plants. So, the differences between the predicted final density of the nematodes in the moisture experiment and the cultivar experiment and between the measured and the predicted final density in the cultivar experiment might be explained by the effect of limited food supply on the growth of the nematode population.

Discussion

For a limited set of environmental conditions – no moisture stress and temperatures between 18 and 25 °C – the model describes experimental results during the first month after seeding of the grass reasonably, using a value for fecundity of 30 eggs per female and a rhizosphere radius of 1 or 2 cm. However, at low temperatures the increase of the population on the roots is underestimated, and it is overestimated when moisture stress occurs.

The underestimation of the population increase at low temperatures is caused by underestimation of the development rate of the nematode. It is necessary to determine the relation between temperature and development rate for *T. dubius*, instead of using a relation determined for other species; the temperature threshold of development seems to be lower for the population of *T. dubius* used in the experiments than for *Tylenchus emarginatus* and *Pratylenchus penetrans*. At the same time, the effect of temperature on mortality should be determined. At high temperatures, mortality during development is certainly not negligible; although the development rate of *T. dubius* is probably highest at 30 °C, the population declines at this temperature an only little reproduction occurs (Malek, 1980).

The overestimation of population increase at moisture stress may have various causes. In the model, soil moisture acts indirectly by its influence on root growth. Since root growth only influences migration, the influence of soil moisture is limited to the migration period. The results of population increase under moisture stress were better described with a lower value for the rhizosphere radius. However, it is questionable whether the effect of moisture stress can be explained by a direct relation between soil moisture and the rhizosphere radius. Nematode mobility is influenced by soil moisture, but the mobility is highest at intermediate moisture levels (Vrain, 1986). Therefore it is doubtful whether the mobility of *T. dubius* was lower in the simulated experiments under moisture stress than at optimal water supply for the host. In any case, a rhizosphere radius dependent on soil moisture cannot explain any effects of soil moisture that occur after the migration period, as its effect is limited to this period. Extreme moisture conditions did not occur in the simulated experiments. Therefore, a direct effect of soil moisture on development and reproduction of the nematodes in the rhizosphere is not expected (Vrain, 1986).

The overestimation of population increase at moisture stress may also be due to the assumption that no overpopulation occurs. The overestimation of the final population in the experiment at 18 °C and the cultivar experiment indicates that this assumption only holds during a short period. When root growth is slower, as is the case at lower soil moisture levels, food shortage is likely to occur earlier and at lower initial population densities. Development rate, oviposition rate and mortality are probably all affected by food shortage. Fecundity is probably not affected, as Fisher (1969) showed for *Aphelenchus avenae*. To incorporate food shortage in the model, detailed information is needed about the availability of young roots. The applicability of the model will be much greater when this information is incorporated, as more situations and longer periods may be simulated. However, it is questionable whether this is necessary for an accurate simulation of the damage caused by *T. dubius*, because experimental results suggest that damage to *L. perenne* is mainly caused by nematode activity during the first weeks after sowing (Den Toom, 1988a).

Before extending the population model, the length of the period during which population increase determines the amount of damage to the host plant should be estimated. This can be done by simulating the growth of the host in a model in which population density is introduced as a forcing function. Various density curves may be evaluated.

To improve the explanatory value of the model, certain parameters need to be determined more accurately.

Fecundity is the most important parameter in the model. The population increase of *T. dubius* cannot be explained with the low values for fecundity reported for *Tylenchorhynchus* in literature. The value of 30 used in the simulations is only a rough estimate. Since this estimate was obtained from an experiment in which the growth of the host was probably already limited by pot volume, and given the assumed absence of mortality, a still higher value might be expected.

The estimate of the rhizosphere radius depends on fecundity; a higher value of the fecundity would have caused a lower estimate for the rhizosphere radius. Although measurement of this parameter is preferable, it might be sufficient to fit the rhizosphere radius when fecundity and the relation between temperature and development rate have been determined more accurately.

Den Toom (1988b) suggested that the differences in population increase of *T. dubius* on fast- and slow-growing cultivars of *L. perenne* might be caused by the effect of slow plant growth on nematode migration to the roots, rather than by differences in degree of cultivar resistance. The simulations of population increase on 'Idole' and 'Pelo' support this hypothesis, but they also indicate that growth of the individual roots might be an important factor determining the growth rate of the nematode population. Therefore it might be better to hypothesize that differences in population increase on fast- and slow-growing cultivars of *L. perenne* are determined by quantitative rather than qualitative differences between the cultivars.

The model underestimates the number of females, but the numbers of juveniles and males are described reasonably well. This indicates that the juvenile sex ratio and the longevity of the males are probably well estimated and that the duration of the period in which oviposition mainly occurs is about equal to the longevity of the reproductive females assumed in the model. However, the lifetime of the adult female is probably much longer than assumed in the model. The life time of the adult females of other species of nematode may approximately equal the length of their life cycle or even be 6 to 10 times longer, whereas oviposition mainly occurs during the first part of adulthood (Mamiya, 1971; Gowen, 1970). A better estimation of the longevity of the females and the course of the individual oviposition rate during ageing is necessary when periods in the order of a few times the generation time are simulated.

The quality of the model output greatly depends on the quality of the input relations. Therefore, the number of eggs in the initial populations deserves attention, because quantitative information on this is lacking.

The model presented here can be adapted for other species of ectoparasitic nematodes and host species by changing the input relations and values of the parameters.

Samenvatting

Simulatie van het waardplant/parasiet systeem Lolium perenne/Tylenchorhynchus dubius. 1. Populatiedynamica van Tylenchorhynchus dubius

Om het populatieverloop van de nematode *Tylenchorhynchus dubius* op *Lolium perenne* gedurende de eerste weken na inzaai van het gras te kunnen verklaren, werd een verklarend dynamisch simulatiemodel ontwikkeld met gebruikmaking van gegevens uit de literatuur.

De resultaten van enkele experimenten werden gesimuleerd om de waarde van onbekende parameters te schatten en om het model te testen. Experimenten bij temperaturen tussen 18 en 25 °C waarin geen vochtstress optrad werden goed door het model beschreven. De populatietoename werd onderschat voor lage temperaturen en overschat in geval van vochtstress. Betere gegevens over het totaal aantal eieren dat een vrouwtje kan leggen en over de relatie tussen temperatuur en ontwikkeling van de nematode zijn nodig om de verklarende waarde van het model te verbeteren.

Om het model bruikbaar te maken voor simulatie van periodes langer dan een paar weken, moet het effect van wortelgroei op ovipositiesnelheid en ontwikkeling van de nematode ingebouwd worden. Dit effect is waarschijnlijk ook nodig om de gevolgen van vochtstress op de populatietoename te kunnen verklaren.

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