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Simulation of the host/parasite system Lolium perenne/Tylenchorhynchus dubius. 2. The effect of T. dubius on L. perenne

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Abstract

The effect of the ectoparasitic nematode *Tylenchorhynchus dubius* on various processes that determine the growth of the grass *Lolium perenne* was studied using dynamic simulation. An equation was formulated for the relation between nematode density in the rhizosphere and the cell penetration rate per nematode. Various hypotheses on the effect of cell penetration on plant growth processes were formulated and then introduced in a SUCROS-type growth model of the host. The plausibility of the hypotheses was tested by their ability to simulate experimental results with given population data.

The simulations showed that it is unlikely that all cells penetrated by *T. dubius* will die. The effect of *T. dubius* cannot be attributed to the nematodes' consumption of dry matter. Growth reduction may be attributed to the nematode negatively affecting the roots' permeability.

Additional keywords: ectoparasitic nematodes, perennial ryegrass, damage.

Introduction

The nematode/grass system *Tylenchorhynchus dubius/Lolium perenne* was studied to elucidate the effect of the plant parasitic nematode on the grass under various environmental conditions (Den Toom, 1988). An explanatory dynamic simulation model comprising submodels of the population dynamics of the nematode and the growth of the host plant is being developed. The submodels are linked by the effect of the nematode on the processes that determine the growth of the host and by the effect of the host on the population dynamics of the nematode.

The latter effect was discussed in a previous paper in which a preliminary model of the population dynamics of *T. dubius* was presented (Den Toom, 1989). The present paper deals with the simulation of the effect of the nematode on the host; it describes attempts to couple data on the nematode population to a SUCROS-type model of the growth of the host.

Two basic relations were needed for this coupling: 1) the relation between nematode density in the rhizosphere and the daily feeding activity per nematode, and 2) the effect of individual feeds on the carbon flow processes in the host. As knowledge on these relations is incomplete for *T. dubius* (as for most other plant parasitic nematodes), various hypotheses were formulated and their plausibility was evaluated.

Plant model

The plant model used in this study is based on SUCROS (Van Keulen et al., 1982; Spitters et al., 1989). Photosynthesis is calculated from incoming radiation as a driving force. The assimilates are partitioned over shoot and root according to constant partitioning coefficients. The model was adapted to simulate the growth of grass in pots in a climate room. It was extended with a relation that accounts for the effect of reduced soil moisture content on photosynthesis. It was assumed that the reduction of the rate of photosynthesis is equal to the reduction in transpiration rate and that the photosynthetic properties of the leaves and assimilate partitioning are not affected by reduced soil moisture content. This assumption only holds for a reduction of less than about 40% in water uptake (Van Keulen, 1982). The relation between soil moisture and the reduction factor for transpiration is based on Feddes et al. (1978).

Ageing of the roots was introduced in the model because young roots are attractive to *T. dubius* and old roots are not attacked. Aging was simulated with an escalator boxcar train (Goudriaan and van Roermund, 1989). It was assumed that epidermal cells of *L. perenne* live for 16.5 days at 21 °C unless killed by external factors (Kirk and Deacon, 1986). The temperature dependency of root ageing was approximated by a Q_{10} value of 2.

To calculate the number of epidermal cells per unit root mass a value of 2.21×10^4 mg^{-1} was used, based on the epidermal cells having an outer surface area of 3.8×10^{-3} mm^2 (measured on cv Pelo), a root diameter of 0.4 mm (Kutschera et al., 1982) and a root length per unit dry mass of 66.7 mm/mg (H. Mulder, unpublished results).

The model is written in CSMP.

Relation between nematode density and penetration rate

Description. The active stages of *T. dubius* (second stage juveniles to adult males and females) feed mainly on epidermal cells in the root hair zone and the zone of elongation and to a lesser extent on root hairs and root tips (Bridge and Hague, 1974; Laughlin and Vargas, 1972; Sharma, 1971; Wyss, 1973). The nematodes penetrate the cells with their stylet and partly remove the cell contents. The feeding period is short, in the order of ten minutes, and the searching time, i.e. the time between retraction of the stylet and successful penetration of the next feeding site, is in the order of seconds to minutes (Bridge and Hague, 1974; Wyss, 1973).

Nematode density was assumed to have no influence on the mean feeding period, because feeding nematodes are usually not disturbed by encounters with searching nematodes (Wyss, 1973). The mean searching period was assumed to increase with increasing nematode density.

The penetration rate per nematode, PR_n, was defined as the number of cells penetrated per unit of time by one nematode. It is the inverse of the sum of the feeding period and the searching period.

The ratio between feeding period and searching period at a given moment is equal to the ratio between the number of feeding nematodes and the number of searching nematodes. So, the searching period can be calculated when feeding period and the numbers of feeding and searching nematodes are known.

The following method for calculating the number of feeding nematodes is analogous to the kinetic derivation of the Langmuir isotherm equation. This equation describes the relation between the number of occupied adsorption sites and the concentration of molecules at adsorption/desorption equilibrium.

A cell can be occupied by only one nematode at a time. Therefore, the number of occupied cells equals the number of feeding nematodes N_f (1)[1]. The rate VR (d^{-1}) at which occupied cells are vacated is proportional to the number of feeding nematodes.

$$VR = k_v \cdot N_f \tag{1}$$

The proportionality constant, k_v (d^{-1}) is the inverse of the feeding period per cell.

The occupation rate, OR (d^{-1}), of consumable epidermal cells, E_h (1), is proportional to the concentration of searching nematodes on the young roots and the number of consumable epidermal cells not occupied by feeding nematodes. The nematode concentration in the rhizosphere is defined as the ratio between the number of searching nematodes, N_s (1), and the total number of epidermal cells, E_t (1).

$$OR = k_o \cdot \frac{N_s}{E_t} \cdot (E_h - N_f) \tag{2}$$

The proportionality constant, k_o (d^{-1}) is equal to the inverse of the searching period at unlimited food supply. It is assumed that the kinetics of the feeding and searching processes are so fast that equilibrium exists between the two processes. Then VR equals OR and equations (1) and (2) may be combined to give:

$$N_f = \frac{K \cdot E_h \cdot N_s/E_t}{1 + K \cdot N_s/E_t} \tag{3}$$

in whicht K ($d \cdot d^{-1}$) is the ratio between k_v and k_o.

N_t is the total number of nematodes in the rhizosphere of young roots. Substituting ($N_t - N_s$) for N_f in equation 3 leads to a quadratic equation for N_s with the solution:

$$N_s = \frac{\sqrt{(1 + \frac{K}{E_t}(E_h - N_t))^2 + \frac{4K}{E_t} N_t} - (1 + \frac{K}{E_t}(E_h - N_t))}{2K/E_t}$$

The other root of the quadratic equation (with the minus sign before the square root) is not valid because it gives a negative value for N_s.

Quantification. The feeding period per cell at room temperature on *L. perenne* averages just under 7 minutes. The searching period at low nematode density is in the range of a few seconds to a few minutes (Bridge and Hague, 1974). In the calculations a feeding period of 7 minutes and a minimal searching period of 30 seconds were assumed at 20 °C. This corresponds with a K value of 14.

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[1] (1) following a variable or parameter means that it is dimensionless (i.e. has dimension 1).

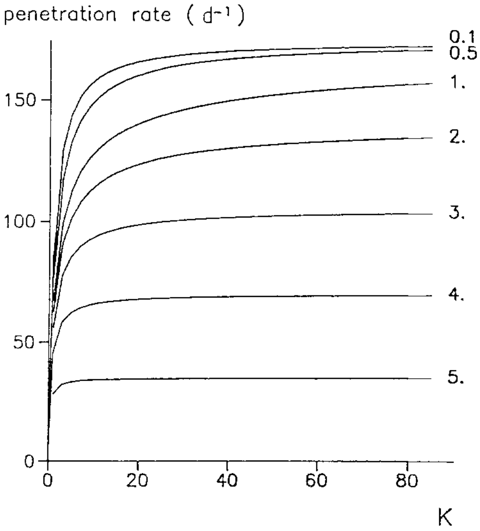

Fig. 1. Effect of the ratio K between the feeding period and the minimal searching period per nematode per cell on the calculated number of cells a nematode penetrates daily, for nematode concentrations in the rhizosphere of young roots ranging from 0.1 to 5 nematodes per epidermal cell.

The influence of temperature on feeding period and searching period was calculated with equation (5)

$$P_T = P_{20} / (a\ T - b) \tag{5}$$

in which P_T is the length of the period at temperature T (°C), P_{20} is the length of the period at 20 °C, a is a constant with value 0.062 ($°C^{-1}$) and b is a constant with value 0.26 (1). This relation was derived from observations made by Boag (1980) on the influence of temperature on the rate of oesophagus contractions in three nematode species. The equation is only valid for temperatures in the range of 10 to 25 °C. K is temperature-independent, because of the assumption that temperature influences feeding period and searching period in the same way.

Figure 1 shows the sensitivity of PR_n to K at various values for the nematode concentration in the rhizosphere (N_t/E_t). When the nematode concentration is high, the penetration rate is not sensitive to the value of K. At lower nematode concentrations the penetration rate is mainly sensitive for K values up to 15. The fate of penetrated cells influences the fraction of consumable epidermal cells in the young roots (E_h/E_t). Figure 2 shows how PR_n is influenced by the fraction of consumable epidermal cells. Figure 3 shows that PR_n decreases rapidly when the number of nematodes surpasses the number of epidermal cells, especially when the consumable fraction is low.

Effect of individual feeds on plant growth processes

Fate of penetrated cells. Wyss (1973) and Brzeski (1971) both studied the effect of penetration by *T. dubius* on cells of a *Brassica* species through a light microscope and observed no leakage of cell contents as a consequence of penetration. Brzeski (1971) reported that the cytoplasm had regenerated within a few hours after the nematode left the cell, and no visible traces of feeding activity remained. In contrast, Wyss (1973) observed that cyclosis of penetrated cells slowed down and stopped within a few hours

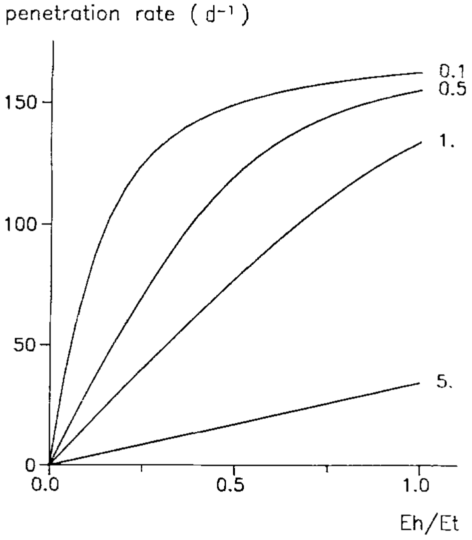

Fig. 2. Effect of the fraction of healthy epidermal cells E_h/E_t on the calculated number of cells a nematode penetrates daily, for nematode concentrations in the rhizosphere of young roots of 0.1, 0.5, 1, and 5 nematodes per epidermal cell.

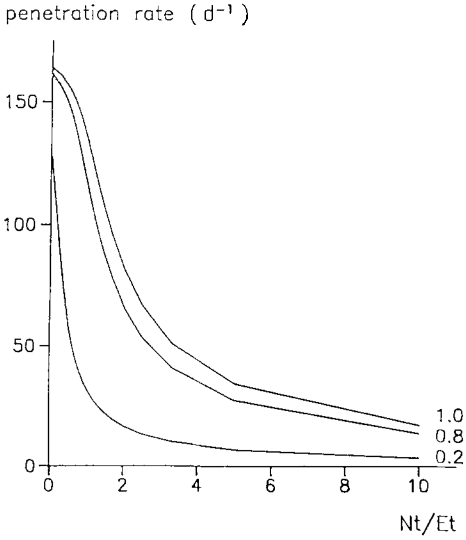

Fig. 3. Effect of the nematode concentration in the rhizosphere of young roots (N_t/E_t) on the calculated number of cells a nematode penetrates daily, when the fraction of healthy epidermal cells is 1.0, 0.8 or 0.2.

after the nematode had left.

As the literature is inconclusive on this point, the death of all penetrated cells, the recovery of all penetrated cells, and – an intermediate option – the death of some of the penetrated cells were all considered in the hypotheses on the effect of nematodes on plant growth processes.

It was assumed that the number of affected cells equals the number of penetrated cells, because there are no reports of visible influences of penetration on neighbouring cells.

Effect on growth processes. Bridge and Hague (1974) and Wyss (1973) observed no changes in the branching pattern of the roots, nor other morphological effects on root growth. It is therefore unlikely that *T. dubius* introduces or induces hormones that affect root morphogenesis.

Boote et al (1983) have classified pest effects on carbon flow processes. Nematodes are classified as assimilate sappers or turgor reducers.

T. dubius acts as an assimilate sapper when the cell mass removed by nematodes is replaced by assimilates to repair the cells. Additional assimilates are probably needed to account for the costs of repair.

Unless *T. dubius* affects the plant by injecting or inducing toxic substances that act directly upon stomatal behaviour and as a consequence on transpiration, it can only act as a turgor reducer if the resistance to water uptake is located at least partly in the epidermis and if the permeability of the epidermis depends on the condition of the epidermal cells. The traditional view is that the main resistance to radial water flow in the roots is located in or near the endodermis, but this has not yet been proved conclusively (Passioura, 1988). According to Drew (1987) the location of the main resistance might depend on the physical environment.

The relative importance of the symplastic and apoplastic pathways for water transport across the root is not yet clear either (Drew, 1987; Passioura, 1988). Cyclosis is needed for the symplastic pathway. The conductive properties of the cell walls, in which the apoplastic pathway is located, might be influenced by the condition of the adjacent plasma membranes.

Thus *T. dubius* may act as a turgor reducer through its direct effect on epidermal cells, both if cells die and if the penetrated cells recover.

Hypotheses. The following hypotheses on the effects of *T. dubius* on crop growth processes were tested.
1) All penetrated cells die.
2) All penetrated cells recover. The growth rate of the host plant decreases, because part of the assimilates are used to repair penetrated cells (respiration hypothesis).
3a) All penetrated cells recover. The permeability of the penetrated cells is reduced during recovery. Consequently, the rate of photosynthesis falls via a fall in transpiration.
3b) Some of the penetrated cells die. The permeability of dead cells is reduced. Consequently the rate of photosynthesis falls via a fall in transpiration.

Simulations

Each hypothesis was introduced separately in the plant model, and its ability to simulate the effect of *T. dubius* on dry matter production of *L. perenne*, as measured in pot experiments (Den Toom, 1988), was evaluated.

General information. Table 1 gives an overview of the simulated treatments. For a first screening of each hypothesis the treatments of experiment T18 were simulated. In treatment T18NW the measured effect of *T. dubius* on shoot growth of *L. perenne* was only moderate; a 30% reduction after 14 and 22 days and a 10% reduction after 36 days from the start of the experiment at an initial population density of 13 nematodes per g soil. Seinhorst and Kozlowska (1979) found a 20% reduction of shoot growth at a comparable initial nematode density; a maximum reduction of 90% was found at an initial nematode density of 200 nematodes per g soil. Therefore, the hypotheses tested are only plausible if they permit a range of initial densities of nematodes higher than that of T18NW to do more damage than found in T18NW.

Table 1. Explanation of the treatment codes of the simulated experiments (Den Toom, 1988).

Experiment code	Temperature (°C)	Nematode treatments[1]	Moisture treatments[2]
T18	18	N, C	W
T25	25	N, C	W, D

[1] N = soil inoculated with *T. dubius*; C = non-inoculated control.

[2] W = wet (maximum soil moisture content 25%); D = dry (maximum soil moisture content 12%).

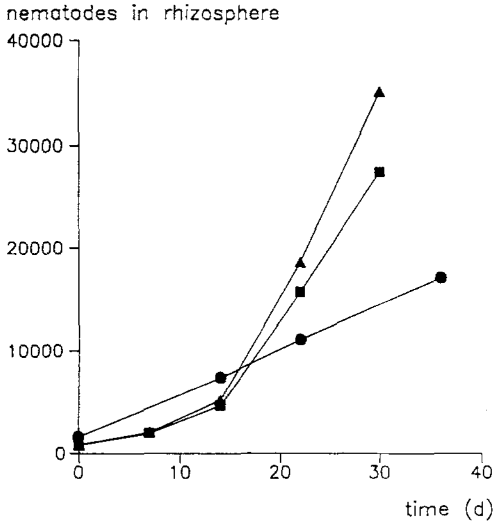

Fig. 4. Course of the *Tylenchorhynchus dubius* population in the rhizosphere of young roots in time, used for the simulation of T18NW (●), T25NW (▲), and T25ND (■).

If the results of the first screening justified further simulations, the treatments at 25 °C were simulated to examine the effects of temperature and moisture stress.

Unless indicated otherwise, the parameters on assimilate partitioning and specific leaf area at 18 °C and 25 °C were based on data from the controls T18CW and T25CW, respectively. Soil moisture content was introduced as a function of time; temperature and radiation as constants.

Figure 4 shows the course in time of the nematode population in the rhizosphere of the young roots as used as input in the simulations. The initial population of nematodes in the rhizosphere was calculated from the initial density in the pots and initial root mass, assuming a rhizosphere radius of 1 cm (Den Toom, 1989). For T18 the nematode population was determined by this initial value and the data on population density on the sampling dates, assuming that the total population was residing in the rhizosphere of the young roots at the sampling dates. For T25 the first sampling date was 22 days after emergence of the grass. To estimate intermediate population density, it was assumed that growth was exponential between the calculated initial density and the first sampling date.

Unless indicated otherwise, the penetration rate in the simulations was calculated with the method described above.

Hypothesis 1. The hypothesis that all penetrated cells die was tested without making assumptions on the effect of cell death on plant growth processes. The effect of nematodes was introduced by basing the values for the parameters on assimilate partitioning and specific leaf area on data measured in the nematode treatment T18NW instead of the control T18CW.

The fraction of living epidermal cells on the young roots and the PR_n are simulated with population data from T18NW. The fraction of living epidermal cells indicates whether and to what extent a higher population can cause more damage; if this fraction is zero at a certain population density, a higher population cannot cause more damage, because no feeding sites are left. Figure 5a shows that the simulated fraction

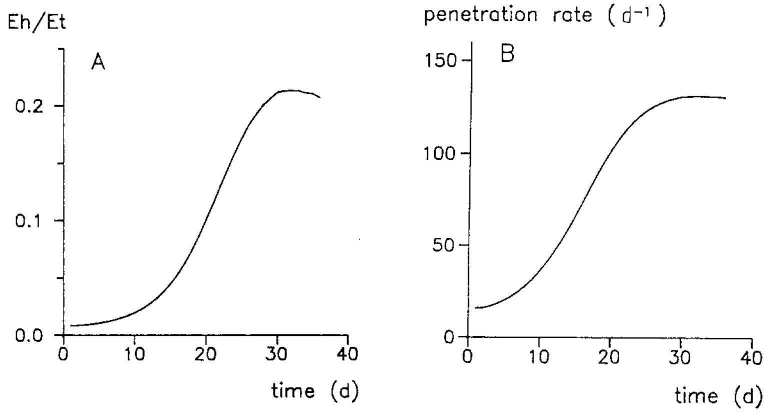

Fig. 5. Consequences of death of all penetrated cells on the fraction of living epidermal cells (A) and the penetration rate per nematode (B) for T18NW.

of living epidermal cells was initially so low that a higher nematode population could hardly affect more epidermal cells. However, differences between various densities could already be observed on the seventh day in an experiment (Seinhorst and Kozlowska, 1979).

In the case of unlimited food supply PR_n should be about 160 cells per day. Figure 5b shows that PR_n is less than a quarter of this value during the first two weeks of the simulation. Because the reduction of PR_n would be even larger at higher nematode densities, it is doubtful whether initially higher populations could remain higher than the population of T18NW. This suggests that differences between T18NW and higher population densities might not even occur at later sampling times.

The simulations show that it is unlikely that all penetrated cells die.

Hypothesis 2. All penetrated cells recover. The costs of recovery were calculated as the dry mass consumed by the nematodes multiplied by a conversion factor to account for the costs of transforming assimilates into dry matter.

The daily dry matter consumption per nematode at 20 °C was estimated to be 0.02 μg per day. This value was calculated from dry matter production, sex ratio and longevity of males and females, assuming that consumption is six times production (Petersen and Luxton, 1982). At 20 °C, the longevity of females is 44 days including an oviposition period of 14 days during which 2 eggs per day are produced, the longevity of males is 34 days (Den Toom, 1989). At a sex ratio of 0.5, a stable population consists of 56% females and 44% males, because of the differences in longevity. The dry mass of the nematodes was calculated from data on the length and width of *T. dubius* (Sharma, 1971) using Andrassy's formula for the calculation of fresh mass (Andrassy, 1956) and assuming a dry matter content of 25 % (Yeates, 1979). The resulting values were 0.09, 0.14 and 0.005 μg for males, females and eggs, respectively.

In the calculations for T18NW the value for daily dry matter consumption per nematode at 20 °C was used. It was assumed that the daily dry matter consumption per nematode was not influenced by nematode density. Thus, the daily dry matter consumption per nematode was certainly not underestimated.

Table 2. Respiration hypothesis. Measured and simulated shoot mass in the nematode treatment as a fraction of shoot mass of the control on the sampling dates of experiment T18W.

	Time[1]		
	14	22	36
Measured	0.70	0.68	0.90
Simulated (DCN[2] = 0.02)	0.98	0.99	0.99
Simulated (DCN = 0.40)	0.63	0.69	0.90

[1] Time in days after emergence = days after start of simulation.

[2] DCN = daily dry matter consumption per nematode ($\mu g \cdot .d^{-1}$).

However, simulated shoot growth was hardly affected (Table 2). The extra maintenance respiration caused by the nematodes was about 1% of the total assimilates available for growth and maintenance at the start and decreased with time to 0.1%. When a daily dry matter consumption of 0.4 μg per nematode was used, the simulated nematode effect was comparable with the measured effect (Table 2). However, it is unlikely that the daily dry matter consumption per nematode was underestimated by a factor of 20. Therefore, the effect of *T. dubius* on the production of *L. perenne* cannot be wholly attributed to an effect on maintenance respiration.

Hypotheses 3a and 3b. It was assumed that the permeability of non-functioning epidermal cells equals the permeability of old root cells. It was assumed that the permeability of old roots is 0.3 times that of young roots (De Wit et al., 1978). The level to which the permeability of the total root system is reduced by nematodes (R_{nem}) was calculated with equation 6:

$$R_{\mathrm{nem}} = \frac{Y_{\mathrm{h}} \times 1.0 + (Y_{\mathrm{a}} + O) \times 0.3}{(Y_{\mathrm{h}} + Y_{\mathrm{a}}) \times 1.0 + O \times 0.3} \tag{6}$$

in which Y_{h} is the mass of young roots with healthy epidermal cells, Y_{a} the mass of young roots with epidermal cells affected by nematodes and O is the mass of old roots. R_{nem} and the reduction factor resulting from reduced moisture content in the soil were multiplied to compute the total reduction of photosynthesis.

Hypotheses 3a and 3b differ with respect to the relation between the nematode population and the affected root mass.

For hypothesis 3a it was assumed that all penetrated cells are less permeable during a recovery period that is in the order of a few hours. During the recovery period the cells cannot be penetrated. Table 3 shows the effect of the length of the recovery period on shoot production of T18NW. The results are within the limits of the measurements when recovery periods of 2, 3 and 4 hours were used. The correspondence between simulations and measurements was best with a recovery period of 3 hours. Therefore, this value was used in the subsequent simulations.

For hypothesis 3b the percentage penetrated cells that die as a result of penetration depends on the physiological age of the cells. It was assumed that 0,5%, 10%, 20%,

Table 3. Sensitivity analysis for the period in which penetrated cells do not function in hypothesis 3a for experiment T18. Simulated shoot mass. Figures in parentheses represent standard deviations of the measurements.

	Time[1]		
	14	22	36
Measured	141 (46)	724 (191)	2868 (532)
Simulated			
NP[2] 1	192	892	3299
2	166	792	3153
3	139	681	2978
4	112	557	2755
5	92	459	2550

[1] Time in days after emergence = days after start of simulation.

[2] NP = period during which the cells do not function (hours)

40% and 80% of the penetrated cells in the successive age classes die. All living cells can be penetrated.

The consequence of both hypotheses on shoot production of T18NW is shown in Fig. 6, together with the shoot production of the control T18CW. The difference between the two hypotheses is illustrated by the course of R_{nem} in time (Fig. 7). The ir-

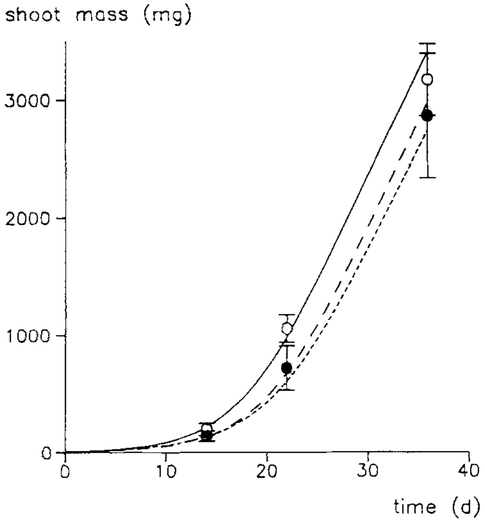

Fig. 6. Shoot production of T18NW simulated with hypotheses 3a (– – – –) and 3b (---------) and shoot production of the control T18CW (————). Points represent measurements; vertical bars represent standard deviations of the measurements. ● T18NW, ○ T18CW.

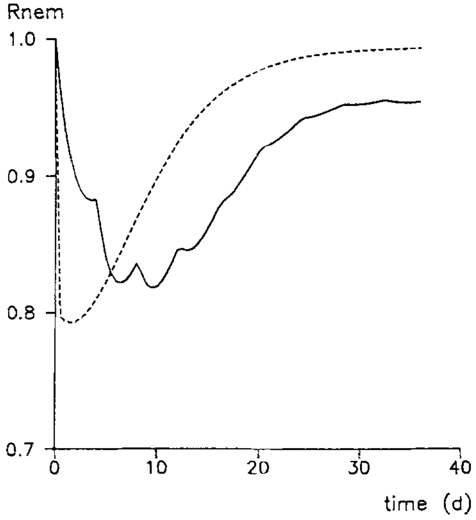

Fig. 7. Course of R_{nem} with time for T18NW simulated with hypotheses 3a (---------) and 3b (————).

regularities in the curve of R_{nem} at hypothesis 3a are the result of young root mass being simulated with a boxcar train; if more boxcars had been used the curve would have been smoother. For both hypotheses, the effect of *T. dubius* on water uptake was highest during the first half of the experiments. With hypothesis 3a all penetrations are equally effective and their effect is short-lived. With hypothesis 3b the effect per penetration initially increases with time. The effect per killed cell lasts until the cell becomes part of the old root mass. Therefore, the maximum decrease of water uptake was higher and occurred earlier with hypothesis 3a than with 3b. In both cases the minimum value of R_{nem} was much higher than the theoretical minimum of 0.3, which occurs when all young roots are affected. The penetration rate decreased by no more than 3% in both cases and the fraction of non-affected roots did not fall below 70% for hypothesis 3a and 74% for hypothesis 3b. So, under both hypotheses higher initial populations can cause more damage and can multiply to higher densities than the population in T18NW.

As both hypotheses gave reasonable results for T18, the experiment at 25 °C was simulated to examine the effects of temperature and moisture stress.

For hypothesis 3a the effect of temperature on the length of the recovery period needs to be explicitly incorporated. The rate of repair is expected to increase with temperature. Therefore, penetrated cells should have a shorter recovery period at higher temperatures. However, the shoot production of T25NW was overestimated instead of underestimated when the recovery period was 3 hours (Fig. 8).

In hypothesis 3b temperature influences death of the penetrated cells through its effect on root ageing. This hypothesis gave better results for the shoot production of T25NW (Fig. 8). The disparity between measurements and simulations might have been caused by the fact that estimates rather than measured data were used to calculate the effect of temperature on root ageing and the feeding activity of *T. dubius*.

In the dry treatments T25CD and T25ND moisture stress occurred. The effect of moisture stress on the control T25CD was simulated reasonably, but the effect of *T. dubius* on shoot production was underestimated with both hypotheses (Fig. 8). Shoot production of the nematode treatment T25ND even exceeded shoot production of

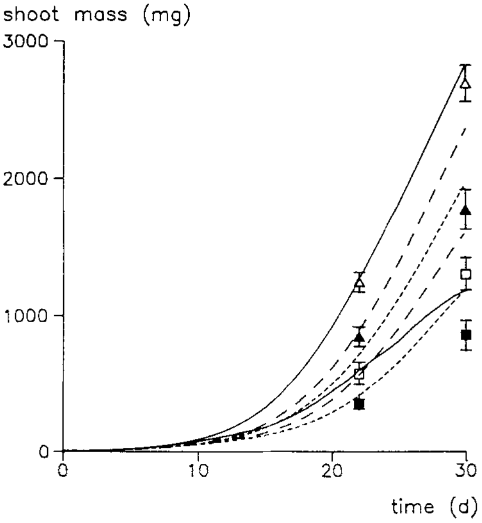

Fig. 8. Shoot production of T25NW and T25ND simulated with hypothesis 3a and 3b, and shoot production of the controls T25CW and T25CD. Points represent measurements; vertical bars represent standard deviations of the measurements. ▲ T25NW, △ T25CW, ■ T25ND, □ T25CD. ——— control, – – – 3a, -------- 3b.

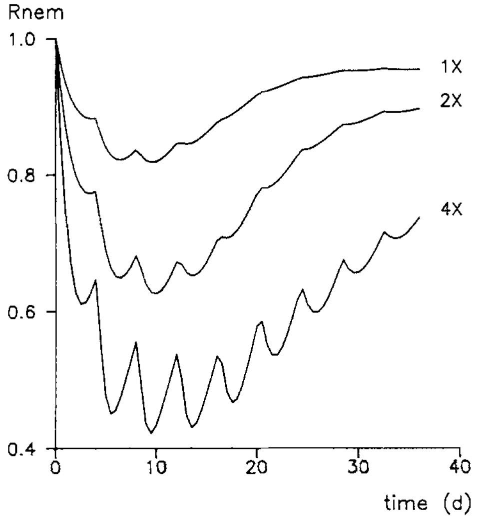

Fig. 9. Influence of population density of *T. dubius* on R_{nem} calculated with hypothesis 3b. From top to bottom, normal population density of T18NW, double density, and four times the normal density, respectively. Other circumstances as for T18NW.

T25CD for hypothesis 3a. The latter effect was permitted by the fact that the daily fall in moisture content in the nematode treatment was somewhat smaller than in the control.

An overestimation of the shoot production of T25ND with hypothesis 3a could have been expected, given the overestimation for T25NW with this hypothesis.

With hypothesis 3b, the effect of the nematodes on shoot production of treatment T25NW on the first sampling date was slightly overestimated. Therefore, it is unlikely that the negative effect of the nematodes on the permeability of the roots was underestimated for T25ND. Probably, the assumption that assimilate partitioning and photosynthetic properties of the leaves are not affected by reduced water uptake is not valid for treatment T25ND; in this treatment, the reduction of the water uptake as a result of moisture stress was more than 40% only incidentally, but the combined effect of nematodes and moisture stress surpassed this critical value for longer periods. Therefore, the model might be improved by incorporating a (reversible) effect of prolonged water stress on assimilate partitioning and photosynthetic properties of the leaves.

R_{nem} under hypothesis 3b was simulated for population densities of 1×, 2× and 4× the population density of T18NW at non-limiting water supply (Fig. 9). The two higher nematode densities not only caused a lower R_{nem}, but the period during which R_{nem} was low was also longer.

Conclusions and general discussion

Although Wyss (1973) observed that penetrated cells died, my simulations show that it is unlikely that all cells penetrated by *T. dubius* die. Wyss worked with isolated root systems, and therefore lack of assimilates may have precluded cell recovery. Although important for the recovery of the cells, the assimilates needed for repair constitute such a small part of the daily assimilate production that they cannot explain the effect of *T. dubius* on the growth of *L. perenne*.

Seinhorst (1981) states that *T. dubius* does not affect water uptake of *L. perenne* at initial nematode densities up to 45 individuals per g soil. He postulated that at lower nematode densities the growth rate should be affected without water consumption being affected.

My simulations show that the effect of *T. dubius* on plant growth at initial nematode densities as low as 13 (T18) and 7 (T25) individuals per g soil could be attributed to a reduction of water uptake. The course of the simulated reduction factor R_{nem} in time (Fig. 9) shows that the length of the period during which a pronounced effect of the nematode on plant properties is likely to be found, increases with increasing initial population density of the nematode. The longer the first sampling is postponed, the less likely it is to find that nematodes at low densities have a pronounced effect on plant properties. As Seinhorst based his theory on an experiment in which the first sampling took place 37 days after the start of the experiment (Seinhorst and Kozlowska, 1979), his observations do not indicate that different mechanisms are operating at low and high nematode densities.

Of the two simulated possibilities of nematode influence on water uptake, the possibility that the permeability of the roots is reduced as a result of the death of some of the penetrated cells is the most likely. To explain the effect in terms of the decreased permeability of recovering cells, requires that these cells have a recovery period of about 3 hours. This is a rather long recovery period, although it falls within the vague boundaries set by Brzeski (1971). Moreover, contrary to the expectations a longer recovery period was needed in my simulations at 25 °C than at 18 °C. A more accurate measurement of the recovery period would show whether temporary disfunctioning of the penetrated cells could contribute to the effect of *T. dubius* on plant growth, or whether growth reduction is only caused by the death of some of the penetrated cells.

My assumptions on the permeability of young and old roots and of affected and non-affected cells were arbitrary. The difference in permeability between various regions along the roots has not been completely quantified (De Willigen and Van Noordwijk, 1987; Drew, 1987). The difference need not be as large as assumed here, but if the reduction in permeability of affected epidermal cells and old parts of the roots becomes less than about 50%, the hypothesis that the effect of *T. dubius* is mainly caused by a direct effect on water uptake is no longer plausible. In that case the nematode density at which the maximum effect is reached is too close to the density at which the moderate effect measured in the simulated experiments was obtained.

An effect of the nematodes on the permeability of the roots might also affect plant growth by influencing nutrient uptake. This hypothesis could not be tested with the present model, because the model assumes there is no nutrient shortage. If such an effect did occur in the simulated experiments, it was so slight that no clear symptoms of nutrient shortage occurred.

Hypotheses implying that the effect of nematodes is caused by induction of hormones or introduction of growth-reducing substances (Seinhorst, 1981) are meaningless unless the crop growth process affected is indicated. Only hypotheses that are quantified at the process level can be quantitatively tested.

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Samenvatting

Simulatie van het waardplant/parasiet systeem Lolium perenne/Tylenchorhynchus dubius. 2. Het effect van T. dubius op L. perenne

Het effect van de ectoparasitaire nematode *Tylenchorhynchus dubius* op het gras *Lolium perenne* werd bestudeerd met behulp van dynamische simulatie. Er werd een vergelijking opgesteld om de snelheid waarmee de nematode epidermiscellen op de wortels aanprikt te berekenen uit nematodendichtheid in de rhizosfeer. Er werd een aantal hypotheses geformuleerd voor de manier waarop de groeiprocessen in de plant door aanprikken van de cellen beïnvloed worden en deze werden ingebouwd in een op SUCROS gebaseerd groeimodel voor het gras. Door middel van berekeningen met het model werd nagegaan in hoeverre de hypotheses het effect van gegeven nematodenpopulaties op de plant zoals dat in proeven gevonden was konden verklaren.

Uit de simulaties bleek dat het onwaarschijnlijk is dat alle door *T. dubius* aangeprikte cellen dood gaan. Het effect van *T. dubius* kan niet toegeschreven worden aan onttrekking van droge stof. De groeireductie kan wel toegeschreven worden aan een door de nematoden veroorzaakte verhoging van de wortelweerstand voor wateropname.

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