Neth. J. Pl. Path. 94 (1988) 33-44

Influence of temperature and soil moisture on the relation between Tylenchorhynchus dubius and Lolium perenne

A.L. DEN TOOM

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

Accepted 12 November 1987

Abstract

The relation between the ectoparasitic nematode *Tylenchorhynchus dubius* and the growth and production of *Lolium perenne* during the first month after sowing, was studied in pot experiments at several temperatures and moisture levels.

The nematode reduced the growth of the grass, mainly as a result of activity during the first weeks after seeding. The percentage decrease of dry matter yield was smaller when temperature was more favourable for plant growth. Decreased moisture content of the soil enhanced the effect of nematodes at 10 °C.

Additional keywords: ectoparasitic nematodes, perennial ryegrass, reseeding.

Introduction

The problems encoutered when reseeding pastures in the Netherlands might be due to nematodes (Van Bezooijen, 1979). A survey of Dutch pastures in 1977 showed that grassland contains large numbers of plant-parasitic nematodes (J. van Bezooijen, personal communication). The populations consist mainly of ectoparasitic nematodes. Short periods without a host hardly influence the population density of ectoparasitic nematodes (Simons, 1973). So these populations will also be present at reseeding. The repercussions of these ectoparasitic nematodes on the growth and production of newly sown grass are not well defined. For example, in experiments with the nematode *Tylenchorhynchus dubius* on *Lolium perenne*, Seinhorst and Kozlowska (1979) did not find yield reduction at densities lower than 0.8 nematodes per gram of soil at 18 °C, whereas Sharma (1971) found a decrease in dry matter production of 35% at a density of 0.2 nematodes per gram at 25 °C. These conflicting results may be due to differences in environmental conditions between the experiments.

In this paper the relation between nematode density and growth and yield reduction is described in the host/parasite system *L. perenne/T. dubius*. *L. perenne* is the prevailing species in seed mixtures used for reseeding grassland. *T. dubius* is one of the most common and numerous ectoparasitic nematodes in Dutch pastures (J. van Bezooijen, personal communication). This nematode feeds on epidermal cells of the apical meristem, the zone of elongation and the root hair zone and on the root hairs (Klinkenberg, 1963; Wyss, 1973). It has been found that on various hosts, reduction of dry matter yield is accompanied by effects on shoot/root ratio, morphology, or

development (Laughlin and Vargas, 1972; Sharma, 1971). Given the location of nematode attack, effects on water balance and uptake of nutrients might be expected. By quantifying the aforementioned effects and evaluating their consequences for crop growth, the relation between *T. dubius* and *L. perenne* can be elucidated.

Materials and methods

At three temperatures and at various moisture treatments, grass growing on soil inoculated with nematodes was compared with grass growing on non-inoculated soil (moisture experiments; T10, T18 and T25). In another experiment (density experiment, N25) the influence of different initial densities of the nematode population on the plant was studied. An overview of these experiments is given in Table 1.

Soil and nematodes. A population of *T. dubius* was multiplied on *L. perenne* grown in containers of a steam-sterilized sandy soil. The containers were kept in a greenhouse, at 18 °C. Similar containers of non-inoculated soil were treated in the same way to provide soil for the controls. Before the soil was used in an experiment, the plants were removed from the containers and the soil was sieved. The moisture content was determined by measuring the weight loss of a sample after drying in an oven for 24 h at 100 °C. Moisture content of the soil was expressed as mass percentage water per unit dry soil. The relation between moisture content and pF is shown in Fig. 1.

Moisture experiments. At the start of the experiments, pots ($9 \times 9 \times 9.5$ cm^3) with a net volume of 400 ml were filled with either inoculated or non-inoculated soil at a dry bulk density of 1.2 g ml^{-1} and 16 seeds of *L. perenne* cv. Pelo were sown per pot at a depth of 0.5 cm.

NPK 20-20-20 fertilizer (458 mg) containing trace elements was supplied to each pot as a watery solution. In addition, in T18 a second application of half of this fertilizer dose was given the day after the third sampling time, because of the fast growth of the

Table 1. Experimental conditions and factors. All experiments were carried out in eight replications and had a randomized block design. Daylength was 16 h in all experiments.

Experiment code	Temperature[1] (°C)	Irradiance[2] (W m^{-2})	Relative humidity (%)	Moisture treatments[3]	Nematode treatments[4]	Sampling times (days after emergence)
T10	10	43	73	W, D	N, C	20, 43
T18	18	108	70	W, D, E	N, C	14, 21, 36, 48
T25	25	108	70	W, D	N, C	22, 30
N25	25	92	70	D	C, N1, N2, N3, N4	16, 30

[1] Day temperature equal to night temperature.
[2] Measured at soil level.
[3] W = wet; D = dry; E = extra dry.
[4] N = soil inoculated with *T. dubius* (N1 . . . . N4 = increasing initial densities of the nematode); C = non-inoculated control.

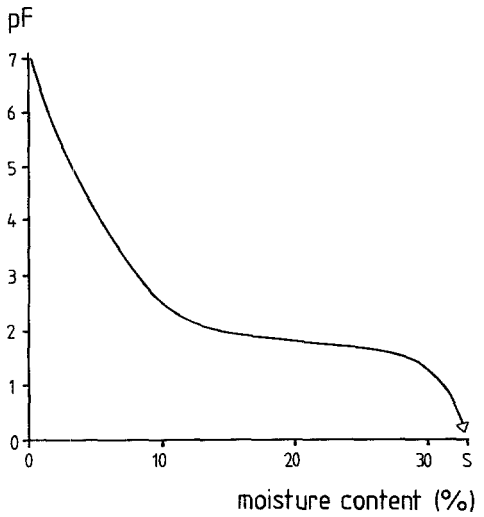

Fig. 1. pF curve of the soil used in the experiments. Horizontal axis: moisture content of the soil (mass of water as a percentage of dry mass of the soil).

plants and the relatively long duration of this experiment. The soil was covered with a layer of gravel to reduce evaporation. The pots were placed under controlled conditions (Table 1). After emergence, the plants were thinned to 12 per pot in experiment T18. Because this number was found to be large relative to the volume of the pot, in the other experiments the number of plants was reduced to 9.

At the start of the experiment the moisture content of the pots was determined by weighing each pot (with known mass of dry soil, pot and gravel) and adjusted to the moisture levels mentioned in Table 2. As soon as the moisture content in one of the pots in the wet treatment fell below the minimum values mentioned in Table 2, all pots

Tabel 2. Moisture treatments.

Experiment	Treatment[1]	Maximum[2]		Minimum[3]	
		%	pF	%	pF
T10	W	25	1.6	15	1.9
	D	16	1.9		
T18	W	25	1.6	11	2.3
	D	16	1.9		
	E	9	2.7		
T25	W	25	1.6	12	2.2
	D	12	2.2		
N25	D	12	2.2	8	3.0

[1] See Table 1 for treatment codes.
[2] Maximum: moisture content of the soil immediately after watering.
[3] Minimum: if moisture content in the wet treatments of the moisture experiments or the control of the density experiment fell below the values indicated, frequency of watering was increased for all treatments of the experiment.

of all treatments were watered in the same way as at the start of the experiment. The frequency of watering ranged from once in four days to once in three days in experiment T10 and from once in two days to twice a day at higher temperatures. In experiment T18 the initial moisture contents of the soil in treatments D and E exceeded 16 and 9%, respectively. In these treatments, half of the dose needed to compensate for evapotranspiration was supplied, until moisture content was at the levels mentioned above. It took about a week to achieve this.

Density experiment. To create a series of nematode densities, inoculated soil and non-inoculated soil were mixed. The resulting densities corresponded to 0, 1, 10, 50 and 100% of the density of the inoculated soil. The experiment was prepared and conducted in the same way as described for the moisture experiments, but to ensure that enough plants would emerge at the high nematode densities used in this experiment, 20 seeds were sown per pot instead of 16.

Nematode counts. The population density of the nematodes was determined on the day of emergence (initial density) and at each sampling time. For this purpose four pots were elutriated with an Oostenbrink elutriator on the day of emergence, two pots from each treatment at the intermediate sampling times and three pots from each treatment at the final sampling time. In experiment N25, juveniles and adult males and females were counted separately on the day of emergence and at the final sampling time.

Crop observations. At the sampling times mentioned in Table 1, destructive sampling took place. The above-ground parts were severed at the soil surface. The number of leaves per pot was counted. Fresh mass per pot was determined and a subsample was taken to measure leaf area. The rest of the shoot was dried in an oven at 100 °C for 16 hours.

Soil was washed of the under-ground parts (roots and stembases) – henceforth called roots – and they were dried. At the third sampling time of T18 and the final sampling time of the other experiments the N, P and K contents were measured in a sample from each treatment.

Results

Nematodes. The nematode population increased exponentially in all nematode treatments, except for the dry treatment of experiment T18 in which no significant multiplication was found. The relative growth rate of the populations increased more than proportionally with temperature (Table 3). In experiment T18, decreased moisture content of the soil led to a lower relative growth rate.

In the density experiment, the relative growth rate (RGR) of the nematode population was lowest at the highest density (Table 4). The percentage of juveniles increased from about 60 to about 80 at all densities.

Crop measurements

Emergence. Time of emergence varied with temperature: 15 days at 10 °C, 5 days at

Table 3. Initial density, final density and relative growth rate (RGR) of the nematode population under different moisture conditions.

Experiment	Treatment[1]	Initial density[2]	Final density[3]	RGR[4] (d^{-1})
T10	NW	5.3a[5]	12.4b	0.020
	ND		12.8b	0.021
T18	NW	6.2a	31.7b	0.033
	ND		23.5c	0.028
	NE		8.1a	0.006
T25	NW	3.3a	35.1b	0.079
	ND		27.4b	0.070

[1] See Table 1 for treatment codes.
[2] Mean of four replicates, expressed as thousands per pot (480 g dry soil in a volume of 400 ml).
[3] Mean of three replicates, expressed as thousands per pot (480 g dry soil in a volume of 400 ml).
[4] Based on four observations in time for T18 and three for T10 and T25.
[5] For each experiment values followed by a different letter differ significantly at $p < 0.05$ (Student's t-test).

Table 4. Initial and final population densities of the nematodes and relative growth rate of the nematode population (RGR) in soils inoculated with different concentrations of nematodes.

Treatment[1]	Initial density[2]				Final density[2]				RGR (d^{-1})
	m	f	j	tot	m	f	j	tot	
C	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.000
N1	0.1	0.2	0.4	0.7	0.2	0.4	1.8	2.3	0.042
N2	1.3	1.3	4.6	7.3	1.8	3.2	29.8	34.7	0.052
N3	5.0	7.3	22.2	34.5	6.2	8.6	70.3	84.8	0.030
N4	12.5	16.1	43.8	72.4	9.9	11.1	86.0	106.7	0.013

[1] See Table 1 for treatment codes.
[2] Number of males (m), females (f), juveniles (j) and total number of nematodes (tot) expressed in thousands per pot. The differences between the treatments are significant (Student's t-test, $p. < 0.05$).

18 °C and 4 days at 25 °C. Neither nematodes nor moisture conditions influenced the time of emergence or number of emerged plants.

Dry matter production. In the density experiment, dry matter yield decreased significantly in all nematode treatments except the one with the lowest initial density. Fig. 2 shows the relation between the logarithm of initial density and dry matter yield at the final sampling time. The correlation coefficient found by linear regression was 0.99; whereas a correlation coefficient of 0.94 was found for regression of dry matter yield on final density of the population.

In the moisture experiments, nematodes had significantly decreased dry matter yield at all sampling times of all experiments, except for the last sampling time of experi-

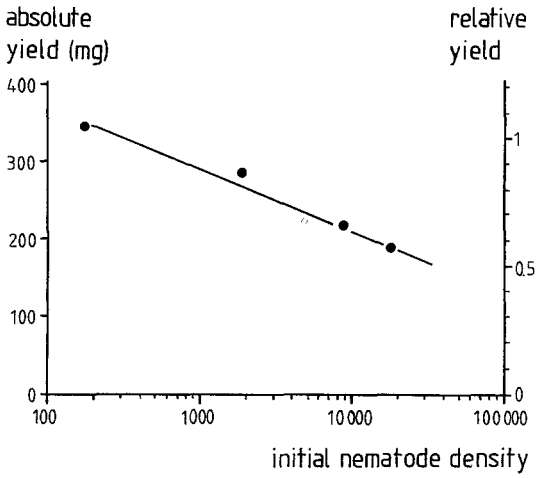

Fig. 2. Relation between initial nematode population per pot and final yield of the nematode treatments in the density experiment N25. Dry matter yield is expressed in mg per pot on the left-hand vertical axis and on the right-hand vertical axis as a fraction of dry matter yield of the control.

ment T18. At this sampling time no negative effect of nematodes was found in the wet treatment, and the negative effect was small in the medium treatment. The decline of the effect of nematodes with increasing water content was probably due to growth reduction in the controls, caused by the restricted room for growth in the pots. To facilitate evaluation of the influence of temperature, moisture and time on the effect of nematodes, dry matter yield of the nematode treatments was expressed as a fraction of dry matter yield of the corresponding controls (relative yield). In experiment T10 both moisture treatments had a relative yield of 0.70 at the first sampling time. Relative yield decreased with time to 0.40 in the wet treatment and 0.33 in the dry treatment. At the first three sampling times of T18 the relative yield was about 0.80 in all moisture treatments. At the final sampling time it was 1.00 in the wet treatment, 0.93 in the medium treatment and 0.80 in the dry treatment. In T25 the relative yield was about 0.60 in both moisture treatments at both sampling times. The relative yield was constant with time in N25 and ranged from 1.00 at the lowest nematode density to 0.55 at the highest nematode density (Fig. 2).

Growth analysis. Growth was analysed to elucidate the effect of nematodes on dry matter yield. The relative growth rate (RGR) of the plants could not be calculated directly from data on dry matter yield, because insufficient data were available. Therefore, the RGR of the plants was calculated from transpiration data. The transpiration of the plants was calculated from the transpiration of the pots, by subtracting the evaporation. Daily evaporation was assessed from transpiration of the pots before emergence. Initially, cumulative transpiration increased exponentially with time (Fig. 3). By plotting the logarithm of cumulative transpiration against time, the RGR of the plants can be calculated as the regression coefficient of the linear part of this curve. This procedure is only valid if there is a constant ratio between transpiration and leaf area and between leaf area and dry mass (i.e. a constant transpiration coefficient, TC). Although this was not the case for the total duration of the experiments, the differences in TC between the first two sampling times of T18 were so small that this assumption might be reasonable for a shorter period.

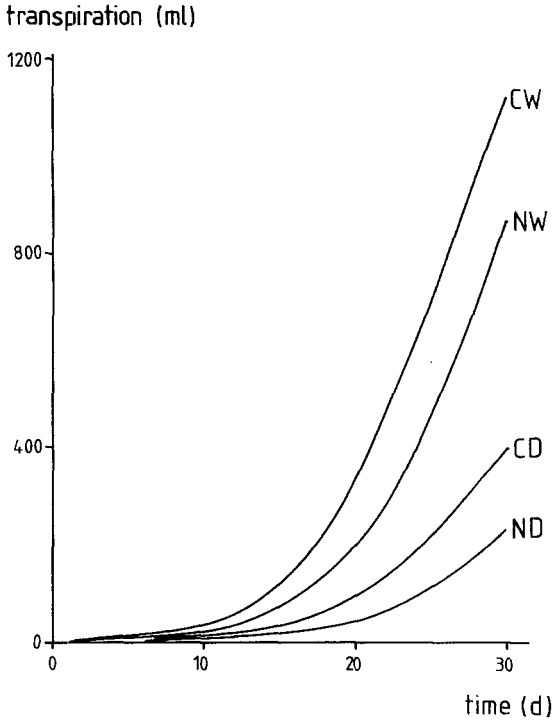

Fig. 3. Course of cumulative transpiration in time in experiment T25. Cumulative transpiration is expressed in ml per pot, and time in days after emergence. CW: wet control, NW: wet nematode treatment, CD: dry control, ND: dry nematode treatment.

Relative rate of increase of the plant mass at the later sampling times was calculated from the increase in the logarithm of cumulative transpiration between the watering times preceding and following the sampling time. Leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) were calculated from measurements at the sampling times; net assimilation rate (NAR) was derived from RGR and LAR. The results of growth analysis for the first sampling time are shown in Tables 5 and 6.

The largest RGR was found in experiment T18, indicating that this temperature was most favourable for growth of perennial ryegrass. Nematodes caused a lower RGR during exponential growth. After the period of exponential growth the relative rate of increase of plant mass decreased with time in all treatments. The relative rate of increase of dry mass of the nematode treatments was generally higher than in the controls after the period of exponential growth, but in T10 it was still lower than in the controls at the final sampling time.

The lower RGR during exponential growth was due to decreased LAR in experiments T18 and N25. In experiment T25 the first sampling took place about a week after the end of the period of exponential growth. At this time no causes of reduced RGR could be found anymore. The decrease in LAR was caused by a decrease in LWR in T18 and by a decrease in SLA in T18 and T25. In T10, LWR was reduced by nematodes, but this did not result in a decrease of LAR in the wet treatment, because SLA was increased by nematodes. Generally, the influence of lower moisture content on RGR, LAR, LWR and SLA at the first sampling had the same direction as that of nematodes. In the experiments T25 and N25, LWR was highest in the nematode treatments at the later

Table 5. Growth analysis of the moisture experiments for the first sampling time, and relative growth rate during exponential growth.

Experiment	Treatment[1]	Time[2]	RGR[3]	NAR[4]	LAR[5]	LWR[6]*	SLA[7]*	TC[8]*
T10	CW	20	0.18	0.7	241	0.75	323	139
	NW	20	0.16	0.6	284	0.73	389	152
	CD	20	0.16	0.6	254	0.70	360	123
	ND	20	0.16	0.7	240	0.67	365	101
T18	CW	14	0.35	2.6	133	0.62	216	192
	NW	14	0.35	3.1	112	0.60	188	210
	CD	14	0.33	2.9	113	0.61	186	141
	ND	14	0.32	3.8	93	0.56	167	140
	CE	14	0.31	3.1	111	0.61	184	112
	NE	14	0.26	3.4	77	0.52	148	86
T25	CW	16	0.31					
		22	0.15	1.0	149	0.62	242	227
	NW	16	0.30					
		22	0.16	0.9	175	0.64	273	232
	CD	16	0.25					
		22	0.16	1.0	149	0.59	253	141
	ND	16	0.24					
		22	0.18	1.2	152	0.60	254	122

[1] See Table 1 for treatment codes.
[2] Duration of period of exponential growth (d) and sampling time in days after emergence (if a second value is indicated, this is the sampling time).
[3] Relative growth rate (d^{-1}).
[4] Net assimilation rate (mg cm^{-2} d^{-1}).
[5] Leaf area ratio (cm^2 g^{-1}).
[6] Leaf weight ratio (g g^{-1}).
[7] Specific leaf area (cm^2 g^{-1}).
[8] Transpiration coefficient (g g^{-1}).
* Results of analysis of variance for the effect of nematodes ($p < 0.05$):
LWR T10, T18, T25: significant;
SLA T10, T25: interaction, T18: significant;
TC T10, T18: not significant, T25: interaction.

sampling times. In experiments T18 and T25, SLA was significantly higher in the nematode treatments at the final sampling times. This effect was caused by a higher dry matter content in the controls, which in turn was probably caused by the overcrowding of the roots.

The influence of nematodes on TC at the first sampling time varied with moisture content of the soil. In the dry treatments, nematodes caused a decrease, whereas a tendency towards increase was found in the wet treatments. Lowering the moisture content caused the TC to decrease both in the controls and in the nematode treatments. At the final sampling times, a significant increase in the TC was found in experiment

Table 6. Growth analysis of the density experiment N25 for the first sampling time, and relative growth rate during exponential growth.

Treatment[1]	Time[2]	RGR[3]	NAR[4]	LAR[5]	LWR[6]*	SLA[7]*	TC[8]*
C	16	0.23	2.5	186	0.67	276	142
N1	16	0.23	3.0	160	0.68	240	138
N2	16	0.22	2.7	162	0.66	252	129
N3	16	0.19	2.7	140	0.69	206	117
N4	16	0.17	2.7	124	0.70	176	113

[1] See Table 1 for treatment codes.
[2] Duration of period of exponential growth (d) and sampling time in days after emergence.
[3] Relative growth rate (d^{-1}).
[4] Net assimilation rate (mg cm^{-2} d^{-1}).
[5] Leaf area ratio (cm^2 g^{-1}).
[6] Leaf weight ratio (g g^{-1}).
[7] Specific leaf area (cm^2 g^{-1})
[8] Transpiration coefficient (g g^{-1}).
* Results of analysis of variance for the effect of nematodes ($p < 0.05$):
LWR : not significant
SLA : significant
TC : significant

T10 and the wet treatment of experiment T25. This does not necessarily imply an increase in transpiration per unit dry matter produced; it may also mean that part of the dry matter produced had died.

Development. Generative development could not occur because the plants were not vernalized. If assessed from the number of leaves, development was reduced to the same extent as growth; the relation between number of leaves and dry mass of the shoot was described by the same curve for all treatments and all experiments. This means that the mass invested in each successive leaf is not influenced by environmental conditions. The number of leaves per tiller was not influenced. Adventitious roots were formed at about the same time as tillering. This process had started by the first sampling of all experiments, except for the nematode treatments of experiment T10.

NPK content. Both nematodes and lower moisture content caused the contents of N, P and K to increase. The slower the growth rate of the plant, the higher the contents of N, P and K.

Discussion and conclusions

Tylenchorhynchus dubius causes growth reduction of *L. perenne*. Clear symptoms do not occur. Growth retardation is accompanied by a proportional reduction of vegetative development. The influence of nematodes on the contents of N, P and K resembles the general effect of growth retardation.

Growth analysis showed that growth retardation is mainly connected with a decrease in LWR and SLA during the period of exponential growth. The effect on LWR was most important at the lower temperatures, whereas the effect on SLA occurred at higher temperatures. In the dry treatments, including the density experiment, TC was initially decreased by nematodes, whereas no effect occurred in the wet treatments. According to the functional equilibrium theory of Brouwer (1962), a decrease in the LWR is a response to decreased uptake of water and/or nutrients. Nematodes reduce water uptake in another way than reduced moisture content of the soil; in the controls, decreased moisture level always caused a decrease of the TC and sometimes a decrease of the SLA. The reduction of water uptake by the nematodes is most severe in the first period of growth of the host, since the effects of nematodes on LWR, SLA and TC disappear later on, or even change direction.

The percentage decrease of dry matter yield in the nematode treatments did not increase after the formation of adventitous roots had started. So the plant seems to be most susceptible to damage by nematodes in the period in which it depends completely on the seminal roots. This may be because of differences in the morphology of the two root systems; possibly the death of epidermal cells hampers root elongation more in the thin seminal roots than in the thicker adventitious roots. Because the nematodes can only feed on young roots, the increase over time in the fraction of old roots may also explain the decrease in the plant's susceptibility.

In the density experiment a linear relation was found between the logarithm of initial density of the nematode population and final dry matter yield of the plant. This relation, which indicates that the effect per nematode decreases with nematode density, has been found for many nematode/host combinations, both in pots and in the field (Oostenbrink, 1966). So it is reasonable to assume that such a relation also applies to the *T. dubius/L. perenne* nematode/host combination at environmental conditions other than those in the density experiment, although the values of the parameters will change.

The relation between nematode density and dry matter production is influenced not only by environmental conditions, but also by the condition of the nematode population at the time of sowing. In the dry treatment of T25 both effect per nematode and RGR of the nematode population were larger than at comparable initial densities in the density experiment, whereas environmental conditions were about the same. The main difference between the two experiments was the much higher density in the stock population of the density experiment. Probably, high nematode density causes irreversible changes in reproductive potential and food requirements of the nematodes involved. Since population density in the stock populations did not vary much for the moisture experiments, it is assumed that differences in effect on dry mass between these experiments are due solely to differences in nematode numbers and environmental conditions and not to differences in condition of the stock populations.

The effect of *T. dubius* on dry matter production was smaller when temperature was nearer to the optimum for growth of *L. perenne*. A decrease in the moisture content of the soil hardly increased the effect of nematodes, except in T10. In this experiment the effect of nematodes on relative yield at the second sampling was enhanced by suboptimal water supply, whereas no difference between the moisture treatments was found at the first sampling. This suggests that the greater damage in the dry treatment resulted from the longer duration of the susceptible period. The same explanation may hold

for the influence of sub- and supra-optimal temperatures on damage. But the lack of effect of suboptimal water supply at the higher temperatures shows that conditions that decrease the growth rate of the plant do not necessarily enhance the effect of nematodes. A smaller susceptibility may have compensated for the longer duration of the susceptible period in the dry treatments. Because water supply in the dry treatments was regular, the plants were able to adapt to suboptimal moisture content of the soil. As nematodes cause an effect comparable to moisture stress, this adaptation may have reduced the plant's susceptibility to the effect of nematodes. Incidental moisture stress will probably have more influence on the effect of nematodes.

Environmental conditions affect the relation between nematodes and their host also by directly influencing the nematode. At the first sampling time the effect in T25 was more marked than in T10. Since the feeding rate of nematodes increases with temperature (Boag, 1980), this may be caused by the nematodes having a higher feeding rate at higher temperatures. However, the results at the final sampling suggest that the influence of environmental conditions on the host is more crucial for the amount of damage than their direct influence on the nematode. It is therefore concluded that a given population of *T. dubius* will cause the smallest percentage decrease in the dry matter yield of *L. perenne* when environmental conditions are most favourable to the growth of the grass.

Acknowledgements

The author wishes to thank ing. B. Kroesbergen for determining the pF curve and Professor Dr R. Rabbinge for critically reading the manuscript.

Samenvatting

Invloed van temperatuur en vochtgehalte van de grond op de relatie tussen Tylenchorhynchus dubius en Lolium perenne

De relatie tussen de ectoparasitaire nematode *Tylenchorhynchus dubius* en de groei en produktie van *Lolium perenne* gedurende de eerste maand na inzaai werd bestudeerd in potproeven bij verschillende temperaturen en vochtgehaltes van de grond.

De nematode veroorzaakte groeireductie die vooral een gevolg was van nematodenactiviteit in de eerste weken na inzaai. Het procentuele effect op de droge-stofopbrengst was kleiner naarmate de temperatuur dichter bij de optimumtemperatuur voor de groei van de plant lag. Bij 10 °C versterkte een lager vochtgehalte van de grond het effect van de nematoden.

References

Bezooijen, J. van, 1979. Nematodes in grasses. Mededelingen van de Faculteit Landbouwwetenschappen Rijksuniversiteit Gent 44/1: 339-349.

Boag, B., 1980. Effects of temperature on rate of feeding of the plant parasitic nematodes *Rotylenchus robustus*, *Xiphinema diversicaudatum* and *Hemicycliophora conida*. Journal of Nematology 12: 193-195.

Brouwer, R., 1962. Nutritive influences on the distribution of dry matter in the plant. Netherlands Journal of Agricultural Science 10: 399-408.

Klinkenberg, C.H., 1963. Observations on the feeding habits of *Rotylenchus uniformis*, *Pratylenchus crenatus*, *P. penetrans*, *Tylenchorhynchus dubius* and *Hemicycliophora similis*. Nematologica 9: 502-506.

Laughlin, C.W. & Vargas, J.M., 1972. Pathogenic potential of *Tylenchorhynchus dubius* on selected turfgrass. Journal of Nematology 4: 277-279.

Oostenbrink, M., 1966. Major characteristics of the relation between nematodes and plants. Mededelingen Landbouwhogeschool Wageningen 66-4.

Seinhorst, J.W. & Kozlowska, J., 1979. *Longidorus elongatus* and *Tylenchorhynchus dubius* on *Lolium perenne*. Nematologica 25: 314-321.

Sharma, R.D., 1971. Studies on the plant parasitic nematode *Tylenchorhynchus dubius*. Mededelingen Landbouwhogeschool Wageningen 71-1.

Simons, W.R., 1973. Nematode survival in relation to soil moisture. Mededelingen Landbouwhogeschool Wageningen 73-3.

Wyss, U., 1973. Feeding of *Tylenchorhynchus dubius*. Nematologica 19: 125-136.