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The influence of cyst nematodes and drought on potato growth

5. Effects on root distribution and nitrogen depletion in the soil profile

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Abstract. In two experiments in the Wageningen Rhizolab with potato cv. Mentor planted in soils with or without potato cyst nematodes (*Globodera pallida, W*) the number of roots per cm^2 was observed two weekly by video camera, in horizontally placed minirhizotrons at depths varying from 5 to 100 cm. In both experiments initial root growth was more rapid in the top soil of the uninfected soil. In the first experiment under optimal water supply, root formation continued longer in the top 30 cm of infested soil leading to twice as many roots at the end of the growing season as in uninfested soil. In the subsoil from 30 to 100 cm, however, root formation was strongly reduced by cyst nematodes leading to an uneven distribution of roots throughout the profile. In the second experiment potato cyst nematodes only increased rooting in the top soil with reduced irrigation. Potato cyst nematodes did not affect the water use efficiency of the crop whereas reduced irrigation increased water use efficiency by about 22%. Without potato cyst nematodes the soil profile was depleted of mineral nitrogen until a depth of 1 m whereas with high initial population densities no nitrogen was taken up in the subsoil between 30 and 100 cm. The spational heterogenity of roots and nitrogen in the soil is an important mechanism of damage. This finding may lead to improved cultural practices and breeding for tolerance.

Introduction

Studies of above-ground crop reactions to differences in environmental factors are more numerous than that of below-ground reactions. Some of the most relevant recent studies are discussed here. Reports often indicate that the potato has a shallower and often less extended root system than many other crops. Water extraction from deeper soil layers (over 30 cm) is less with potato than with crops such as barley, maize and sugarbeet [van Loon, 1981]. A plough pan which hardly bothered other crops, was not penetrated by the relatively weak potato roots [van Loon, 1981]. In a deep homogenous marine-clay soil, however, Vos and Groenwold [1986] found potato roots to reach as deep as 80 to 100 cm below the hill. Between 50 and 60 days after emergence, root decay commenced, starting in the upper horizons. Samples taken by auger showed root densities between 1 and 2 cm cm^{-3} in the hill but less than 1 cm cm^{-3} beneath the furrow, maximum root length varied between 3.4 and 7.1 km m^{-2}.

Beside mechanical impedance and limited oxygen supply, low soil temperatures and metal (aluminium) toxicity are major abiotic factors that restrict the exploration and exploitation of the soil [Goss et al., 1993]. They reviewed root growth and distribution in relation to nutrient availability and uptake but did not discuss the consequences of biotic (e.g. potato cyst nematode) factors on root growth and distribution.

Evans [1982] grew four cultivars of potatoes in plots of land which had either few or many potato cyst nematodes per unit weight of soil following the growth of resistant or non-resistant cultivars in the previous season. Shoot to root ratios (S/R) were decreased by nematode attack but the magnitude of this effect was similar in the four cultivars tested with S/R-values varying from 11.9 to 5.6 at 9 weeks from planting in lightly and heavily infected soil respectively. The root weights of two susceptible cultivars (Maris Peer and Pentland Dell) decreased, whereas the root weights of two tolerant cultivars (Pentland Crown and Cara) increased after infection. Under heavy attack, the rooting density in the top 75 cm of the tolerant cv. Cara was more than doubled whilst that of susceptible cultivars was less than half.

Fasan and Haverkort [1991] observed in container experiments that both drought and potato cyst nematodes led to decreased S/R ratios of potato cv. Mentor. With drought, shoot dry matter decreased more than root dry matter but with potato cyst nematodes the decrease of S/R was only due to a reduction of the shoot dry matter whereas the total root dry mass production was not affected by nematode attack.

Lescynski and Tanner [1976] described irrigated field-grown Russet Burbank with up to 2300 m of root length per plant distributed mainly in the top 40 cm. Clearly there is variation in root system size (overall length and rooting depth) depending on cultivar, soil type, whether or not there is a soil pan, whether the crop is irrigated or if it is affected by potato cyst nematodes. A comprehensive study of the development of the potato root system was carried out by Evans et al. [1977] who used cv. Maris Piper (tolerant) and Pentland Dell (intolerant) infected by four different levels of potato cyst nematodes. Heavily attacked plants had much less extensive root systems than lightly attacked ones, with root density particularly decreased below the ridge soil; lateral roots were more decreased than main roots. Maris Piper had deeper, more extensive, more branched roots under heavy nematode attack than Pentland Dell. Evans and Haydock [1990] provided a more detailed comparison of root growth in Cara (tolerant and Pentland Crown (less tolerant). Cara rooted deeper and showed twice the length of roots against a transparent window than Pentland Crown; the differences were enhanced by nematode attack.

Huisman et al. [1969] screened 118 potato clones for tolerance of potato cyst nematode attack in the field and found that the cultivar Multa significantly out-yielded all others tested. Examination of the root anatomy showed differences in the degree of necrosis between more and less tolerant cultivars. Non-resistant, less tolerant cultivars showed extensive necrosis around feeding cells after the nematodes matured, but little during their development. Tolerant cultivars showed little necrosis at any time and vigourously growing callus formed around the feeding cells. Resistant cultivars showed severe necrosis around the feeding sites as soon as they were initiated and this caused the enclosed feeding cells to deteriorate.

From literature it appears that studies of potato root systems after nematode attack are relatively few and mainly report on the changes of root mass and shott/root ratios. The objectives of the present research were to study the effect of potato cyst nematode (*Globodera pallida*) on temporal and spatial root distribution and dynamics of root growth and its consequences for mineral nitrogen depletion in the rooted and non-rooted parts of the soil profile. The study was carried out in the Wageningen Rhizolab [van de Geijn et al., 1994] where frequent and non-destructive root and soil mineral nitrogen content observations are possible from 5 to 100 cm soil depth.

Materials and methods

Two experiments were carried in four compartments of the Wageningen Rhizolab with cultivar Mentor and the potato cyst nematode *G. pallida.* The first experiment with different nematode densities was carried out in 1991 (Expt. 1) and the second comparing the effect of drought and cyst nematodes on root distribution was carried out in 1992 (Expt. 2).

Root, water and mineral nitrogen recording. The Wageningen Rhizolab, a versatile facility for root study [van de Geijn et al., 1994], completed in 1990 consists of 16, 2 m deep, compartments with an area of 1.25 $\times$ 1.25 m^2. Eight compartments are situated on either side of a 2 m wide underground corridor. Twelve 1.3 m long glass tubes of 6 cm diameter (minirhizotrons) are placed horizontally at depths varying from 5 to 175 cm with the opening on the corridor side. Through these openings a specially adapted video camera was inserted every 2 weeks to record a 1.3 $\times$ 1.8 cm^2 area at 36 positions on the upper face of each tube. Details of the root recording system are given by Smit et al. [1994]. The photograph shown in Plate 1 illustrates the recorded image and how data are interpreta: a: no roots recorded, b: 5 roots recorded, c: 9 roots recorded and d: 8 roots recorded. After the growing season the number of roots (including their side branches) per video image was counted, and the mean value per cm^2 of the 36 positions was plotted versus the soil depth of each tube. Water was applied by drip irrigation based on automated soil moisture measurements and tensiometry once or twice per week to replace the water taken

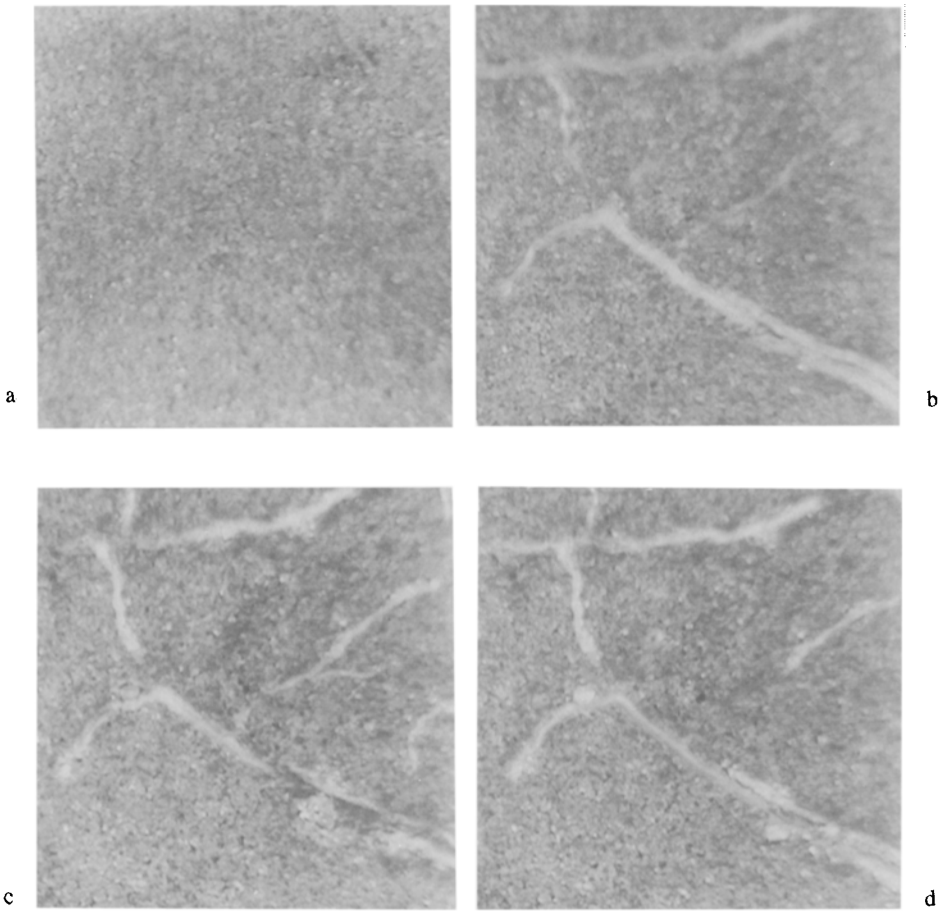

Plate 1. Formation of roots and cysts observed at the same minirhizotron position with 40 living eggs g^{-1} soil in Expt. 1. (a) 20; (b) 52; (c) 116; (d) 165 days after planting.

up by the crop [van de Geijn et al., 1994] and its amount was recorded. Samples of soil water were extracted two weekly at the various soil layers with 10 cm intervals and were analyzed for the mineral (NO_3^- and NH_4^+) N content [van de Geijn et al., 1994].

Plant and soil treatment. The bottom 1 m of each compartment was filled with coarse sand without organic matter where no roots grew. On top of this a 70 cm layer of humic sandy soil was added without potato cyst nematodes. The top 30 cm was taken from a field from the North East of the Netherlands on which potatoes were grown in the previous season and consisted of a light sandy soil with an initial nematode density (P_i of 40 live eggs per g soil for Expt. 1 and 15 eggs per g for Expt. 2, determined following procedures described by Haverkort et al. [1992]. Part of the soil was irradiated with 1 MRad gamma radiation which killed all nematodes but left fungi and bacteria unaffected [Haverkort and Fasan, 1991]. At the start of the experiments, the soil water content was near field capacity.

Expt. 1 contained the following treatments:

Compartment 1: no living potato cyst nematode eggs present, irradiated soil only;
Compartment 2: 1 part of untreated soil was thoroughly mixed with 15 parts of irradiated soil leading to a P_i of 2.5 living eggs per g soil;
Compartment 3: 1 part of untreated soil mixed with 3 parts of irradiated soil (P_i = 10);
Compartment 4: untreated soil with a P_i of 40.

In Expt. 2 P_i-values of 15 and 0 eggs per g soil were arrived at through similar irradiation and mixing procedures. In this experiment nematode infection was studied in comparison to and in combination with drought, whereby the droughted treatments at each application (once or twice per week) only received half the amount of water of the controls; the following treatments were created:

Compartment 1: P_i = 0, optimal water supply;
Compartment 2: P_i = 15, optimal water supply;
Compartment 3: P_i = 0, water supply half of Compartment 1 from planting onward;
Compartment 4: P_i = 15, water supply half of compartment 2.

Three weeks before transplanting seed potatoes of cv. Mentor which is moderately tolerant of potato cyst nematodes *G. pallida*, were placed 5 cm deep in trays filled with sand. When the plants were about 15 cm tall, they were detached from the mother tuber and transplanted (henceforward referred to as 'planting') in a 20 cm × 25 cm planting pattern (30 plants per compartment). A similar planting pattern was adapted for the guard rows surrounding the compartment. Fertilizer (NPK) was applied prior to planting at rates recommended for starch potato production based on soil analysis. Transplanting took place on May 17 1991 for Expt. 1 and on April 28 1992 for Expt. 2. At the single final harvest of Expt. 1 on October 29 1991 and of Expt. 2 on September 14 1992, total fresh matter of tubers and non-tuber plant parts was weighed (roots excluded) and their dry matter content determined by drying samples overnight at 105 °C.

The limited availability of Rhizolab space did not allow for replication of treatments but the material (plants and soil) was very homogenous and cyst nematodes and water were applied such as to create a wide range of treatments assuring that differences observed between the compartments were not coincidental.

Results and discussion

Dry matter production and tuber numbers. Table 1 shows that at P_i = 40 eggs g^{-1} soil tuber yield and number were about one third of the control treatment without nematodes. Second lowest yields in Expt. 1 were recorded at Pi = 10 whereas tuber yields were hardly affected and total dry matter production was decreased at only 10% with 2.5 eggs per g soil. Increased nematode densities were associated with increased harvest indices, from 0.69 at Pi = 0 to 0.80 at Pi = 40, indicating [as was also reported by Evans and Haydock, 1990] that cyst nematode infection induced the potato plants to senesce earlier.

Dry matter yields and tuber numbers were less in Expt. 2 than in Expt. 1 because harvest took place 6 weeks earlier in 1991 than in 1992 and the foliage was confined to the planted area with netting whereas in 1991 the haulms spilled over the planted experimental area because plants in the guard rows grew less abundantly. Under optimal water supply, a P_i of 15 eggs g^{-1} decreased tuber dry matter yields by 20% compared with the pest free (1.46 kg m^{-2} versus 1.83 kg m^{-2}) whereas the same P_i reduced tuber yields by 30% when only 50% water was supplied (1.23 kg m^{-2} versus 1.74 kg m^{-2}). At P_i = 0, reduced water only slightly reduced tuber yield. (2608 g versus 2738 g per compartment) mainly because drought reduced haulm growth and increased the harvest index (0.69 versus 0.61). An increase in water-use efficiency [Vos and Groenwold, 1986; Haverkort and Fasan, 1991], probably also reduced the effect of drought.

Table 1. Total and tuber dry matter production (root mass excluded), harvest index (tuber dry weight as proportion of total dry weight), number of tubers and water use efficiency (WUE) at final harvest on October 29, 1991 (Expt. 1) and September 14, 1992 (Expt. 2)

Expt.	Treatment	Total (kg)	Tuber (kg)	Harvest index	Number of tubers	WUE (g l–1)
1	Pi = 0 eggs g^{-1}	4.53	3.13	0.69	320	5.51
	Pi = 2.5 eggs g^{-1}	4.05	3.01	0.75	242	5.96
	Pi = 10 eggs g^{-1}	2.67	2.00	0.75	206	5.79
	Pi = 40 eggs g^{-1}	1.33	1.00	0.80	116	5.94
2	Pi = 0 eggs g^{-1}, water 100%	2.98	1.83	0.61	121	4.85
	Pi = 15 eggs g^{-1}, water 100%	2.26	1.46	0.65	106	4.65
	Pi = 0 eggs g^{-1}, water 50%	2.53	1.74	0.69	100	5.98
	Pi = 15 eggs g^{-1}, water 50%	1.85	1.23	0.66	79	5.52

Root observations in Expt. 1. Fig. 1a shows the number of roots per cm^2 of the minirhizotron surface observed in the top soil (mean values of the 36 positions of the five tubes placed in the upper 30 cm). In the absence of nematodes the number of roots was greatest at 50 days after planting; from then on rooting did not increase in this treatment. In infested soils the intensity increased until 120 days after planting before it levelled off and reached double the number of roots (about 2 per cm^2 of the control treatment without nematodes. Little difference was observed between the various nematode densities from $P_i = 2.5$ to 40 living eggs per g soil. Nematodes apparently led to a strong increase of the ramification of roots in the top soil. Subsoil numbers of roots (mean values of the 36 positions of the four tubes placed between 30 and 100 cm depth), contrary to what was shown in the topsoil, decreased with increasing nematode densities, especially at $P_i = 40$ (Fig. 1b). Maximum subsoil numbers of roots were reached at about 80 days after planting at $P_i = 0$. From then on a slight decrease (due to root decay) was observed in the control whereas at P_i =

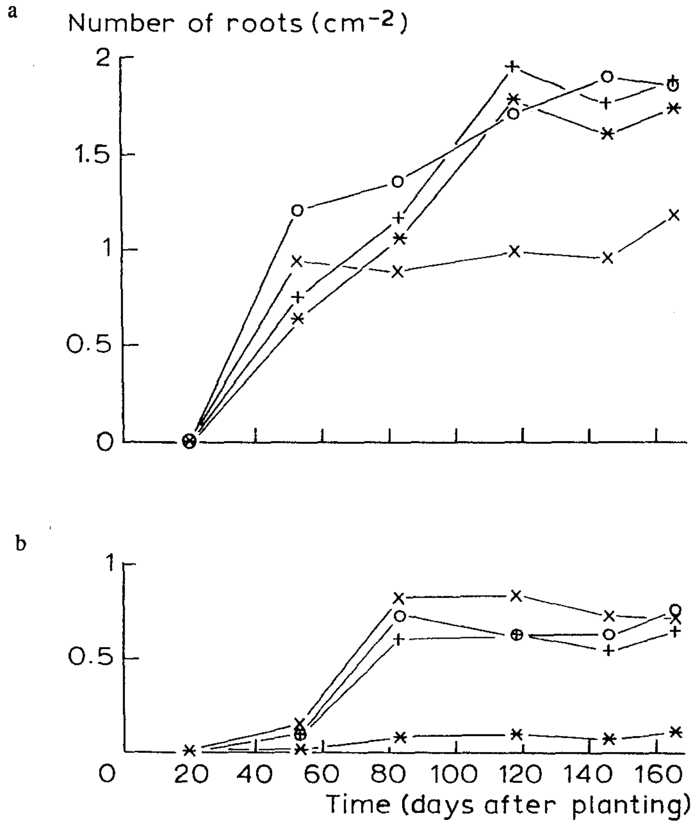

Fig. 1. Number of roots with time in Expt. 1. (a) top soil 0–30 cm; (b) subsoil 30–100 cm. × $P_i = 0$, o $P_i = 2.5$, + $P_i = 10$ and * $P_i = 40$ viable eggs per g soil.

2.5 and $P_i = 10$ still a slight further increase was observed. From these results it can be concluded that potato cyst nematodes lead to an increase in rooting intensity in the topsoil and to a decreased intensity in the subsoil. This phenomenon is explained assuming that potato cyst nematodes lead to increased branching of roots in the infected top soil (which decay subsequently as they are not recovered when soil auger samples are washed [Haverkort, 1993] and to a decreased penetration into the subsoil.

Fig. 2 shows the number of roots with soil depth at 83 days after planting in soils without and with 40 living eggs per g soil. The high nematode density led to a high number of about 1.7 roots per cm^2 at 10 cm soil depth and to few roots below 60 cm depth where hardly any roots were observed. Between 83 and 166 days after planting the number of roots almost doubled at 5 cm depth with the highest nematode density leading to the high number of roots in the infected topsoil observed in Fig. 1. Root numbers increased much less, at all depths, in the treatments without potato cyst nematodes and where a relatively even distribution of roots was observed throughout the season. Vos and Groenwold [1986] reported a much stronger decline of root length density with soil depth than we found with regard to root numbers. This may be due to differences in soil type (they observed roots in a clay soil with different horizons whereas we observed roots in a homogeneously packed compartment) and in cultivar. Moreover, their method (auger sampling) may well have led to a loss of thinner roots expected to be present below 30 cm soil depth. Nematodes apparently led to continued formation of new roots until the end of the growing period. It is not clear from the observations whether all roots

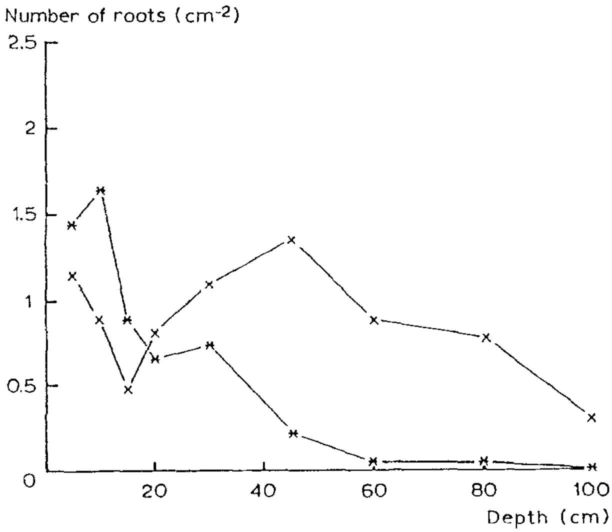

Fig. 2. Number of roots with soil depth in Expt. 1. at 83 days after planting. × $P_i = 0$ and * $P_i = 40$ viable eggs per g soil.

observed still were alive so it is possible that continuously new roots were formed because the older ones died off. All treatments showed much fewer roots at 15 cm to 20 soil depth than at surrounding shallower or deeper soil layers. The reasons for this 'dip' are not clear but may have to do with a change in root direction from horizontal to vertical root growth or, more likely with a reduced presence of roots at this depth possibly due to absence of water (which was supplied weekly to the top of the soil) and to the absence of nitrogen (which was partly taken up by the roots and which partly may have leached to deeper soil layers, Fig. 6), thus inducing plants to form less roots at this soil layer.

Root observations in Expt. 2. A nematode density of 15 living eggs per g soil with adequate water supply, contrary to the finding in Expt. 1 (Fig. 1a), did not lead to an increase of the number of roots in the top soil in Expt. 2 (Fig. 3a). Although it is not clear why no increase was observed we think that this discrepancy was due to the high soil compaction which

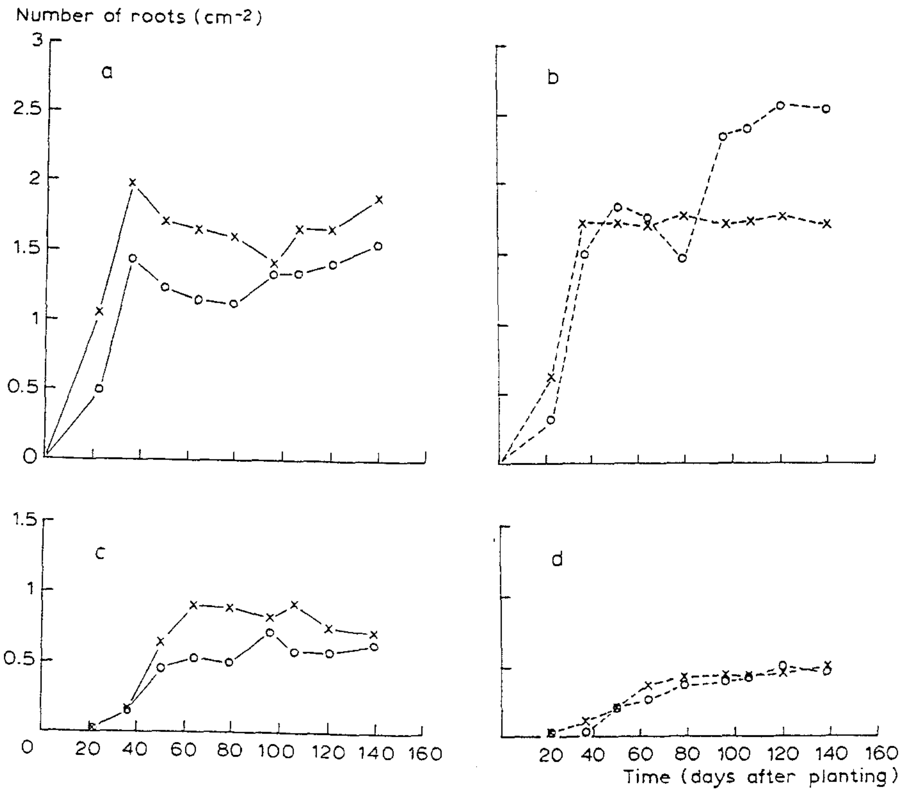

Fig. 3. Number of roots with time in Expt. 2. in the topsoil from 0–30 cm (a and b) and in the subsoil from 30–100 cm and (c and d) under adequate water supply (a and c, × $P_i = 0$, o $P_i = 15$ eggs g^{-1}) and under 50% of adequate water supply (b and d).

occurred when the compartments were filled for the first experiment. The high soil compaction may also have led to the slow initial development of the crop in Expt. 1 and especially may have induced root growth in the infested top soil at the expense of root growth in the subsoil. Between 30 to 100 cm (Fig. 3c), as in Expt. 1, nematode infection reduced the number of roots. Where only half the amount of water of the control treatment was given (Fig. 3b) the response in the top soil (a strong increase in rooting intensity associated with cyst nematode infestation) was similar to that in Expt. 1. Root numbers in the subsoil in the droughted treatments (Fig., 3d), however, were very low (less than 0.5 roots per cm^2) both in the infested and uninfested soils.

Fig. 4 shows the numbers of roots as a function of soil depth at 96 days after planting. Similar to Expt. 1, the control treatment (no cyst nematodes, no drought) showed the most even distribution pattern of roots in the soil with intensities varying from about 0.5 root per cm^2 at 1 m depth to about 1.5 roots per cm^2 in the top soil. Drought led to an increase in the number of roots in the topsoil, contrary to what might be expected under field conditions. In our system the plants were watered very regularly (about twice per week) and only give half the amount of water of he controls (with and without nematodes). This reduced, but regularly applied amount of water, likely remained in the topsoil inducing the plants to root growth just there, whereas in field conditions with longer and more severe dry

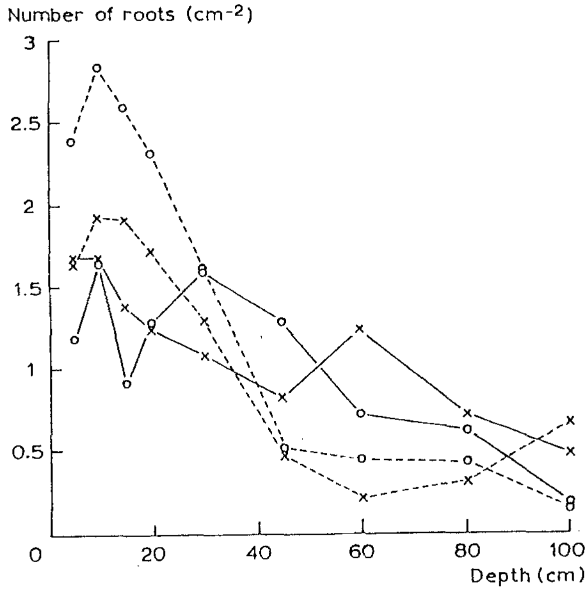

Fig. 4. Number of roots with soil depth in Expt. 2. at 96 days after planting. × P_i = 0, o P_i = 15 eggs g^{-1}, ———— 100% irrigation, --------, 50% irrigation.

spells, plants depend on deeper roots for their water supply from deeper soil layers.

This study showed that potato cv. Mentor subjected to potato cyst nematodes. *Globodera pallida* is induced to form new roots in the topsoil for a much longer period than in uninfested soil. Towards crop senescence this led to about twice the number of roots. Root growth below 30 cm, however, was slowed but continued much longer in the uninfested soil.

Water use and nitrogen depletion. As was found under field conditions [Haverkort et al., 1992] there was no interaction between drought and cyst nematode infection as total dry matter production was not reduced more than proportionate to water use. The cumulative amount of water supplied to the crop in Expt. 1 is shown in Fig. 5. At harvest on October 29 1991 the control ($P_i = 0$) compartment had used 822 l the $P_i = 2.5$ compartment 680, the $P_i = 10$ compartment 461 and the $P_i = 40$ compartment had used 224 l of water per m^2. Potato cyst nematode infection clearly reduced the amount of water taken up by a potato crop as was shown before [e.g. Haverkort and Fasan, 1991] in container experiments under semi-controlled conditions. The water-use efficiency (WUE, g of total dry matter produced per l of water used (Table 1)) was hardly affected by potato cyst nematode infection as it varied between 5.51 g l^{-1} and 5.94 g l^{-1} at $P_i = 40$. Drought, however did affect the water-use efficiency to a greater extent (Table 1): the WUE of the well watered treatments in Expt. 2 were 4.75 g l^{-1} on average (somewhat lower than in Expt. 1 because temperatures and light intensity were higher in 1992 than in 1991) whereas the droughted

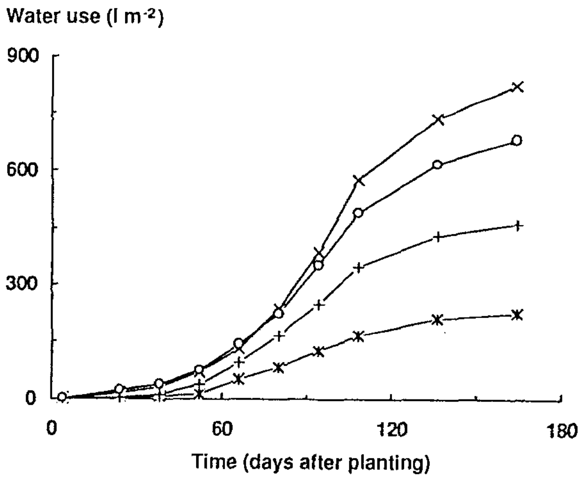

Fig. 5. Cumulative water use with time in Expt. 1. × $P_i = 0$, o $P_i = 2.5$, + $P_i = 10$ and * $P_i = 40$ viable eggs per g soil.

treatments (mean values of infected and uninfected compartments) showed a WUE of 5.75 g l^{-1} on average.

A possible unability of the roots to take up water under the conditions of the experiments not likely contributed to the reduction in growth of the potato crops, as in Expt. 1. the crop was watered according to its needs. Water tension in the rooted zone was never less than half field capacity and the water-use efficiency was not affected by the nematode infection. Hence, the unavailability of nutrients, notably of nitrogen in the soil may have been responsible for reduced crop growth. Fig. 6 shows the cumulative amounts of soluble mineral N at various soil depths with time. In the absence of nematodes (Fig. 6a) the upper 20 cm was depleted within 30 days after planting and at P_i = 2.5 (Fig. 6b) within 47 days after planting.

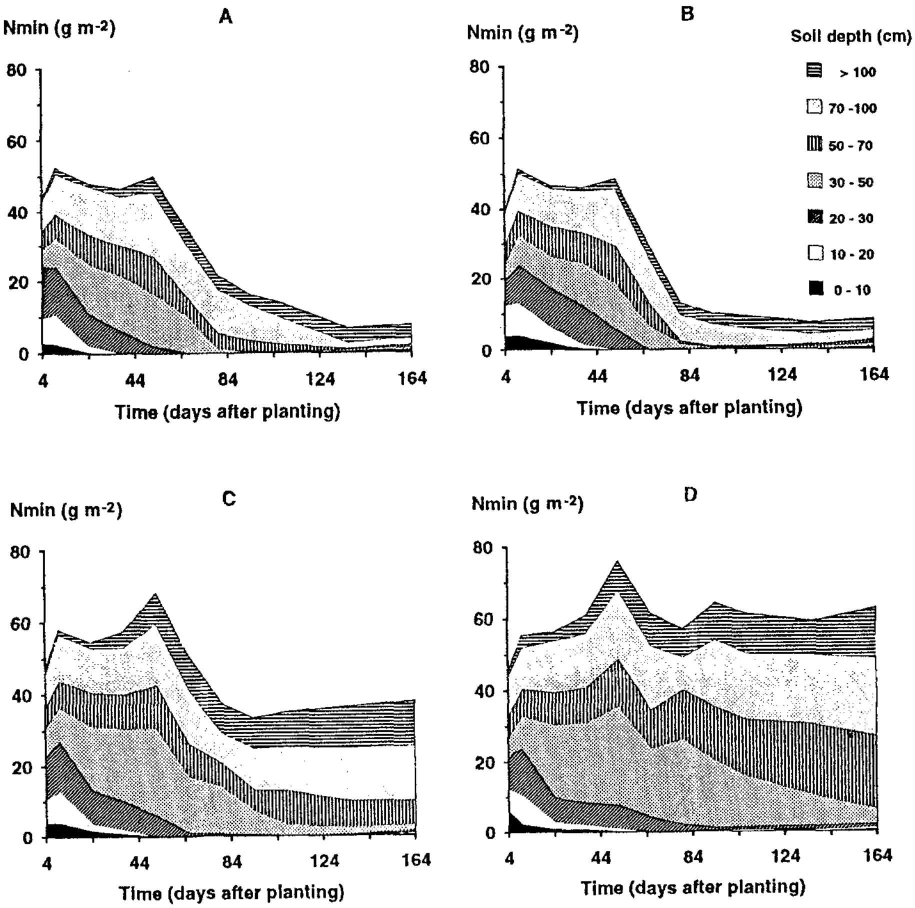

Fig. 6. Cumulative soil mineral nitrogen in various soil layers with time in Expt. 1. 6a P_i = 0, 6b P_i = 2.5, 6c P_i = 10 and 6d P_i = 40 viable eggs per g soil.

At the end of the growing season in these compartments the crops growing at these low nematode densities had almost taken up all the mineral nitrogen in the soil profile at less than 10 g m^2 was left. No leaching of nitrogen from the upper layers to lower layers had taken place in these compartments. In the compartments with the highest nematode densities (P_i = 10 and 40, Figs. 6c and 6d) nitrogen depletion in the infested upper 30 cm was much slower than in the compartments with low nematode densities. This is explained by the reduced presence of roots in the heavily infested top soil at 60 days after planting (Fig. 1a). With time, from day 60 onward, root densities in the heavily infested topsoil increased well above those of the control (Fig. 1a) but the nitrogen in the topsoil from day 60 onward had either been taken up or had leached to the lower soil horizons where less roots were present (Fig. 1b). Evidence of nitrogen movement from the topsoil to the subsoil is most apparent in the P_i = 40 compartment (Fig. 6d) where the amount of mineral nitrogen per m^2 strongly increased in the horizons deeper than 50 cm. Mineralization of organic N during the growing season, likely contributed to this effect but could not be separated from leaching.

The results indicate that major mechanisms of the yield reduction following infection with potato cyst nematodes are: firstly a slow initial root growth in the top soil when nitrogen is still present there, secondly a continued proliferation of roots in the topsoil in the second part of the growing season when most of the nitrogen in the topsoil is depleted because it has been taken up or leached to the subsoil and thirdly the reduced presence of roots in the subsoil in the second half of the growing season where nitrogen is amply available but beyond reach of the roots.

Our results are in line with those of Evans et al. [1977] who also reported a strong decline of roots below the ridge after nematode infection. Our results also corroborate the observations of increased root weights in infected soils [Evans, 1982] and decreased shoot/root ratios [Evans, 1982 and Fasan and Haverkort, 1991]. Beside the changes in spatial distribution induced by cyst nematodes, our research also shed light on the changes of temporal dynamics: the high top soil root densities are caused by a prolonged formation of roots and not by a more rapid early root formation. Continuous nematode attack in the top soil induced the plants to continuous formation of new roots in the top soil and may have reduced their ability to form roots at greater soil depths reducing their ability to take up nitrogen. Tolerance of potato cyst nematode might be improved by cultural practices which assure the presence of water and nutrients where the roots are throughout the growing season, i.e. the topsoil through regular irrigation and split nitrogen applications to avoid leaching and through breeding for cultivars with deeper root systems.

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