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Effects of potato-cyst nematodes (*Globodera pallida*) and soil pH on root growth, nutrient uptake and crop growth of potato

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Abstract

Potato-cyst nematodes (*Globodera pallida*) cause severe yield losses in potato. Plants infected with potato-cyst nematodes generally have reduced concentrations of nitrogen, phosphorus and potassium in the foliage. This study investigated whether reduced growth of nematode-infected potato is caused by nutrient limitation.

Experiments in the field and in containers showed that phosphorus concentration correlated best with total crop biomass at early stages of growth. The role of phosphorus in nematode damage was further investigated in the field and in the Wageningen Rhizolab. The experimental field was infested with potato-cyst nematodes and two levels of nematode density were established by fumigation with a nematicide. Prior applications of calcium carbonate resulted in pH_{KCl} levels of 4.8 and 6.1. Two levels of phosphorus fertiliser were applied: either 0 or 225 kg P ha^{-1}. In the Wageningen Rhizolab, soil of both pH levels from the field was used after treatment with 1 MRad gamma irradiation to kill the nematodes. Subsequently, half of the soil was inoculated with cysts to give a nematode density of 30 viable juveniles per gram of soil.

In the field, nine weeks after planting, the total crop biomass ranged from 107 g m^{-2} for the treatment with nematodes at pH_{KCl} 6.1 without phosphorus fertiliser to 289 g m^{-2} for the fumigated treatment at pH_{KCl} 4.8 with phosphorus fertiliser. The differences in total biomass for the various treatments were explained by differences in foliar phosphorus concentration. Nematodes induced or aggravated P deficiency and reduced total biomass. This was not the only damage mechanism as at high, non-limiting levels of foliar phosphorus concentration, nematodes still reduced total biomass.

In the Wageningen Rhizolab, directly after planting, the number of roots visible against minirhizotrons was reduced by nematodes. However, the increase of root number in the nematode treatment continued longer than in the control, until root number was higher than that of the control. The compensary root growth of the nematode treatment was restricted to the top 30 cm and nematodes reduced rooting depth.

High soil pH reduced growth, mainly by reducing the availability of phosphate. Both nematodes and high soil pH reduced nutrient uptake per unit root length. Our results lead us to suggest an interaction between nematodes and soil pH, with nematode damage being higher at pH_{KCl} 6.1 than at pH_{KCl} 4.8.

Introduction

Potato-cyst nematodes (*Globodera* spp.) are major pests of potato in the Netherlands and cause severe yield losses. These losses depend on the population density of the nematode at planting, the potato cultivar, the weather and the soil type (Evans and Haydock, 1990; Trudgill, 1986).

Potato-cyst nematodes survive in the soil as eggs within a cyst. When a host crop is grown, exudates from the roots stimulate the eggs to hatch (Triffitt, 1930). Subsequently, the juveniles invade the roots, thereby destroying root cells, and induce a feeding site (Jones, 1981). Nematode infection has a direct effect on root elongation, as root length is reduced within a few days (Arntzen et al., 1994; Rawsthorne and Hague, 1986).

When measured in field experiments, crops infected by potato-cyst nematodes generally have a reduced root weight several weeks after planting. However, nematodes reduce top growth more than root growth, resulting in a reduced ratio of top weight to root weight (Evans, 1982; Trudgill and Cotes, 1983). This indicates that nematodes not only reduce root elongation but also impair physiological functioning of the roots.

Yield loss following nematode infection is often associated with reduced light interception by the crop due to reduced crop leaf area. Infected crops show delayed canopy closure and senesce earlier than uninfected crops (Haverkort et al., 1992; Mulder, 1994; Trudgill et al., 1990). The effects at the end of the growing season are but the end-result of primary responses originating in the root system when juveniles penetrate the roots. At the beginning of the season, growth of nematode-infected crops can be reduced due to a reduced photosynthetic rate and due to a dry matter distribution unfavourable for the formation of leaf area. Thirty days after planting of four potato cultivars in pots of soil with 100 eggs of *G. pallida* per gram of soil, photosynthetic rates per unit leaf area were 70% lower than in uninfected controls (Schans and Arntzen, 1991). The photosynthetic rates increased again in the following weeks. Schans (1991) and Schans and Arntzen (1991) asserted that cyst nematodes primarily affect the hormonal balance of the plant, leading to impaired crop photosynthesis. Additionally, nutrient deficiency can affect photosynthetic rates (Nátr, 1992) and crops infected by potato-cyst nematodes generally have reduced foliar concentrations of nitrogen, phosphorus and potassium (Evans and Franco, 1979; Trudgill et al., 1975a,b). Trudgill (1980) showed in a pot test that nematode damage interacted strongly with the availability of N and of P. Doubling the amount of N and P provided, more than doubled top weight when the nematodes were not controlled, but had little effect when the nematodes had been controlled with a nematicide. The effects of increased availability of N and P were apparent at both 7 and 14 weeks after planting, when additional fertilisation increased foliar nutrient concentrations and reduced nematode damage. These results were corroborated by field experiments at sites infested by potato-cyst nematodes, where application of compound fertiliser increased growth more in the absence of a nematicide than with a nematicide (Trudgill, 1987).

Another indication of decreased nutrient uptake caused by potato-cyst nematodes is the interaction between nematode damage and soil pH (Haverkort et al., 1993). In a container experiment, nematodes reduced tuber yield by 19% at pH_{KCl} 4.5, but by 44% at pH_{KCl} 6.5. Soil pH affects the solubility of ions in the soil and thereby the availability of phosphorus. On acid soils, below a pH_{KCl} of 4.5, phosphorus availability is reduced by increased availability of aluminium. At high soil pH, increased concentrations of calcium result in increased phosphorus fixation. The increased yield loss caused by potato-cyst nematodes at pH_{KCl} 6.5 compared with pH_{KCl} 4.5 may be explained by an effect of both soil pH and nematodes on the uptake of phosphorus.

Our objective was to examine the effects of potato-cyst nematodes and soil pH on potato growth and the role of nutrients in nematode damage. The effect of fertilisation on growth and on the reduction of nematode damage can be through increased initial growth and earlier canopy closure, or by increasing canopy persistence. We focused on the early stages of crop growth, particularly on the role of nutrients in nematode damage during these stages. We sought to answer the following questions: (1) do nematodes induce nutrient limitation during early crop growth? If so: (2) which nutrients are involved, (3) which nutrient is most limiting, (4) is nematode induced nutrient deficiency remediable, and (5) how does soil pH influence the effects of nematodes on nutrients?

Materials and methods

Three field, two container experiments and an experiment in the Wageningen Rhizolab studied the effects of potato-cyst nematodes (*Globodera pallida*) on above and below-ground growth and nutrient uptake (details are in Table 1). The experimental fields were naturally infested with potato-cyst nematodes. Two levels of infestation were obtained by soil fumigation of half the area with the nematicide Monam (active ingredient sodium methyldithiocarbamate, 51%), applied by rotary spading injector. For the container experiments, soil was taken from infested fields and half of it was irradiated with 1 MRad gamma radiation to kill the nematodes for the control treatment. Nematode densities prior to planting were determined in soil samples. Cysts were extracted by using the Schuiling centrifuge and, after removing adhering organic matter by acetone, the number of cysts was counted. The cysts were crushed to expose eggs and juveniles and

Table 1. Details of the experiments

Year	Experiment 1 1989	Experiment 2 1990	Experiment 3 1990	Experiment 4 1991	Experiment 5 1995	Experiment 6 1995
Site	Eeserveen field	Eeserveen field	Wageningen containers	Wageningen containers	Vlagtwedde field	Wageningen Rhizolab
Soil type	sandy	sandy	peaty	peaty	sandy	sandy
Organic matter	6.5%	6.5%	10%	22%	6%	6%
Soil pH_{KCl}	5.2	5.2	5.5	4.5, 6.5	4.8, 6.1	4.6, 6.1
Soil treatment	Monam,[1] 500 l ha^{-1}	Monam,[1] 500 l ha^{-1}	irradiation, 1 MRad	irradiation, 1 MRad	Monam,[1] 600 l ha^{-1}	irradiation, 1 MRad
Nematode density (viable eggs/g dry soil)	6 and 26	6 and 58	0 and 19	0 and 27	between 2 and 57	0 and 30
Other treatments	irrigation: with, without	irrigation: with, without	drought: none, early	soil pH: 4.5, 6.5	P-fertilisation: with, without	soil pH: 4.6, 6.1
Cultivars	Mentor Astarte Darwina Desiree Elles	Mentor Darwina Desiree Elles	Mentor	Mentor	Mentor	Mentor
Planting date	April 20	April 17	April 24	May 2	April 21	May 12[2]
Planting pattern	0.3 × 0.75 m	0.3 × 0.75 m	6 plants/ container	6 plants/ container	0.3 × 0.75 m	0.2 × 0.25 m.
Harvest date	July 19	July 18	June 6	June 24	June 21, Aug. 15, Sept. 14	Aug. 21
Number of replicates	2	2	3	3	6	—

[1]Active ingredient: sodium methyldithiocarbamate 51%; [2]Planting of plantlets.

mixed with water. In duplicate samples of the solution the number of viable eggs and juveniles, with a distinct border between the oesophagus and intestinal region (LaMondia et al., 1986), were then counted. In Exp. 5, the total number of cysts per sample was counted and 300 cysts were soaked for one week in tap water and crushed. The eggs were put in fresh potato root diffusate for 10 days and after that, the total number of emerged juveniles was counted. With this procedure, more than 95 percent of the viable eggs are detected (H. Regeer, pers. comm.).

Total crop biomass excluding fibrous roots was measured between 43 and 116 days after planting and nutrient concentrations in the leaves were determined. Dry weight was determined by drying samples of the plants for 24 h at 105 °C. Total nitrogen concentration in the dry matter was determined using the Dumas-method (Macro N, Foss Heraeus), phosphorus concentration was assessed colorimetrically (Starrcol) after destruction with H_2SO_4/HNO_3 and potassium concentration was measured by atomic sorption (AS Varian AA10).

The crops were adequately protected against *Phytophthora infestans* by spraying the fungicide maneb/fentin acetate several times, according to current farming practice.

Experiments 1 and 2

The effects of nematodes and drought on growth of different cultivars were studied in two field experiments in Eeserveen, the Netherlands (Table 1). Nematode densities prior to planting were determined by taking soil samples (100 g) of each plot to a depth of 30 cm.

Differences in soil water availability were obtained by irrigating one half of the area at regular intervals by overhead sprinkler irrigation. Irrigation was applied mainly from mid-July onwards.

The trials were laid out in a split–split-plot design with two replicates, irrigation was in the main plots, fumigation was in the subplots and cultivars were in the sub-subplots. Eight plants per plot were harvested.

Prior to planting and following soil analysis and recommendations, the field was fertilised with 180 kg N, 52 kg P and 125 kg K per hectare. By the end of June an additional 30 kg N per hectare was applied. More details about these experiments are given by Haverkort et al. (1992).

Experiment 3

The effects of nematodes and early drought were studied in a container experiment under a rain shelter in Wageningen (Table 1). Polyester containers, measuring 0.6 m × 0.9 m by 0.4 m high were filled with sandy soil from an experimental field near Assen, the Netherlands. Nematode densities prior to planting were determined in a bulked soil sample of 350 g.

At planting, the total mineral nitrogen content of the soil was 11.3 g per container. The P and K status of the soil were not determined. Additional fertilisation consisted of 4.1 g P and 10.5 g K per container. Six tubers were planted per container. At planting, the soil was at field capacity and the control treatments were watered twice a week to maintain soil moisture. For the early drought treatment, containers were not watered until 43 days after planting (d.a.p.).

The experiment was carried out in three blocks within which were randomised containers with or without nematodes and watered or not watered. Containers were placed in three rows with one guard container at both ends of each row. Space between the containers was about one meter. More details on this experiment are given by Fasan and Haverkort (1991).

Experiment 4

Effects of nematodes and soil pH were studied in containers under a rainshelter in a similar set-up as Exp. 3. Soil with a pH_{KCl} of 4.5 and 6.5 was taken from an experimental field in Tweede Exloërmond, the Netherlands. On this field, different levels of soil pH were obtained by application of various amounts of calcium carbonate over several years. Nematode densities prior to planting were determined in a bulked soil sample of 350 g.

At planting, the total mineral nitrogen content of the soil was 11.2 g per container. The P and K status of the soil were not determined. Additional fertilisation consisted of 5.6 g, N, 4.1 g P, 7.1 g K and 1.6 g Mg per container. More details on this experiment are given by Haverkort et al. (1993).

Experiment 5

The effects of nematodes, soil pH and phosphate fertilisation on crop growth and foliar nutrient concentrations were studied in a field experiment in Vlagtwedde, the Netherlands (Table 1). The pH of the soil, measured as pH_{KCl}, was 5.0 in 1984 and by applying various amounts of calcium carbonate over four years pH values of 5.2 and 6.9 were obtained. Since 1987 no calcium carbonate was applied and pH values decreased to 4.8 and 6.1.

There were six blocks, each of which was split for the two levels of soil pH. Perpendicular to this, each block was split and one half was fumigated. The four subblocks were further split into two plots that received either zero or 225 kg P per hectare, applied as triple superphosphate. The phosphorus fertilizer and a basal dressing of 230 kg N and 125 kg K were applied prior to the soil fumigation. Plot size was 8 m × 4.5 m.

Nematode densities prior to planting were determined by soil core sampling. Of each plot, 15 cores to a depth of 25 cm were taken, a total of about 400 g of soil. The availability of phosphorus was determined 11 weeks after fertilisation and after ridging of the 75 cm spaced rows by measuring the amount of water-extractable soil phosphate (Pw) (Sissingh, 1971) in a soil sample of about 300 g. The soil was sampled by taking ten soil cores in the centre of the ridge to a depth of 30 cm.

Seed potatoes, class A, grade 35–55 mm, were planted on April 21 at a spacing of 30 cm within rows and 75 cm between rows. Before canopy closure, 61 days after planting, a group of twelve plants per plot was harvested. After foliage death, 146 days after planting, tubers of 24 plants per plot were harvested. At the first harvest, total fresh weight of the above-ground plant parts was determined and a sample of ten stems was taken and divided into stems and leaves. Leaf area was determined with a LiCor 3100 Area Meter (Li-Cor Inc., Lincoln, Nebraska, USA). Tubers and the underground part of the stem with stolons and thick roots were dug up and rinsed.

Root length at 61 days after planting was assessed by taking soil core samples of 4.77 cm diameter in the centre of the ridge between plants at three depths (0–15, 15–30 and 30–45 cm). In each plot two replicate samples were taken. The soil samples were stored at $-18\,^{\circ}C$ until processing. After thawing, the roots were rinsed free of soil by hydropneumatic elutriation (Smucker et al., 1982) and root length was determined

by the line intersect counting method (Tennant, 1975). Total root length (km m^{-2}) was calculated by multiplying root length density (cm cm^{-3}) by the volume of soil per square metre of surface area for each soil layer of 15 cm. For this, a homogeneous horizontal distribution of roots was assumed, and a triangular shape for the ridges of 20 cm high and 75 cm wide.

As an estimation for the uptake of N, P and K per unit root length, total nutrient uptake at 61 days after planting was divided by the total root length at that time.

Experiment 6

This experiment was carried out in the Wageningen Rhizolab. For a detailed description of research methodology and main functions of this facility we refer to Van de Geijn et al. (1994) and Smit et al. (1994). The following is a brief description.

The experiment was carried out in four compartments of 1.25 m × 1.25 m and 2 m deep. The bottom 1 m of each compartment was filled with coarse sand without organic matter. On top of this a 70 cm layer of a sandy soil with 4% organic matter was placed. Soil for the top 30 cm was taken from the field of Exp. 5 before fertilisation and soil fumigation. The pH of the collected soil was 4.6 and 6.1. The Pw of the collected soil was 62 for pH 4.6 and 58 for pH 6.1. The soil of both pH levels was irradiated with 1 Mrad gamma radiation that killed all nematodes (Fasan and Haverkort, 1991). Fungi and bacteria are less affected by this level of radiation (Becking, 1971). The soil of both pH levels was split and one half was inoculated with cysts of *Globodera pallida* to a density of 30 viable juveniles per gram of soil. Before inoculation, the contents of the cysts were determined by putting duplicate samples of 500 cysts in potato root diffusate and weekly counting the number of emerged juveniles. The test ended when only few juveniles emerged.

The soil for the top 30 cm was fertilised with amounts equivalent to 100 kg N, 44 kg P and 166 kg K per hectare. For an equal distribution of nematodes and fertiliser, the soil was thoroughly mixed in a concrete mixer. The mixing did probably not affect nematode viability, because unlike migratory plant-parasitic nematodes, which lack a protective cyst, cyst nematodes are not sensitive to mechanical damage (Boag, 1988).

During filling of the compartments, glass minirhizotrons of 6 cm diameter were installed horizontally at various depths (5, 10, 15, 20, 30, 45, 60 and 85 cm). Horizontal placement reduces effects of the minirhizotrons on spatial distribution of roots, as roots don't track along the glass surface (De Ruijter et al., 1996). To measure soil moisture and temperature, ceramic cups and hydrophilic microporous tubes were installed at several depths. Periodically, soil solution was extracted and mineral nitrogen concentrations were determined with a TRAACS 800 continuous flow analysis system.

Single-stem plantlets were used rather than seed tubers to diminish plant variation. Sixteen days before transplanting, tubers were placed 5 cm deep in trays filled with potting compost. On May 12, the plants were carefully detached from the mother tuber and shoots of equal size were selected. The planting pattern was a 20 cm × 25 cm grid with 30 plants per compartment. The same planting pattern was applied to the guard rows surrounding the compartment.

During growth, soil moisture content was measured regularly by measuring the dielectric constant of the soil and water was maintained by drip irrigation. No rain water reached the compartments as the Rhizolab rain shelter unfolded when rain was detected.

Roots showing at the minirhizotron surface were recorded every 14 days with a video camera (Smit et al., 1994). The video tapes were processed by counting the number of roots visible in each image of 14 mm × 18 mm, 36 images per minirhizotron. Branches were counted as individual roots. For each minirhizotron, the 36 images were averaged and a single number of roots per cm^2 minirhizotron surface was calculated.

Crop development was followed by measuring height. Concentrations of N, P and K were determined in the second leaflet from the top of the topmost fully expanded leaf at several dates. Before foliage death, 101 days after planting, the entire crop was harvested. The total crop biomass (excluding fibrous roots) and foliar nutrient concentrations at harvest were determined.

Statistical analyses

Statistical analyses were performed using Genstat (Genstat 5 Committee, 1993). The measurements in Exp. 5 were analysed using analysis of variance (ANOVA) corresponding to the split-plot design used and by using multiple regression analysis. LSD values were derived from the ANOVAs. The limited availability of the Rhizolab space in Exp. 6 did not allow for replication of treatments. To minimise coincidental

differences between the compartments, uniform planting material and homogenised soil were used. Potatocyst nematodes and soil pH were applied such as to create clear differences between the treatments.

Results

Experiments 1–4

Figure 1 shows the relationship between total crop biomass (excluding fibrous roots) and foliar nutrient concentrations at the periodic harvests in Exps 1–4. Nematodes reduced total biomass and often also reduced foliar nutrient concentrations (open symbols vs. closed symbols). In general, total biomass was positively correlated with concentrations of P and K. Relationships between total biomass and N concentration were less clear and varied between experiments. In Exps 3 and 4, foliar concentrations of nitrogen did not differ between fumigated and non-fumigated treatments, whereas total biomass and P and K concentrations were lower in the non-fumigated treatment (Figure 1C and 1D).

The relationship between foliar K concentration and total biomass was not always positive. In Exp. 2 (Figure 1B) high levels of nematodes reduced total biomass. With nematodes (non-fumigated) a significant negative relationship was found ($P < 0.001$, R^2_{adj} 0.65) and the highest dry matter yields were found at the lowest K concentrations.

In Figure 1, deficiency (left arrow) or sufficiency (right arrow) levels are indicated on the abscissa. These levels were calculated with data on concentrations in leaf blade and in petiole from Lorenz and Tyler (1983; cited by Walworth and Muniz, 1993) and with a leaf composition of 75 percent blade and 25 percent petiole (J. Vos, pers. comm.). As harvest dates varied, levels for midseason are indicated for Exps 1 and 2 and levels for early season were taken for Exps 3 and 4.

As most irrigation in Exps 1 and 2 was applied from mid-July onwards, after the time of the periodic harvest, effects of irrigation were small and not significant. In Exp 3, early drought reduced total biomass and foliar P concentration (Figure 1C). Drought hardly affected foliar K concentration and increased N concentration. With nematodes, drought did not affect total biomass nor foliar nutrient concentrations.

The effect of nematodes on total biomass and on foliar P and K concentrations interacted with the soil pH treatment. Yield loss by nematodes was greater at pH 6.5 than at pH 4.5 and at pH 6.5 yield loss was associated with decreased concentrations of P and K.

Experiment 5

The role of phosphorus in the mechanism of nematode damage was studied further in Exp. 5. Prior to planting, nematode population densities at pH 4.8 were almost twice as high as at pH 6.1 (Table 2). Soil fumigation reduced initial nematode population densities to low levels of 5 and 6 juveniles per gram of soil for pH 4.8 and 6.1 respectively. The availability of phosphorus, expressed as Pw, was 34 percent higher at pH 4.8 than at pH 6.1 (Table 2). Phosphorus fertilisation increased Pw by 34 percent at both pH levels, giving a larger absolute increase of Pw at pH 4.8 than at pH 6.1. Fumigation did not affect Pw.

The different treatments significantly affected total dry biomass at 61 days after planting (d.a.p.) and final tuber yield (Table 3). High levels of nematodes in non-fumigated soil reduced total biomass by 24–40 percent at 61 d.a.p. The relative effects on final tuber yield were similar. There was a significant interaction between effects of soil pH and phosphorus fertilisation on total biomass at 61 d.a.p. Total biomass was higher at pH 4.8 than at pH 6.1 and was increased by phosphate fertilisation, but the increase was greater at pH 6.1 than at pH 4.8. Interactions between soil fumigation and pH or phosphorus fertilisation were not significant. However, the initial nematode density at pH 6.1 was half that at pH 4.8 (Table 2) but gave similar yield reductions as at pH 4.8 (Table 3). When the initial nematode density was taken into account in a multiple regression analysis, significant effects on total biomass were found for the initial nematode density, soil pH and for the interaction between the nematode density and soil pH.

In Figure 2A–C, total crop biomass at 61 days after planting is plotted against foliar concentrations of nitrogen, phosphorus and potassium. There was a positive relationship between total biomass and foliar nutrient concentrations. Foliar N concentrations were reduced by nematodes (Table 3) but the reduced dry matter production could not be attributed to nitrogen limitation, as P fertilisation led to large differences in total biomass at equal N concentrations (Figure 2A). The variation in total biomass was associated with a relatively small variation in N concentration (Figure 2A) and relatively large variation in P concentration (Figure 2B). K concentrations were around or below the indicated deficiency level. A positive trend between total biomass

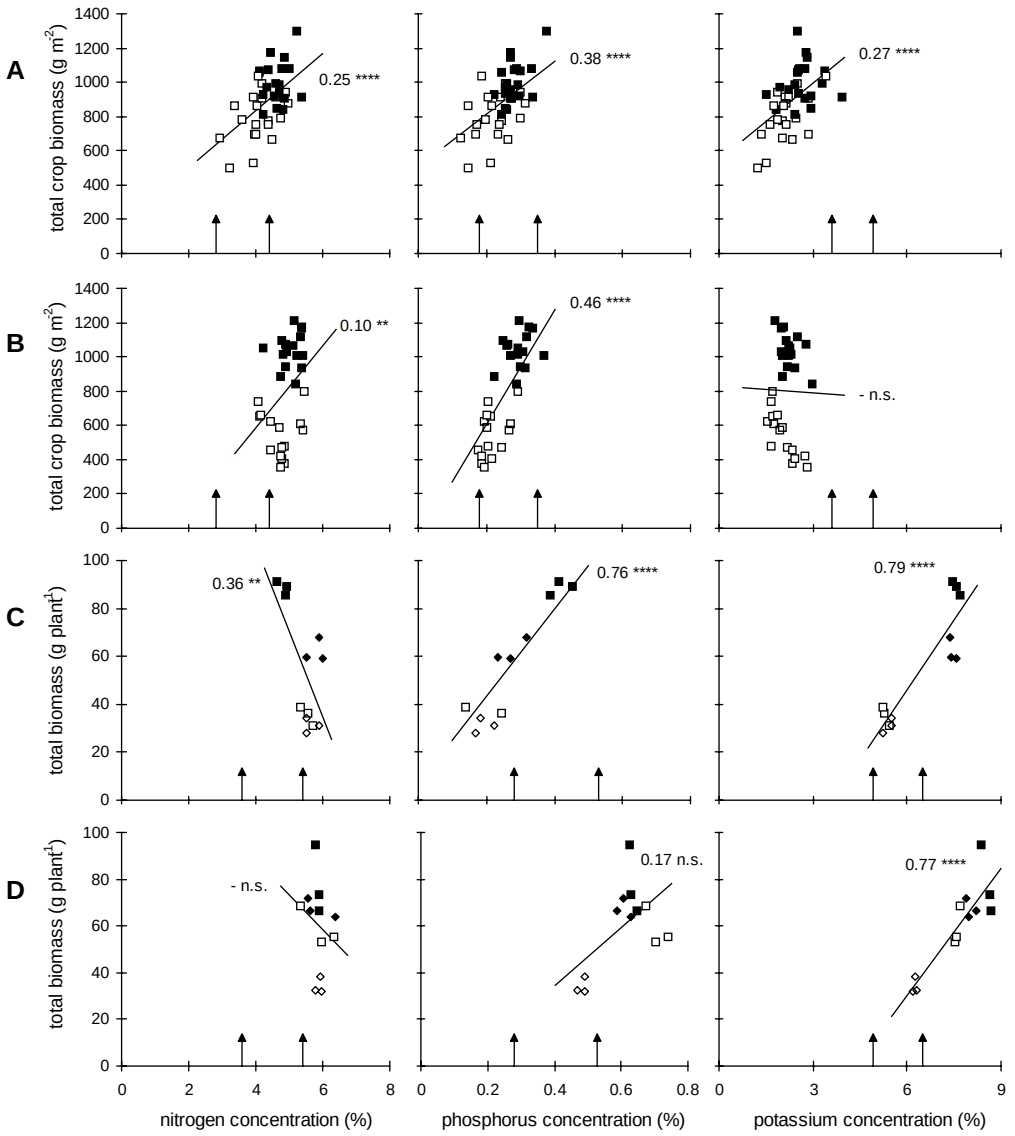

Figure 1. Total biomass (g m^{-2} and g plant^{-1}) vs. nutrient concentrations of the green leaves (%). Closed symbols: fumigated soil, open symbols: non-fumigated soil. Numbers in the graph indicate the R^2_{adj} of the regression, asterisks indicate significancy by which the slope of the regression differs from zero: **** $P < 0.001$, *** $0.001 < P < 0.01$, **$0.01 < P < 0.05$ and *$0.05 < P < 0.10$. (A) Exp. 1, 90 d.a.p.; (B) Exp. 2, 92 d.a.p.; (C) Exp. 3, 43 d.a.p., squares: control, diamonds: drought; (D) Exp. 4, 53 d.a.p., squares: pH_{KCl} 4.5, diamonds: pH_{KCl} 6.5. The arrows on the abscissa indicate deficiency (left arrow) or sufficiency (right arrow) levels according to Walworth and Muniz (1993).

and K concentration was visible but the relationship was weak (Figure 2C). As in Exp. 2, at high levels of nematodes a significant negative relationship was found ($P = 0.028$, R^2_{adj} 0.13) between total biomass and foliar K concentration.

On fumigated soil, the reduced total biomass at pH 6.1 without P fertilisation (Figure 2B, closed circles) was associated with low values of foliar P concentration, close to the deficiency level (left arrow on the abscissa in Figure 2B). P fertilisation increased P

Table 2. Effects of treatments on initial nematode density (juveniles per gram of soil) and phosphorus availability index (Pw) at planting, and their effects on root length density ($cm\,cm^{-3}$) at three depths between plants in the center of the ridge at 61 days after planting. Experiment 1. P− = 0, P+ = 225 kg P ha^{-1}

Treatment			Nematode density	Pw	Root length density		
					0–15 cm	15–30 cm	30–45 cm
pH 4.8	P−	Fumigated	5	58	2.16	2.24	1.66
		Nematodes	47	64	1.25	1.77	0.98
	P+	Fumigated	5	84	2.01	1.86	1.34
		Nematodes	47	80	1.40	1.57	0.62
pH 6.1	P−	Fumigated	6	44	2.11	2.39	1.13
		Nematodes	25	47	1.51	1.93	0.66
	P+	Fumigated	6	63	1.87	2.08	0.81
		Nematodes	25	59	1.08	1.50	0.52
LSD (0.05)			6	10	0.64	0.75	0.48

Table 3. Average values of total crop biomass ($g\,m^{-2}$) and concentrations of nitrogen, phosphorus and potassium in the green leaves (%) in Exp. 5. LSD = least significant difference. P + = 225 kg P ha^{-1}, P − = no phosphorus fertiliser, Fum = fumigated, Nem = nematodes

	Total crop biomass		Damage (%)	Foliar nutrient concentrations					
				Nitrogen		Phosphorus		Potassium	
	Fum.	Nem.		Fum.	Nem.	Fum.	Nem.	Fum.	Nem.
61 days after planting									
pH 4.8 P+	289	219	24	5.81	5.32	0.622	0.506	5.13	4.06
pH 4.8 P−	284	194	32	5.92	4.94	0.561	0.380	4.75	4.03
pH 6.1 P+	249	160	36	5.64	5.00	0.456	0.388	5.47	4.44
pH 6.1 P−	178	107	40	5.45	4.96	0.370	0.302	5.14	4.66
LSD (0.05)	34		21	0.35		0.055		0.59	
116 days after planting									
pH 4.8 P+	1699	1224	28	4.17	3.42	0.151	0.112	2.70	2.49
pH 4.8 P−	1596	1134	29	3.93	3.47	0.132	0.117	3.27	2.53
pH 6.1 P+	1544	981	36	3.85	3.60	0.116	0.113	4.48	3.85
pH 6.1 P−	1210	766	37	3.70	3.75	0.112	0.125	4.23	4.02
LSD (0.05)	208		22	0.41		0.021		0.76	
146 days after planting[1]									
pH 4.8 P+	1439	1028	29	—	—	—	—	—	—
pH 4.8 P−	1374	963	30	—	—	—	—	—	—
pH 6.1 P+	1206	822	32	—	—	—	—	—	—
pH 6.1 P−	1004	598	40	—	—	—	—	—	—
LSD (0.05)	117		18						

[1]Only tubers harvested.

concentration and total biomass (Figure 2B, closed triangles). Nematodes reduced yield and reduced foliar nutrient concentrations within each combination of soil pH and P fertilisation (Table 3 and Figure 2, open vs. closed symbols). At low P concentrations (±0.4%), total biomass was similar for the fumigated and nematode treatment. At high P concentrations (≥0.5%), close to the sufficiency level, yields were higher on fumigated soil than with nematodes (Figure 2B).

Multiple regression analysis showed that variation in total biomass was significantly ($P \leq 0.006$) explained by a quadratic effect of P concentration, by the initial population density of the nematodes and by the interaction between P concentration and nematode density. In Figure 2B, regression lines for the effects of P concentration are drawn for the average nematode densities on fumigated and non-fumigated soil, respectively 5 and 36 living juveniles per gram of soil.

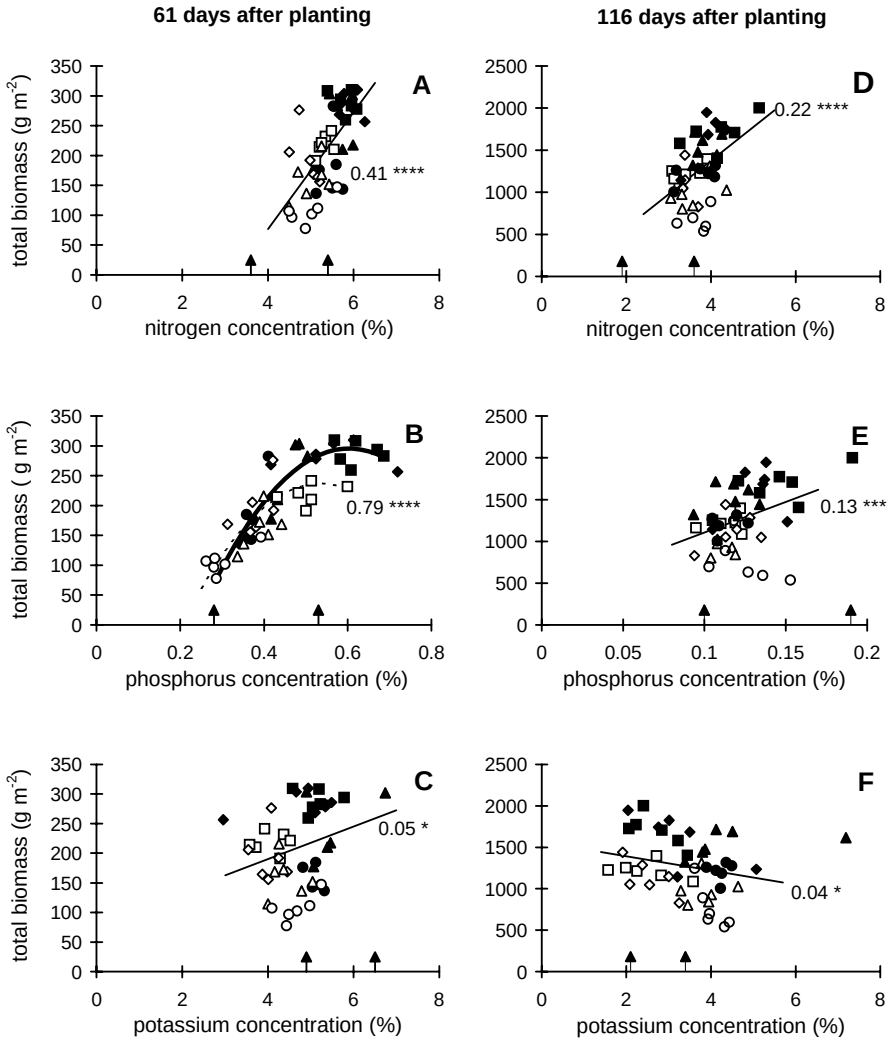

Figure 2. Total crop biomass ($g\,m^{-2}$) vs. nutrient concentrations of the green leaves (%), Exp. 5A, B, C: 61 d.a.p.; D, E, F: 116 d.a.p. Closed symbols: fumigated soil, open symbols: non-fumigated soil. pH_{KCl} 4.8, ◇ P +; pH_{KCl} 4.8, P −; Δ pH_{KCl} 6.1, P +; ○ pH_{KCl} 6.1, P −. Numbers in the graph indicate the R^2_{adj} of the regression, asterisks indicate significancy of the slope of the regression: **** $P < 0.001$, ***$0.001 < P < 0.01$, **$0.01 < P < 0.05$ and *$0.05 < P < 0.10$. The arrows on the abscissa indicate deficiency (left arrow) or sufficiency (right arrow) levels according to Walworth and Muniz (1993). Note the different horizontal axes in Figure 5(B) and 5(E).

Figure 2D–F show the relationship between total biomass and foliar nutrient concentrations at 116 days after planting. By then, about half of the leaves had turned yellow or were dead. Nutrient concentrations in the green leaves had decreased compared to the levels at 61 days after planting (Table 3). Contrary to the first harvest date, at 116 days after planting there was no clear positive relationship between total biomass and foliar P concentration (Figure 2E). Between total biomass and K concentration (Figure 2F) there was a negative relationship. When fumigated or non-fumigated plots were observed separately, this negative relationship was more clear. Despite the absence of a positive relationship between total biomass and foliar nutrient concentrations, the relative effects of the different treatments on total biomass were similar to those at 61 d.a.p. (Table 3).

Root length density (RLD) in soil cores between plants in the ridge was decreased by nematodes (Table 2). Phosphorus fertilisation also reduced RLD

but these reductions were smaller than those caused by nematodes. The effect of soil pH on RLD varied and interacted significantly with depth, mainly because average RLD at 30–45 cm depth was about 30 percent smaller at pH 6.1 than at pH 4.8. At 0–15 and 15–30 cm depth, differences between the two pH levels were small. Nematodes and phosphorus fertilisation did not affect vertical distribution of the roots, as there were no significant interactions with depth. There were no significant interactions between the treatments on RLD. Neither were significant interactions found when the initial nematode population density was taken into account by multiple regression analysis.

At 61 d.a.p., nematodes did not significantly affect the ratio between total root length and total leaf area (RL/LA) per plant (Table 4). RL/LA was affected by both soil pH and phosphorus fertilisation. RL/LA varied between 4.12 km m^{-2} at pH 6.1 without phosphorus fertiliser and 1.67 km m^{-2} at pH 4.8 with phosphorus fertiliser.

The calculated uptake of N, P and K per unit root length was significantly increased by phosphorus fertilisation (Table 4). Soil pH significantly affected uptake of P per unit root length, e.g., without P fertilisation uptake of P was 0.202 g km^{-1} at pH 4.8 and 0.092 g km^{-1} at pH 6.1. Nematodes significantly reduced uptake of P and K per unit root length. There were no interactions between treatments on nutrient uptake per unit root length, even when the differences in initial nematode population density were taken into account.

Experiment 6

Nematodes reduced crop height similarly at both pH levels (Table 5). At the end of the experiment, 101 d.a.p., total biomass was strongly reduced by nematodes at both pH levels. Soil pH affected neither crop height nor total biomass.

Table 4. Effects of treatments on the ratio between root length and leaf area (RL/LA, km m^{-2}) and nutrient uptake per unit root length (g km^{-1}), Experiment 5, 61 days after planting. P− = 0, P+ = 225 kg P ha^{-1}

Treatment			RL/LA (km m^{-2})	Nutrient uptake of the roots (g km^{-1})		
				N	P	K
pH 4.8	P−	Fumigated	2.08	2.09	0.202	2.73
		Nematodes	2.41	1.79	0.136	2.31
	P+	Fumigated	1.75	2.50	0.271	3.41
		Nematodes	1.67	2.43	0.232	2.94
pH 6.1	P−	Fumigated	3.27	1.43	0.092	1.95
		Nematodes	4.12	1.19	0.064	1.49
	P+	Fumigated	1.88	2.42	0.200	3.25
		Nematodes	2.06	2.32	0.167	2.95
LSD (0.05)			0.90	0.67	0.053	0.79

Table 5. Crop height (cm) on June 27 (46 days after planting) and total crop biomass (g m^{-2}, dry weight) on August 21 (101 days after planting) of four combinations of soil pH and nematode infestation level (juveniles per gram of soil), Exp. 6

Treatment		Crop height (cm), June 27	Total crop biomass (g m^{-2}), August 21
pH_{KCl}	Nematodes		
4.6	0	100	2762
	30	72	1693
6.1	0	100	2596
	30	74	1846

The average number of roots per cm^2 minirhizotron surface increased rapidly in the topsoil during the first half of June (Figure 3). The number of roots of both control treatments in the topsoil increased until a maximum on June 15 and declined thereafter. From June 15 onwards, roots were found in the subsoil. Directly after planting, root growth was reduced by both high soil pH and nematodes (Figure 3). Until July, the number of roots per cm^2 minirhizotron surface in the topsoil was higher at pH 4.6 than at pH 6.1. Soil pH did not affect the number of roots in the subsoil.

Nematodes initially reduced the number of roots in the topsoil, but also prolonged root formation and, from mid June onwards, the nematode-infected crops had more roots in the top 30 cm than the uninfected crops. Nematodes decreased the number of roots per cm^2 of minirhizotron surface in the subsoil, below 30 cm. Despite this, nematodes increased total root number (topsoil + subsoil) in the second half of the growing season. The maximum depth at which roots were found was 85 cm for the control treatments and 60 cm for the nematode treatments.

Effects of nematodes on foliar nutrient concentrations changed with time (Table 6). At the first sampling date, 31 d.a.p., concentrations of N_{total}, NO_3 and P in leaflets of the topmost fully expanded leaf were reduced by nematodes, whereas foliar K concentrations were increased or not affected. During growth, foliar nitrogen concentrations of the controls decreased faster than those of the nematode treatment and in July total nitrogen and NO_3 concentrations of the nematode treatment were higher than those of the control. Foliar P concentrations decreased over time and concentrations of the nematode treatment were lower than those of the control. On the first two sampling dates, it was found that nematodes had strongly reduced foliar P concentrations. At later stages of growth, the effects were smaller. The effect of nematodes on foliar K concentration varied. On June 26 and on August 21, foliar K concentrations were reduced by nematodes. On the other sampling dates, no differences were found.

The effect of soil pH on foliar nutrient concentrations varied. On the first sampling date, it was found that high soil pH did not affect N_{total} concentration but increased the concentration of NO_3. P concentration in the foliage was not affected, K concentration was reduced. In the course of time the effects of high soil pH varied but at the end of the experiment on August 21, foliar N and K concentrations were increased whereas foliar P concentration was decreased.

Figure 4 shows the cumulative amounts of soluble mineral nitrogen at various soil depths with time. Nitrogen in soil solution of the top soil layers was soon depleted and by the end of June no soluble mineral nitrogen was found in the top 30 cm. With nematodes, soluble mineral nitrogen decreased at a lower rate

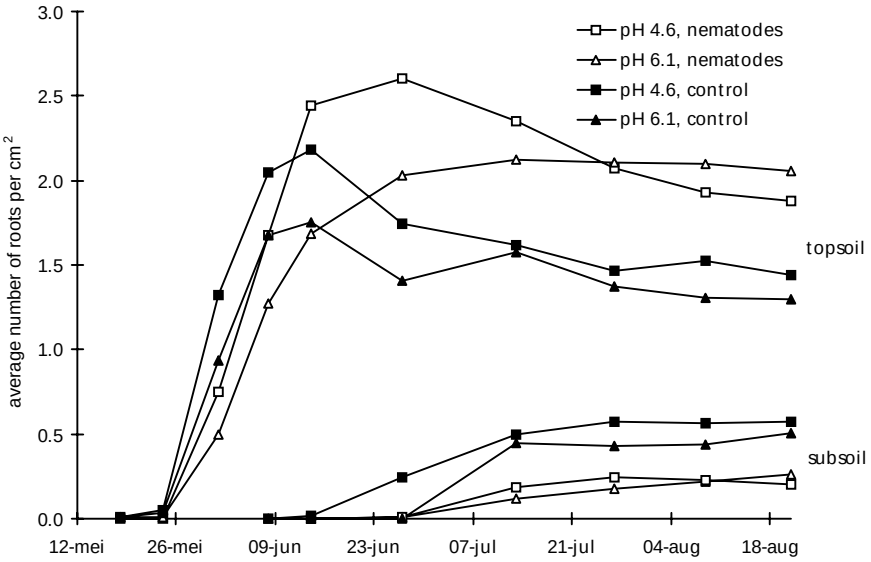

Figure 3. Average number of roots per cm^2 of minirhizotron surface in topsoil and subsoil with time, Exp. 6. For topsoil the observations with the minirhizotrons at 5, 10, 15, 20 and 30 cm depth were averaged, for subsoil the minirhizotrons at 45, 60 and 85 cm depth.

Table 6. Nutrient concentrations (g kg^{-1}) in dry matter of the second leaflet from the top of the topmost fully expanded leaf, Exp. 6

Treatment		Date of sampling				
		June 12	June 26	July 10	July 24	August 21[1]
N_{total} (g kg^{-1})						
pH 4.6	control	74.0	64.3	55.1	51.3	42.9
	nematodes	66.8	60.3	59.0	54.6	45.2
pH 6.1	control	74.2	65.1	58.0	49.5	43.4
	nematodes	67.2	63.6	56.9	52.5	48.0
NO_3 (g kg^{-1})						
pH 4.6	control	4.36	1.28	0.51	0.19	—
	nematodes	4.11	1.28	1.87	0.57	—
pH 6.1	control	6.13	1.99	0.73	0.10	—
	nematodes	4.50	2.39	1.18	0.60	—
P (g kg^{-1})						
pH 4.6	control	7.41	7.09	4.24	4.62	2.55
	nematodes	4.40	5.18	3.70	3.82	2.37
pH 6.1	control	7.05	6.91	3.85	4.56	2.33
	nematodes	4.52	4.59	3.60	4.00	2.02
K (g kg^{-1})						
pH 4.6	control	45.8	40.0	29.5	26.2	45.2
	nematodes	45.2	29.3	32.9	25.8	36.1
pH 6.1	control	40.5	39.7	31.3	27.8	49.2
	nematodes	43.5	33.5	26.2	27.7	41.4

[1] Concentrations in entire green leaves.

and nitrogen in the layer 50–70 cm was not depleted, whereas, in the control treatment, nitrogen in this layer was depleted by July 10, 59 d.a.p. Soil mineral nitrogen in the 70–100 cm layer was lowest with the control treatment at pH 6.1. There were no clear effects of the soil pH treatments on the amount of soluble mineral nitrogen in the different soil layers.

Discussion

Biomass production and nutrient concentrations

Chemical nematicides reduced population densities by an average of 83 percent in the field experiments, and gamma radiation completely killed the nematodes in the container experiments (Table 1 and 2). Both treatments may have killed other soil organisms interacting with the crops, but since nematode densities were high we attributed the effects of fumigation and gamma radiation on crop growth to differences in nematode density.

We found in most cases positive relationships between total biomass and foliar concentrations of nitrogen, phosphorus and potassium (Figures 1 and 2). This is generally found after infection with nematodes (Trudgill et al., 1975a,b; Trudgill, 1980, 1987), indicating that nematodes reduce both yield and nutrient uptake per unit biomass.

Since we did not vary fertilisation in Exps 1–4, we compared concentrations of N, P and K with deficiency levels from the literature to investigate whether these might have been limiting. The use of critical nutrient concentrations is awkward, as these depend on the sampled plant part, the age of tissue and environmental variables as moisture supply, temperature and light intensity (Bates, 1971). Therefore, the deficiency and sufficiency levels can only be used to get an indication of which element may have been limiting. Between the different experiments, the range of concentration levels varied and the lowest values of P and K were sometimes below deficiency levels from the literature. This may be a result of including old leaves with low nutrient levels in the bulked sample. The K concentrations in Exps 1 and 2 were all lower than the deficiency level. However, it is not plausible that K was limiting growth in Exp. 2, as there was no positive relationship between

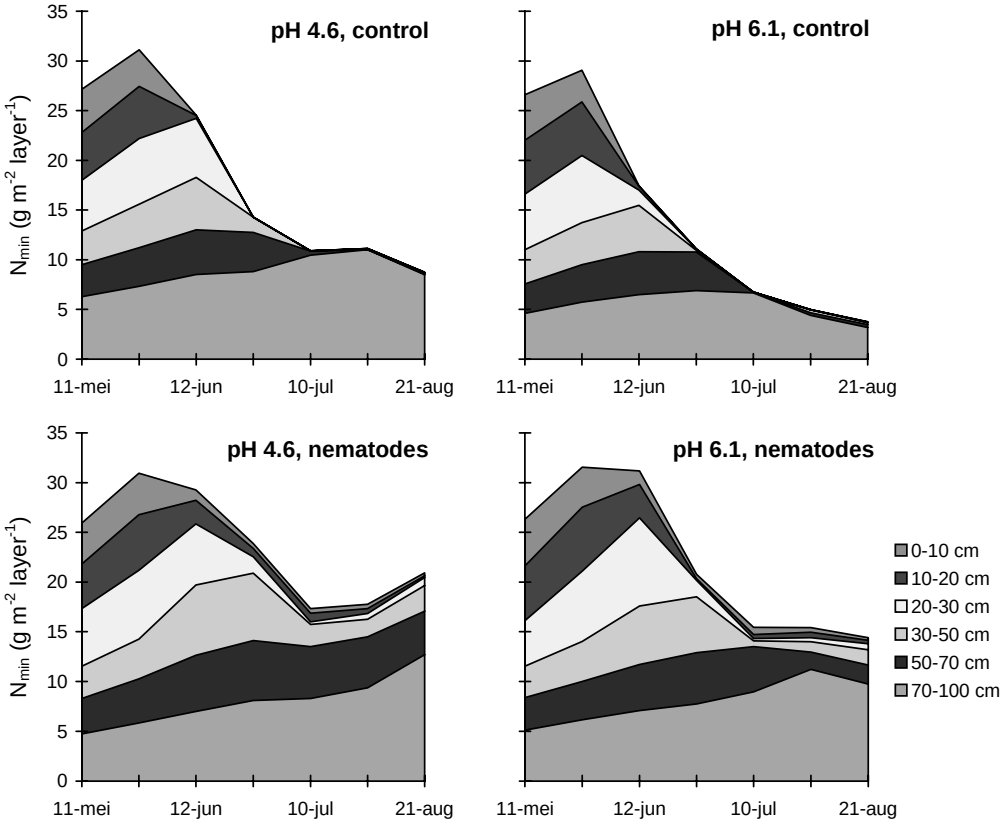

Figure 4. Amounts of soluble mineral nitrogen in various soil layers with time in Exp. 6.

total biomass and K concentration. In this experiment, differences in total biomass may have been caused by differences in P uptake. As P concentration of the treatments with the lowest total biomass was in most cases near the deficiency levels, and in most cases a positive relationship between total biomass and P concentration was found, the role of P in nematode damage was studied in more detail in Exp. 5 by varying soil pH and phosphate fertilisation.

In Exp. 5, we found that total biomass was strongly correlated with P concentration at 61 d.a.p. On fumigated soil at pH 6.1 without P fertilisation, yield was reduced by P limitation as fertilisation increased P concentrations and yield. The Pw value of this treatment was 44, relatively high according to the Netherlands fertiliser recommendation scheme (Anon, 1992). However, potato is responsive to P, and Van Noordwijk et al. (1990) calculated that for non-P-limited growth on four sandy soils Pw values were required from 44 to 87. Our experiments support this, as phosphorus fertilisation increased biomass production.

Effects of soil pH

In Exp. 5, the initial nematode density differed between levels of soil pH and was almost twice as high at pH 4.8 than at pH 6.1 (Table 2). The effects of soil pH are therefore best studied within the fumigated treatment, where nematode densities were equally low for both levels of soil pH.

High soil pH reduced total biomass and final tuber yield in Exp. 5 (Table 3), also found previously by Mulder (1994). This was likely caused by phosphorus deficiency, as the effects of soil pH on growth were largely reflected in foliar P concentration (Figure 2B) and total biomass was strongly increased by phosphorus fertilisation. Phosphorus deficiency may have resulted from low phosphorus availability, as the Pw value was lowest at pH 6.1.

In Exp. 6, the reduced root number at high soil pH may result from a reduced root elongation (Tang et al., 1996), but apparently the root system was still able to sustain plant growth as high pH had no effect on

crop height nor total biomass. The reduced root length at pH 6.1 in the deepest sampled soil layer of Exp. 5 was not caused by a reduced root elongation, but rather resulted from reduced overall crop growth and subsequent smaller root system, as the ratio of root length to leaf area (RL/LA) was increased.

The ratio of root length to leaf area allows assessment of energy allocation and gives information on growth-limiting factors (Brouwer, 1983; Körner and Renhardt, 1987). The increased ratio at pH 6.1 indicates that growth was restricted by insufficient below-ground resource capture. Evidently, phosphorus uptake was restricted, as phosphorus fertilisation reduced the RL/LA from 3.27 to 1.88 km m^{-2}, a level similar to the 2.08 km m^{-2} at pH 4.8 (Table 4).

We conclude that the effect of soil pH was mainly due to differences in the availability of phosphorus.

Effects of potato-cyst nematodes

The effect of nematodes on growth could largely be attributed to P limitation, as P concentrations similar to that of the limiting concentration of the treatment 'pH 6.1 without P fertilisation on fumigated soil' gave similar yields (Figure 2B). Lower P concentrations showed a further yield decrease. However, not all damage by nematodes could be attributed to P limitation. At high P concentrations of the fumigated treatment, variation in P concentration did not lead to variation in total biomass, indicating that at this time P concentrations higher than 0.5% were not limiting. At these non-limiting concentrations, nematodes reduced total biomass. Apparently potato-cyst nematodes reduced crop growth by different mechanisms. At low levels of phosphate availability, phosphorus was limiting and 'other' mechanisms acted at high phosphate levels. Reduced crop growth after nematode infection without nutrient limitation was also found in Van Oijen et al. (1995).

Uptake of phosphorus strongly depends on total root length (De Willigen and Van Noordwijk, 1987) and nematodes could cause damage by reducing total root length. The 'time course' study in the Wageningen Rhizolab (Exp. 6) showed that nematodes reduced the number of roots against the minirhizotrons directly after planting and delayed the increase of root number (Figure 3). This agrees with studies on effects of nematodes on root growth *in vitro*, where nematodes reduced root elongation within a few days (Arntzen et al., 1994; Rawsthorne and Hague, 1986). However, root number of the nematode-infected crops increased over a longer period, and at about one month after planting there were more roots with nematodes than with the control. This compensatory root growth was probably a response to phosphorus deficiency, as nematodes strongly reduced foliar phosphorus concentrations (Table 4). By the time that the nematode treatments had more roots than the controls, the differences in foliar phosphorus concentrations were small. Thus, the nematode treatments had an increased number of roots, sustaining a decreased foliage.

Increased root to shoot ratios are often found after nematode attack (Evans, 1982; Trudgill and Cotes, 1983). However, in Exp. 5 this was not found which can result from the single sampling date on which observed differences were the result of processes from the previous nine weeks. The results give evidence that nematodes affect the functioning of the roots and reduce uptake per unit root length (Table 4). The resulting initial P deficiency was likely counteracted by compensatory root growth, as at 116 d.a.p. there was no relationship between total biomass and foliar P concentration. This, however, could not compensate for the initial growth reduction by the nematodes. At the end of the growing period, 146 d.a.p., nematodes reduced tuber yields by 29–40 percent.

Nematodes affect spatial root distribution and often reduce root growth in deeper soil layers, thereby diminishing access to water and nutrients (Evans and Haydock, 1990). In a Rhizolab experiment similar to Exp. 6, Haverkort et al. (1994) found that nematodes increased root growth in the topsoil and strongly reduced root formation in the subsoil. As nitrogen in soil solution of the top soil was soon depleted, Haverkort et al. (1994) concluded that reduced growth and early senescence of an infected crop may be caused by nitrogen deficiency at the end of the season. In our experiments, nematodes slightly reduced root growth in the subsoil (Figure 3). We also found that nitrogen in soil solution of the top soil was soon depleted (Figure 4). However, crop growth was also reduced and thereby the demand for nitrogen. The increased foliar nitrogen concentrations with nematodes at the end of Exp. 6 indicate that N was not limiting.

Interaction between soil pH and potato-cyst nematodes

The greater nematode density in Exp. 5 at pH 4.8 than at pH 6.1 (Table 2) compromises our ability to provide

a quantitative description of nematode damage in relation to soil pH.

The effect of soil fumigation on total biomass and final tuber yield was similar at both pH levels (Table 3). However, when the initial nematode density was taken into account in a multiple regression analysis, a significant interaction between the effects of initial nematode density and soil pH on total biomass was found. There were no significant interactions between the effects of soil pH and either the soil fumigation treatment or the initial nematode population density on root length density or nutrient uptake per unit root length. This may be explained by the single measurement date in Exp. 5, when the observed differences were the result of accumulated effects on root elongation, nutrient uptake per unit root length and compensatory root growth.

The interaction between nematode density and soil pH on total biomass corroborates the previously found interactions by Haverkort et al. (1993) and Mulder (1994). In addition to the results described by Haverkort et al. (1993), the effects of the treatments of this experiment on foliar nutrient concentrations are shown in Figure 1D. The low yields of the combined effect of soil pH and nematodes coincide with reduced foliar concentrations of P and K. Though these concentrations are relatively high compared to the indicated deficiency level, nutrient uptake seems responsible for this interaction effect. This is supported by Trudgill (1987), who found that nematode damage was highest at low fertilisation levels. The interaction in Exp. 5 may therefore result from the low phosphorus availability at pH 6.1.

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