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The influence of potato cyst nematodes (*Globodera pallida*) and drought on rooting dynamics of potato (*Solanum tuberosum* L.)

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Abstract

Minirhizotron root video observations of two experiments (in 1991 and 1992) in the Wageningen Rhizolab were used to investigate the extent to which potato cyst nematodes (*Globodera pallida*) without (1991) or with accompanying drought (1992) influenced the rooting dynamics of potatoes. The main effect of potato cyst nematodes in 1991 was a retarded root length. At a depth of 10 cm and without nematodes, the maximum total root length was produced 60 days after planting. At a depth of 45 cm, this point was reached after 80 days. With nematodes (2.5, 10 and 40 living larvae per gram of soil), however, the date at which maximum root length was produced was retarded with at least 20 days, depending on the infestation level of the soil. At a depth of 45 cm, nematodes at the highest infestation level also eventually resulted in a shorter root length. At a depth of 10 cm, nematodes resulted in a somewhat greater root length. The effects of nematodes on the longevity of potato roots were analysed by following the fate of individual root segments. It was concluded that in the first experiment (1991), the rate at which roots decayed was higher without nematodes than with nematodes. Combining the data for root length production with root length decay, it was found that without nematodes, the standing living root length was only higher in the first part of the season. Also, from the second experiment (in 1992), in which the effect of nematodes was studied in combination with drought, potato roots did not show a reduced longevity with nematodes. The yield of potatoes in the presence of nematodes is discussed.

Keywords: Drought; Infestation level; Minirhizotrons; Potato cyst nematode (*Globodera pallida*); Root growth; Root turnover Wageningen Rhizolab

1. Introduction

Potato cyst nematodes (*Globodera pallida*) are known to have a negative influence on the yield of potato plants. Although the effects of an infestation of these nematodes depend on the degree of tolerance of the potato cultivar and the interaction with other environmental factors, often the root system of the potato plant is thought to play a role in yield formation under these circumstances.

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Certain tested tolerant potato cultivars, such as Maris Piper and Cara, showed a more extensive and deeper rooting and more branched roots than less tolerant cultivars such as Pentland Dell and Pentland Crown (Evans et al., 1977; Evans and Haydock, 1990). In intolerant cultivars, a high incidence of necrosis was found on roots after the nematodes matured, whereas in tolerant cultivars, callus formation was observed to surround the sites where nematodes had entered the roots (Huijsman et al., 1969). Also, Arntzen et al. (1994) found a relationship between rooting characteristics (the rate at which roots induced hatching and the growth of roots after inoculation) and the degree of tolerance of potato cultivars.

Fasan and Haverkort (1991) reported a decreased shoot/root ratio with both nematodes and drought, but with nematodes, it was only due to a reduction of the aerial part of the dry weight, whereas with drought, both shoot and root weight decreased, but shoot weight more than root weight.

Evans et al. (1975) suggested that stomatal closure and, consequently, a reduced photosynthesis rate are the main mechanisms through which drought, but also nematodes, cause lower potato yields. A higher stomatal resistance was also associated with increased abscisic acid (ABA) contents, originating from the root cap cells, in leaves (Fatemy et al., 1985). Thus, water stress might be one of the main factors reducing plant growth on nematode infested soils. In addition, Evans et al. (1975) reported that Pentland Dell (a less tolerant potato cultivar than other cultivars) when strongly infested by nematodes, started to senesce earlier than lightly infested plants. Irrigation had little effect on the water relations of these nematode infested plants. An earlier senescence of the leaf canopy was also mentioned by Haverkort and Trudgill (1995) as one of the main factors causing a yield reduction. It seems possible that the earlier senescence is induced by the root system as nematodes can affect the size or functional properties of the potato roots. Trudgill and Cotes (1983) and Trudgill (1987) mention that invading juveniles of the potato cyst nematode decrease the effectiveness of the potato root system leading to a chronic deficiency of one or more nutrients and a consequential reduction in the rate of top growth.

Moreover, Evans et al. (1975) suggested that roots of infested plants lived shorter than non-infested plants. In their experiments, a progressive death of roots of Pentland Dell started 11 weeks after planting, earlier and faster than was observed for the resistant cultivar Maris Piper.

Thus, as water and nutrient stress per se can both be induced by a faster decay of the root system, more information about the effect of nematodes on the rooting dynamics of the potato plant could clarify the mechanisms involved in the lower dry-matter production at nematode-infested sites.

In two Wageningen Rhizolab experiments, carried out in 1991 and 1992, roots were observed with minirhizotrons, allowing individual roots to be followed in time. With this method, it was not only possible to quantify total root length production, but it also enabled us to assess quantitatively the rate of root length decay with or without nematodes and drought.

2. Materials and methods

2.1. Experimental conditions

In two experiments conducted in the Wageningen Rhizolab, the potato cultivar Mentor (moderately tolerant of potato cyst nematode) was grown in 1991 with different levels of nematodes, and in 1992, the combination of drought and nematodes was studied. For more details, see Haverkort et al. (1994).

The Wageningen Rhizolab consists of 16 compartments (125×125 cm and 200 cm deep) situated on either side of an underground corridor (van de Geijn et al., 1994). Roots can be observed by horizontally placed minirhizotrons (Smit et al., 1994a). The subsoil of the compartments (-200 to -100 cm) consisted of a white and coarse sand without any organic matter. A humous sandy soil was placed between -30 and -100 cm. To ensure a homogeneous bulk density and a close contact between soil particles and the minirhizotrons, the compartments were filled layer by layer with thin (5 cm) soil layers compressed manually to a uniform bulk density and measured afterwards. The minirhizotrons were positioned during the filling

procedure, avoiding any voids between minirhizotrons and soil that might affect root growth.

The top 30-cm layer was filled with a light sandy soil from a field infested with nematodes. Starting from an initial infestation of 40 and 15 living larvae per gram of soil in 1991 and 1992, respectively, different nematode infestation levels were obtained before use in the Rhizolab by irradiating with gamma radiation and mixing procedures [for more details, see Haverkort et al. (1991, 1992, 1994)].

The 1991 experiment with four compartments consisted of the following treatments:

N1: without nematodes;
N2: 2.5 living larvae per gram of soil;
N3: 10 living larvae per gram of soil;
N4: 40 living larvae per gram of soil, corresponding to the initial infestation of the used soil.

In this experiment, water was not a limiting factor for plant growth.

In the 1992 experiment (also four compartments), two infestation levels with potato cyst nematodes were combined with two levels of water supply:

N1D1: no nematodes, optimal water supply;
N2D1: 15 living larvae per gram of soil, optimal water supply;
N1D2: no nematodes, 50% of the optimal water supply;
N2D2: 15 living larvae, 50% of the optimal water supply.

Water was applied by drip irrigation. During the whole season, at each application, the droughted treatments received only half of the water supplied to the optimal water treatments. The amount of water was based on the soil moisture content, measured automatically at several depths in the profile with capacitive moisture sensors.

Potato seed tubers were allowed to emerge in sand in the weeks prior to transplanting. Transplants consisted of rooted stems about 15 cm in length but were removed from the mother tuber.

The single stem potato plants were transplanted on 17 May 1991 and 28 April 1992 and harvested on 29 October 1991 and 14 September 1992, respectively. The plant distance was 25 cm by 20 cm. To mimic a crop situation, the compartments were surrounded by guard potato rows.

2.2. Root observations

Root observations were carried out by a minicolour video-camera (Bartz Technology, Santa Barbara, CA) equipped with a visible-light system (4.5-mm incandescent bulbs). The camera system was inserted into glass minirhizotrons 130 cm long, outer diameter 5 cm, placed horizontally at varying depths between 5 and 150 cm (Smit et al., 1994a).

Although all depths were observed in both experiments, only depths of 10 and 45 cm were used for this study on root dynamics. To assess differences in rooting dynamics, only six observation dates for the first and seven dates for the second experiment were used. Table 1 shows the observation dates in the Wageningen Rhizolab for 1991 and 1992.

The video-camera had a 1.3×1.8 cm field view on the upper side of each tube. On the glass–soil interface, 20 positions (along 49 cm of the tube) were recorded and stored on a S-VHS JVC BR600 video-cassette recorder. Between each position, a 1.25-cm lap was not recorded.

2.3. Processing of video-images with interactive image analysis

The public-domain image-analysis program NIH-Image v. 1.56 was used (written by Wayne Rasband at the US National Institutes of Health

Table 1
Dates of observation

Year	
1991	1992
17 May (planting)	28 April (planting)
20 June	21 May
9 July	4 June
8 August	18 June
20 September	2 July
10 October	16 July
30 October	13 August
—	15 September
29 October (harvest)	14 September (harvest)

and available from the Internet by anonymous FTP from zippy.nimh.nih.gov or on floppy disk from the National Technical Information Service, Springfield, Virginia, part number PB93-504868) to transfer the video-images to a computer and perform the analysis on root dynamics.

Video images were transferred from the video-recorder to a Macintosh II (20-Mb RAM and 180-Mb hard disk) equipped with a frame-grabber (Data Translation Quick Capture card DT 2255). The digitised images of a single minirhizotron position had a height of 512 pixels, a width of 768 pixels and a size of 390 kb. Each pixel in the image is represented by the grey-scale value, a figure between 0 and 255. In the Image program, pure white is represented by 0 and pure black with a grey value of 255, and intermediate values are represented as intermediate grey tones.

Individual images were rearranged in so-called 'stacks' consisting of six (in 1991) or seven (in 1992) consecutive images of the same position on a minirhizotron. For each depth (tube), 20 stack files were made. To correct small differences in camera positioning between observation dates, an alignment procedure was carried out. By selecting two or more reference points (either roots, characteristic soil particles, soil pores, etc.) and pointing to the same references in the image following in time, a macro in NIH-Image produced a stack file in which exactly the same area could be observed throughout the season. After the alignment procedure, an area of 500×350 pixels ($1.2 \times 0.9\ cm^2$), roughly in the middle of the screen of each stack file, was used for subsequent analysis.

To assess the life span of a single root, exact morphological criteria are needed to classify roots as dead or alive, but, until now, no standardised method has been found in the literature. Nevertheless, we observed some morphological changes that may be related to the physiological properties of roots. The main considered characteristic was root colour. When roots, which were white immediately after appearing, had become brown or black, they were considered to be dead. This was observed in particular for thin roots. It was also often observed that the roots started to shrink after a certain period and then lost contact with the soil particles. In the case of permanent shrinking, this would imply a loss of functionality because nutrient and water uptake would be impaired (Passioura, 1991; Veen et al., 1992). Also, degradation of the root cortex, visible as a decreased sharpness at the border of the roots, loss of colour uniformity and appearance of blots on root surface, was used as a criterion to determine whether a root was dead or alive.

The NIH-Image program was used as an interactive tool to process the minirhizotron video images. With the Image program, it is possible to use seven additional colours in grey-value images. Each of these seven colours was linked to a particular observation date. Beginning with the first observation date, the visible roots were traced with the mouse, drawing a one-pixel-wide line of, for example, the colour red. This line drawing was superimposed on the image of the next observation date. Roots that had become visible on the second observation date were now traced with the second colour (e.g. yellow). If a root (partially) died, the corresponding tracing of this root was removed. The next observation dates were treated accordingly [see also Smit and Zuin (1996)].

On each observation date, after tracing or (partial) removing root segments, the number of pixels of each of the six colours (corresponding to the dates of the appearance of roots) was counted. The number of pixels was converted to length per cm^2 minirhizotron surface, using a method described by Smit et al. (1994b)

2.4. Root parameters and statistical analysis

The Image program allowed us to follow the fate of individual roots appearing in consecutive observation dates and to perform an analysis as described by Cheng et al. (1991). Cumulated length production (total produced length of roots, TPL) and dead roots (total dead root length, TDL) were calculated as a mean of 20 positions for each depth. TPL and TDL were regressed (Gompertz regression equation) on time after planting (t) for each depth and treatment using the Genstat5 program (Payne et al., 1993), forcing through the origin was applied. The percentage of variance accounted by this regression was in two cases 93 and 94% and was higher than 97% in all the others (Table 2).

$$\mathrm{TPL}(t) \text{ and } \mathrm{TDL}(t) = ce^{-e^{-b(t-m)}}, \quad (1)$$

Table 2
Gompertz regression coefficients (see text) of TPL and TDL on time for two depths in 1991 and 1992

Year	Treatment	Depth (cm)	Variable	Regression coefficients						Percentage explained VHRiance
				b		*m*		*c*		
1991	N1	10	TPL	0.0740	(±0.014)	17.80	(±3.221)	1.3330	(±0.028)	98.7
	N2	10	TPL	0.0706	(±0.013)	41.18	(±1.863)	1.4538	(±0.043)	98.5
	N3	10	TPL	0.0252	(±0.006)	63.24	(±6.418)	1.621	(±0.155)	97.7
	N4	10	TPL	0.1028	(±0.037)	45.91	(±2.910)	1.8394	(±0.074)	96.4
	N1	45	TPL	0.1056	(±0.005)	49.709	(±0.187)	1.5092	(±0.004)	100.0
	N2	45	TPL	0.0714	(±0.002)	60.009	(±0.432)	1.5825	(±0.010)	99.9
	N3	45	TPL	0.0645	(±0.003)	65.269	(±0.673)	1.8986	(±0.017)	99.9
	N4	45	TPL	0.1059	(±0.079)	80.83	(±1.850)	0.6190	(±0.019)	99.2
	N1	10	TDL	0.0230	(±0.006)	79.09	(±9.383)	1.201	(±0.171)	97.6
	N2	10	TDL	0.0110	(±0.003)	183.4	(±50.9)	1.379	(±0.847)	99.3
	N3	10	TDL	0.0119	(±0.003)	226.3	(±52.0)	4.83	(±3.970)	99.8
	N4	10	TDL	0.0174	(±0.008)	115.6	(±29.3)	1.605	(±0.685)	96.5
	N1	45	TDL	0.0354	(±0.003)	119.91	(±1.350)	1.4908	(±0.056)	99.9
	N2	45	TDL	0.0370	(±4E−4)	132.31	(±0.236)	1.0766	(±0.007)	100.0
	N3	45	TDL	0.0336	(±0.009)	107.88	(±5.810)	0.6855	(±0.088)	98.6
	N4	45	TDL	0.0749	(±1.7E−17)	131.3	(±3.0E−15)	0.1374	(±1.2E−17)	100.0
1992	N1D1	10	TPL	0.1383	(±0.015)	11.690	(±1.21)	2.1816	(±0.012)	99.9
	N2D1	10	TPL	0.0964	(±0.008)	14.079	(±0.905)	2.1437	(±0.018)	99.7
	N1D2	10	TPL	0.0874	(±0.018)	13.340	(±2.460)	1.9954	(±0.055)	97.4
	N2D2	10	TPL	0.0575	(±0.017)	19.710	(±3.95)	2.4430	(±0.143)	93.4
	N1D1	45	TPL	0.2824	(±5.9E−4)	33.780	(±6.7E−3)	0.8560	(±2.4E−5)	100.0
	N2D1	45	TPL	0.2494	(±9.6E−4)	36.890	(±3.8E−3)	0.7642	(±1.3E−4)	100.0
	N1D2	45	TPL	0.1638	(±0.025)	31.551	(±0.920)	0.2956	(±0.004)	99.6
	N2D2	45	TPL	0.1468	(±0.031)	38.337	(±0.911)	0.5150	(±0.014)	98.9
	N1D1	10	TDL	0.0785	(±0.012)	49.880	(±1.380)	2.0282	(±0.066)	99.0
	N2D1	10	TDL	0.0663	(±0.006)	53.683	(±0.996)	2.0305	(±0.048)	99.6
	N1D2	10	TDL	0.0649	(±0.005)	56.180	(±0.893)	1.9450	(±0.042)	99.7
	N2D2	10	TDL	0.0593	(±0.009)	56.340	(±1.790)	2.0738	(±0.088)	98.8
	N1D1	45	TDL	0.0761	(±0.008)	60.660	(±0.984)	0.8190	(±0.021)	99.5
	N2D1	45	TDL	0.0909	(±0.006)	62.316	(±0.545)	0.7119	(±0.010)	99.8
	N1D2	45	TDL	0.0358	(±0.001)	80.873	(±0.803)	0.3009	(±0.005)	100.0
	N2D2	45	TDL	0.0401	(±0.006)	73.740	(±2.380)	0.4975	(±0.028)	99.2

where c (maximum level of TPL and TDL), b (slope of the curve at $c/2$) and m (time when $c/2$ is reached) are constants, t = time in days after planting, and e is the natural logarithm.

The standing living root length (LRL) in time was calculated as the difference between the regressed values of TPL and TDL:

$$\mathrm{LRL}(t)=\mathrm{TPL}(t)-\mathrm{TDL}(t). \quad (2)$$

The derivative of TDL over time as a fraction of LRL(t) was used to calculate the specific root length decay (SRLD) (Eq. (3)). The derivative was obtained by using the software package Mathematica (Wolfram, 1991).

$$\mathrm{SRLD}(t)=\frac{bce^{\{-e^{[-b(t-m)]}-b(t-m)\}}}{\mathrm{LRL}(t)} \quad (3)$$

3. Results and discussion

3.1. Root length production

In the 1991 experiment, increasing levels of nematodes had a strong negative effect on total and tuber yield (Table 3) and produced a different

Table 3
Total dry-matter production (root mass excluded) and tuber yield (dry mass) at the final harvest on 29 October 1991 and 14 September 1992

Experiment	Treatment	Infestation level (living larvae per gram of soil)	Total dry matter ($kg\,m^{-2}$)	Tuber dry matter ($kg\,m^{-2}$)
1991	N1	0	4.53	3.13
	N2	2.5	4.05	3.01
	N3	10	2.67	2.00
	N4	40	1.33	1.00
1992	N1D1	0 (+optimal water supply)	2.98	1.83
	N2D1	15 (+drought)	2.26	1.46
	N1D2	0 (+optimal water supply)	2.53	1.74
	N2D2	15 (+drought)	1.85	1.23

pattern of total root length production as indicated by changes in the regression coefficients (Table 2), and as visualised in Fig. 1. At a depth of −10 cm, root growth started earlier in the control treatment, and this treatment also showed a faster increase

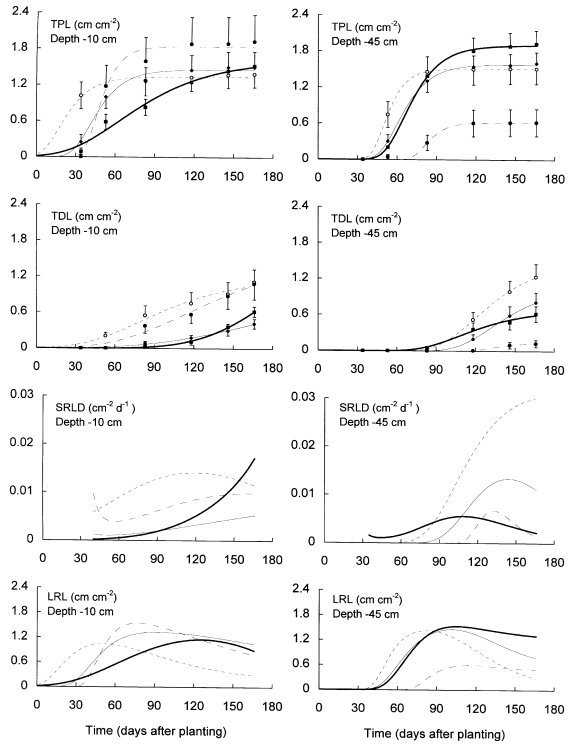

Fig. 1. Root characteristics in 1991 at a depth of −10 and −45 cm. · · : · N1; ———: N2; ———: N3; - - -: N4 (see text). TPL: Total produced length of roots; TDL: total dead root length; LRL: standing living root length; SRLD: specific root length decay.

of root length compared to that in the nematode treatments [especially compared to treatment N3, Fig. 1 (TPL)]. Although, at the end of the season, the differences in total length were minor, the data suggest that slightly more roots were produced with more nematodes. Without nematodes, the same total root length was produced in a shorter time. Thirty-four days after planting, the root length was five times greater in the control than that in infested soil ($1\,cm\,cm^{-2}$ vs. $0.2\,cm\,cm^{-2}$). For treatment N4 (40 larvae per gram of soil), a level of $1\,cm\,cm^{-2}$ was reached 20 days later and the other treatments still later. Also, at a depth of −45 cm, root length production was earlier without nematodes (Fig. 1). In contrast to the observation at −10 cm, the total root length in the N4 treatment was reduced severely throughout the season, and obviously, compensation had occurred in the upper soil layer (see Fig. 1, TPL at −10 cm for this treatment).

In the 1992 experiment, nematodes also reduced the (tuber) yield, under both optimal water supply (D1) and drought conditions (D2), Table 3. Compared to that in 1991, the yield was lower because of the earlier harvest date and because of the fact that the foliage in 1992 was confined with netting to the planted area [see also Haverkort et al. (1994)]. The effect of nematodes on total root length production when the water supply was optimal (N1D1 vs. N2D1) was similar to the effect observed in 1991 at comparable population levels (Fig. 2, TPL) for depths of −10 and −45 cm): at the end of the season, a similar total length of roots had been produced, but without nematodes,

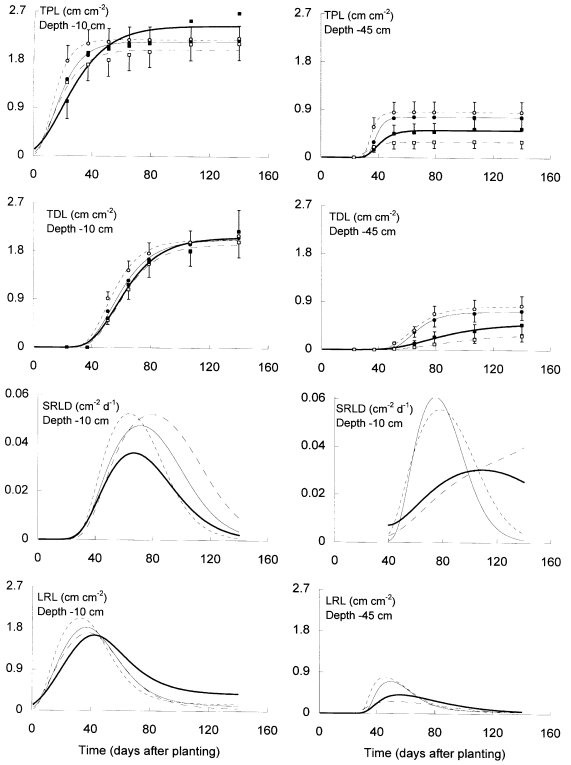

Fig. 2. Root characteristics in 1992 at a depth of −10 and −45 cm. · · ·: N1D1; - - -: N1D2; ———: N2D1; ———: N2D2 (see text). TPL: total produced length of roots; TDL: total dead root length; LRL: standing living root length; SRLD: specific root length decay.

this level was reached earlier. Drought decreased the root length, especially in the deeper soil layer (−45 cm), but an interaction between drought and nematodes became apparent as, during drought, nematodes appeared to stimulate rooting (Fig. 2, TPL).

The presented results indicate that without potato cyst nematodes or drought, root formation in a potato crop takes place in a relatively short period (only 40 days) after planting. After this period, few new roots are formed, which implies that potato roots, once produced, have to be functional during the greater part of the growing season (Figs. 1 and 2; TPL). Nematodes change this pattern: the maximum number of roots is reached later in the season, or the crop continues to grow roots until the end of the season. In this respect, the effect of the nematodes resembles the effect of drought: it has been found for potatoes that drought increased the root:shoot ratio, indicating that root growth was maintained to a greater extent than shoot growth (Jefferies, 1993). In infested soils, new roots produced later in the season will probably be less infected by nematodes, as most of the cysts in the soil will be hatched. Under these conditions, this changed strategy in rooting behaviour might be favourable for the uptake of water and nutrients.

The potato crop does not seem to avoid nematodes with a changed rooting pattern as, in most cases, we did not observe more roots in soil layers with nematodes. On the contrary, in 1991 (highest infestation level) and 1992 (no drought), less rooting was found at −45 cm with nematodes.

3.2. Rooting dynamics

In the 1991 experiment at the considered soil depths, the cumulative curve of the 'total dead root length' was higher without nematodes (Fig. 1; TDL). Also, from the death rate as a proportion of the standing living root length, it can be concluded (Fig. 1; SRLD) that especially deeper in the profile (−45 cm), roots had a shorter longevity in the control treatment than in the presence of nematodes.

In 1992 at a depth of −10 cm (Fig. 2), the effect of drought and nematodes on TDL was minor. At −45 cm, during drought, nematodes increased TDL. However, when the death rate was expressed relative to the living roots, the effect of drought was much more pronounced than the effect of nematodes (Fig. 2; SRLD). At −10 cm, the effect of nematodes on SRLD was only substantial during drought; here, nematodes increased the longevity of the roots. In general, the relative dead rates of the control treatment were higher than in 1991.

Thus, the relative death rate of roots without nematodes in both experiments was at least as high, and usually higher than, with nematodes. This is in contrast to the literature where it is suggested that nematodes shorten the life span of roots (Evans et al., 1975). It can be argued, however, that nematode-induced fast decay of

roots would negatively influence the chances for reproduction for the nematodes themselves, although the required (thermal) time for completion of the life cycle of *Globodera* spp. (Van Haren, 1995) seems to be relatively short compared to the longevity of an average potato root. It is, nevertheless, conceivable that nematodes have a minor influence on the longevity of roots, in contrast to the general idea about the effect of nematodes. The main yield reducing the effect of nematodes would then not be caused by a higher root turnover.

3.3. Standing living root length

Subtracting TDL from TPL yields the standing living root length (Fig. 1, LRL) which shows an optimum curve in time. Nematodes retarded the date at which this optimum was reached, although eventually, a higher optimum was reached. However, in the period until 40 days after planting, the total living root length was much higher without nematodes. Later in the season, the living root length progressively decreased until the end of the season; this decrease started earlier in the control treatment compared to the infested crops. In 1991 at 50 DAP (days after planting) at a depth of 10 cm and 90 DAP at a depth of 45 cm, infested crops (N2 and N3) showed a higher standing living root length than the control crop. The highest population of nematodes (N4), which had a strong effect on plant yield (Table 3), did not have the same effect in both soil layers. This treatment reduced root growth deeper in the profile severely, whereas at a depth of −10 cm, more roots were found.

The 1992 experiment showed similar effects; plants infested with nematodes had a lower living root length in the first part of the season, for both depths and with or without drought. With nematodes, the time at which the maximum value of the standing living root length was reached was postponed (Fig. 2; LRL). Contrary to the results in 1991, the maximum LRL value for any depth was higher in the control treatment (no nematodes, no drought), but it decreased very quickly in the following period. Especially at −10 cm, both during drought and with an optimal water supply, the living root length decreased more rapidly without nematodes. Drought lowered the maximum living root value at all depths.

3.4. Yield formation and nematodes

If nematodes do not induce a faster decay of roots, what would then be the main mechanism by which nematodes impair plant growth? Considering the above, it is unlikely that yield depressions are caused by a higher amount of dry matter invested below ground. It is more likely that there is a less efficient uptake of nutrients or water by (a) a changed rooting pattern and distribution or (b) an impaired root functioning per se (Trudgill, 1987; Haverkort and Trudgill, 1995).

As shown in the present study, nematodes cause a retardation in root growth, which can have a negative effect on early leaf growth. According to Steltenpool and Van Erp (1995), potato crops take up nitrogen for the greater part early in the season, until 80 days after planting. A shift to uptake later in the season means, considering the relation between LAI and N uptake, that an important part of the growing season would be lost for production. If conditions are such that uptake of water and nutrients is proportional to the standing living root length (Figs. 1 and 2; LRL), the differences in tuber yield between the treatments can be explained. Also, Haverkort et al. (1994) have mentioned the possibility that nematodes affect the amount of nitrogen taken up by the plants because of a retardation of root growth.

4. Conclusions

Based on the presented results from the experiments in 1991 and 1992, we conclude that the main effects of the potato cyst nematode on rooting characteristics are a retardation of root growth in time and an extended period of root formation. Drought induced more or less the same effect, but an interaction with nematodes was found. In these experiments, we could not confirm the general idea that nematodes induce a faster decay of roots. On the contrary, in general, the decay of roots was faster without nematodes. Combining the data for

root length production with root length decay, we conclude that without nematodes, the standing living root length was only higher in the first part of the season. After about 60 days of growth, the top soil layer in the nematode treatments showed a higher standing living root length. We conclude from our results that the root longevity in infested potato plants is at least as high as that in non-infested plants, and a higher root turnover cannot be the main yield-depressing factor in nematode-infested fields.

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