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The influence of cyst nematodes and drought on potato growth. 1. Effects on plant growth under semi-controlled conditions

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Abstract

Potatoes were grown under a permanent rain shelter in mobile containers in soil with or without potato cyst nematodes (*Globodera pallida*). The plants were subjected to an early drought stress period starting at planting until 43 days after planting, to a late drought stress period starting at 43 days until senescence at 92 days and to a drought control. Dry matter weight and characteristics of leaves, stems, stolons and roots were determined at periodic harvests. The early drought stress and nematode infection affected many plant organ characteristics in similar ways. Numbers of leaves, specific leaf area, plant height, specific stem weight, leaf area ratio, mean tuber weight and harvest index were reduced by both stress factors at early stages of growth.

Later on, interactions between both stress factors which influence the development rate of the plants led to more diverse plant reactions. Plants of all treatments rapidly senesced at about 90 days after planting. Uninfected plants had then depleted the soil nutrient supply whereas the plants grown in the inoculated soil senesced as a result of the potato cyst nematode infection.

Additional keywords: dry matter partitioning, *Globodera pallida*, organ characteristics, *Solanum tuberosum*.

Introduction

Besides affecting plant water relations (Haverkort et al., 1991) and nutrient uptake (Trudgill, 1987), potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) are known to affect plant development, dry matter partitioning and characteristics of plant organs. Trudgill et al. (1975a), studying the effect of potato cyst nematodes on the cultivar Pentland Dell, reported an earlier senescence, although Seinhorst and Den Ouden (1971) found a delaying effect on senescence which Trudgill et al. (1975b) attributed to an earlier exhaustion of the nutrient supply by the more vigourously growing control. Trudgill et al., (1975b) found with the cultivars Maris Piper and Pentland Dell that potato cyst nematodes reduced the plant height, strongly reduced the number of stems per plant, and reduced the leaf area per plant, mainly because the leaf area per individual leaf was strongly reduced although the number of leaves per stem increased. The number of tubers per stem decreased as well as their individual weight but their dry matter content increased as a result of cyst nematode infection. The amount of dry matter partitioned to the roots was strongly reduced. All these changes occurred to a lesser extent with the more tolerant cultivar Maris Piper. Trudgill (1980) recorded an improved growth of potato cyst nematodes infected plants at the end of the growing season but attributed this to the depletion of the inoculum in the pots.

Several authors recorded a strong reduction of the ratio between the shoot dry weight and that of the root. (Trudgill and Cotes, 1983; Fatemy et al., 1985; Fatemy and Evans, 1986). This indicates that potato cyst nematode infected plants favour the production of root dry matter at the expense of aboveground parts. The total root dry matter of infected plants also declined in these cases while Evans et al. (1977) reported that such a decline in root weight was less with the drought and nematode tolerant cultivar Maris Piper than with the intolerant Pentland Dell. Increased leaf water potentials, stomatal resistances, shoot/root ratios and water use efficiencies (Evans et al., 1975; Haverkort et al., 1991) are indicative of drought stress symptoms in the plant associated with potato cyst nematode infection which generally lead to dwarfed plants and thicker leaves (Wallace, 1987). Fatemy and Evans (1986) reported a smaller leaf area ratio (leaf area relative to total plant weight $cm^2\ g^{-1}$) of potato cyst nematode infected plants than that of the controls after three weeks of growth. The leaf area ratio of the controls, however, strongly decreased in the course of the growing season while that of the infected plants remained constant, resulting in higher ratios of the infected plants after 10 weeks of growth.

The objective of the study reported here was to compare the combined and separate effects of drought and cyst nematode infection on dry matter production, and on characteristics of and dry matter partitioning between leaves, stems, stolons, roots and tubers. To this end, nematode infected plants and control plants were either subjected to a drought stress period early on in growth or to drought stress in the second half of the life of the plant.

Materials and methods

In 48 mobile containers of 40 cm high, 90 cm long and 70 cm wide six seed tubers (cv. Mentor), class E, 35 to 45 mm were planted in each container on April 24, 1990. The containers were placed under a permanent rain shelter which reduced rainfall to zero and global radiation by 25%. It hardly altered other ambient conditions such as temperature and relative humidity of the air. The containers were each filled with 170 l of a sandy humous soil with a pH of 5.45, well mixed with 85 l of a peat soil containing an average of 56 living juveniles of potato cyst nematodes (*Globodera pallida*) per gramme. The infected soil was from the North-East of the Netherlands from a field where potatoes were grown in the previous season. For the nematode control treatment this soil was irradiated with 1 Mrad of gamma radiation which succesfully killed the nematodes. After mixing the soil, there were 24 containers which contained no living cyst nematodes and 24 contained cysts with on average 18.5 living juveniles per gramme. The total nitrogen content of the soil was 11.3 g per container at planting, additional fertilization at planting consisted of 9.5 g P_2O_5 and 12.6 g K_2O per container or per six plants. The amount of nutrients supplied was kept limited because the plants were not allowed to grow too vigourously and they were forced to senesce rapidly.

Evaporation losses were negligible as the containers were covered with a plastic sheet provided with slits to allow the plants to protrude. At planting the soil of the containers was near field capacity. In each of two nematode treatments, the plants were subjected to three moisture treatments. The controls were adequately watered twice weekly throughout the season to make up for the transpiration losses as determined by weekly weighing the containers.

The scheme of the experimental set-up is shown in Fig. 1. Soil water potentials in the controls did not exceed −0.04 MPa (Haverkort et al., 1991). In an early drought stress water was withheld until 43 days from planting. Then half the containers of this treatment was harvested and the other half was well watered until senescence. From 43 days after planting a late drought period started in another set of containers in which the plants received only half the amount of the well-watered controls. The number of leaves and stems of the two central plants in each container was recorded weekly. Shedded leaves were included in the count. The mean height of the plants was determined weekly as the distance between the top and the soil, averaged over all plants in each container. At the first two harvests at the end of the early drought stress (43 days after planting) and in the middle of the late drought stress period (70 days after planting) the numbers of green leaves, yellow leaves, stems, stolons (longer than 5 mm) and tubers (smaller and larger than 5 mm) were recorded as well as their fresh weight. Samples of these plant parts were dried for 20 hours at 105 °C to determine their dry matter content. The leaf areas were determined with a LiCor 3100 Area Meter (Li-Cor Inc., Lincoln, Nebraska, USA). The belowground part of each plant was removed with the aid of a 22 cm diameter, 25 cm high cylinder to obtain the same soil volume (about 50% of the soil volume available) per plant. The roots were rinsed to remove the soil, of about half of the fresh root matter the volume was determined by measuring the increase of water upon submersion and the root length was determined with a COMAIR (Melbourne, Australia) root length scanner. The root surface was then calculated under the assumption of roots to consist of regular cylinders. At the final harvest when the plants were senesced at 92 days after planting, only the number of

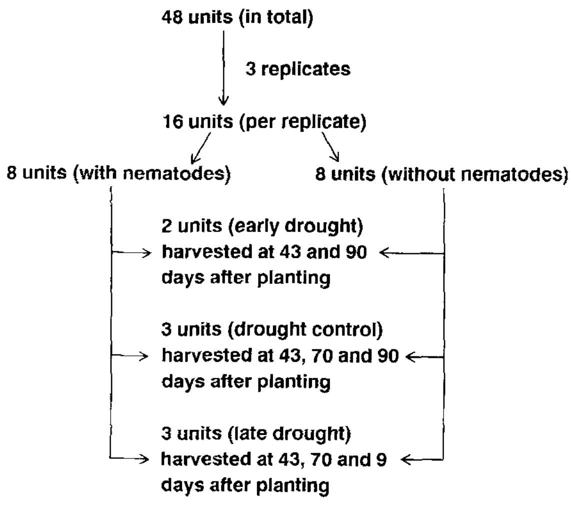

Fig. 1. Experimental scheme, each container with six plants represents an experimental unit.

tubers and tuber fresh and dry matter content were recorded. The harvest index was calculated as the ratio between tuber dry matter and total dry matter. For the final harvest, at almost complete senescence of the plants, tuber dry matter of that harvest and haulm dry matter of the second harvest were used to calculate the harvest index.

About four months after the final harvest, the number of eggs in soil samples of each container was counted to obtain information about the multiplication rate of the cyst nematodes in the various harvest and drought treatments.

Results

Yields and nematode multiplication. At the first harvest at 43 days, total and tuber dry matter production were greatest in the containers with water and without nematodes (Fig. 2), followed by the droughted treatment. The effect of nematodes was far greater than that of the drought. Withholding water did not much further decrease total and tuber dry matter production in the nematode infected treatment because nematode infected plants used less water. At the second harvest, halfway through the late drought period, the effect of the early drought stress period on total and tuber dry matter production was still marked but the late drought stress had hardly affected the plant yield of the containers, irrespective of the nematode infection. Dead leaves

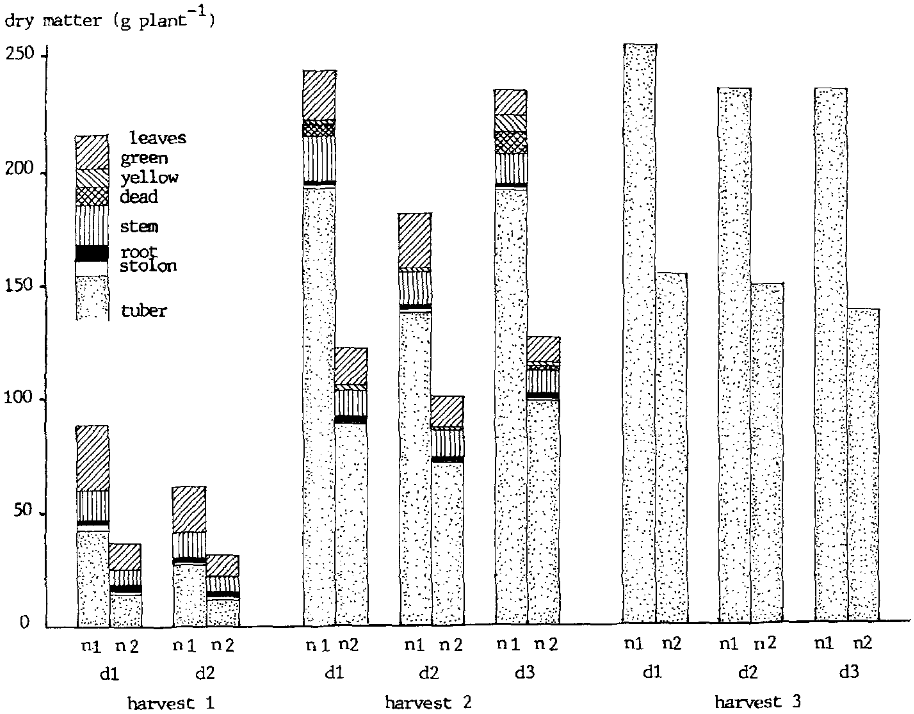

Fig. 2. Cumulative dry matter production of the various plant organs at 43 (harvest 1), 70 harvest (harvest 2) and 92 (harvest 3) days after planting. Legend; nl = nematode control, n2 = infected, dl = drought control, d2 = early drought stress, d3 = late drought stress period.

Table 1. Number of juveniles per g soil observed in the containers at 4 months after termination of the experiment ($LSD_{0.05} = 8.63$).

Drought (d)	Nematodes (n)	Harvest (h, days after planting			Significancies	
		43	70	92		
Control	Control	0.03	0.16	0.04	d	$P < 0.001$
	Inoculated	6.86	16.30	34.64	n	$P < 0.001$
					h	$P < 0.001$
Early	Control	0.08	0.37	0.21	d × n	$P < 0.001$
	Inoculated	6.46	22.60	24.97	d × h	$P > 0.2$
					n × h	$P < 0.001$
Late	Control	–	0.27	0.16	d × n × h	$P = 0.121$
	Inoculated	–	29.01	41.20	repl.	$P > 0.2$

were not observed on the nematode infected and in the uninfected early drought treated plants. At the final harvest at 92 days after planting, only tuber yields were recorded because the plants had senesced. The tuber yields were decreased by about 35% due to nematode infection, but the drought stress effect had almost disappeared.

The 1 MRad gamma irradiation treatment succesfully destroyed the nematode population in the nematode control treatment (Table 1). Soil from this treatment on average contained 0.37 or less eggs per g. The number of eggs in the inoculated well-watered treatments increased from 6.86 when the plants were lifted at 43 days after planting, to 16.3 and 34.6 eggs/g soil when the plants were lifted 70, respectively, 92 days after planting. The early drought period increased the number of eggs per gram from 16.3 to 22.6 when the plants were lifted at 43 days. Later lifting hardly increased the number of eggs in this treatments. The late drought period strongly increased the number of nematodes when the plants were lifted at 70 and 92 days after planting.

Above ground parts. At the first harvest at the end of the early drought period, 43 days after planting, all leaves were still green. At the second harvest, the early drought treated plants yielded 7.10 g of yellow leaves against less than 2 g per plant in the other treatments. At the final harvest towards senescence, all plants showed a few green leaves in the tops of the stems only. The dry matter yield and total leaf area of the green leaves at harvest 1 were reduced more by potato cyst nematode infection than by the early drought stress (Table 2). The interaction of the effects of both stress factors was less than additive, probably because the infected plants used up less soil water and therefore were less drought stressed than the control (Haverkort et al., 1991). They were probably not less infected than the well-watered inoculated plants because from Table 1 similar multiplication rates may be inferred. If the leaf area per plant is calculated as the product of the individual leaf area and the number of leaves per plant, then the decrease due to potato cyst nematodes was largely due to a reduction in the size of the individual leaves whereas drought stress equally reduced both area and number. If the leaf area per plant is calculated as the product of leaf weight per plant and its specific leaf area, then nematodes produced the greatest decrease in leaf weight while drought

Table 2. Characteristics of the green leaves at the first two harvest on 43 and 70 days after planting. Drought treatments: d1 = control, d2 = early drought, d3 = late drought. Statistical significancies: * $P < 0.1$ ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

Characteristic	Without nematodes			With nematodes			Significancies		
	d1	d2	d3	d1	d2	d3	n	d	d×n
Harvest 1									
Dry weight (g per plant)	27.4	20.2		12.1	10.4		***	**	*
Area (cm^2 per plant)	8253	4661		3181	2258		***	**	**
Area (cm^2 per leaf)	150	108		72	58		***	**	ns
Specific area ($cm^2\ g^{-1}$)	301	228		263	218		na	**	ns
Leaf area ratio ($cm^2\ g^{-1}$)	93	74		89	73		ns	*	ns
Number per stem	11.2	7.8		9.7	8.5		ns	**	**
Harvest 2									
Dry weight (g per plant)	22.6	22.3	11.6	17.6	15.7	11.6	**	***	*
Area (cm^2 per plant)	7663	6934	3894	4463	4064	3435	***	***	**
Area (cm^2 per leaf)	187	140	156	92	83	98	***	*	*
Specific area ($cm^2\ g^{-1}$)	341	297	341	286	259	296	***	***	*
Leaf area ratio ($cm^2\ g^{-1}$)	33.8	39.0	25.3	38.3	40.8	31.4	*	***	ns
Number per stem	8.3	4.1	4.7	12.9	13.2	7.2	***	***	ns
Harvest 3									
Total number per stem	12.0	14.4	11.7	15.5	13.5	13.8	**	*	**

equally reduced leaf weight and specific leaf area.

The number of leaves per plant was similarly reduced by both stress factors but as nematodes reduced the number of stems per plant, the number of leaves per stem at the first harvest was not significantly reduced by potato cyst nematodes. Initially the number of leaves per stem was reduced by the nematodes but after 7 weeks the infected plants appeared to have more leaves per stem. In the non-infected plants, the early drought stress period apparently increased the number of leaves per stem at the end of the growing season. At the second harvest halfway through the late drought period and 27 days after the termination of the early drought stress period, the plants subjected to the early drought stress showed a rapid production of the total green leaf dry matter and area per plant. The late drought stress period stopped the formation of new leaves and did not change the specific leaf area (SLA) of the existing leaves. The nematode effect on SLA increased from harvest 1 (−9%) to harves 2 (−6%). The late drought period strongly reduced the number of green leaves and increased the number of yellow leaves per stem. At the first harvest, nematode infection had no influence on the leaf area ratio (total leaf area divided by total plant dry weight) while the nematode infected plants showed significantly higher leaf area ratios than the control.

Early on in plant development as is shown for harvest 1 in Table 3, the weight per individual stem was more than halved by potato cyst nematode infection but this difference diminished to one third at harvest 2. The same holds, to a lesser degree, for the stem length which was similarly affected by both drought and potato cyst nematodes infection at harvest 2 as a result of the influence of potato cyst nematodes on the

Table 3. Characteristics of the stem at the first two harvest on 43 and 70 days after planting. Drought treatments: d1 = control, d2 = early drought, d3 = late drought. Statistical significancies: * $P < 0.1$ ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

Characteristic	Without nematodes			With nematodes			Significancies		
	d1	d2	d3	d1	d2	d3	n	d	d×n
Harvest 1									
Dry weight (g per plant)	15.8	11.7		6.3	5.6		***	**	*
Number per plant	5.4	5.2		4.5	4.5		ns	ns	ns
Length (cm)	52	34		30	24		***	***	**
Specific weight (mg cm^{-1})	62	62		46	52		**	ns	ns
Harvest 2									
Dry weight (g per plant)	18.5	14.4	14.3	11.5	9.6	9.6	***	*	ns
Length (cm	62	54	55	55	48	43	***	***	ns
Specific weight (mg cm^{-1}	59	49	48	54	55	46	ns	*	ns

specific stem weight defined as dry stem weight per cm stem length. The number of stems per plant was not reduced by the drought treatments but nematodes reduced the number from 5.3 to 4.47 (−17%, mean value of harvest 1 and 2).

Below ground parts. The rooting characteristics were not greatly affected by drought or by nematodes. The early drought period reduced the root dry matter, but proportionally less than the total dry matter, leading to a 12% decrease in the shoot/root ratio. Nematode infection strongly reduced shoot but not root dry weight, thereby decreasing the shoot/root ratio by more than 50%. It should be noted here that the roots were only sampled in about 50% of the total soil volume per container. Assuming that most of the roots were within this sample, the shoot/root ratios given in Table 4 are somewhat overestimated. The specific root length and rooting density were not affected within the soil cylinder sampled, but root weight and root length tended to increase due to the presence of nematodes at harvest 2. This may have been due to the depletion of the inoculum before harvest 2 leading to renewed healthy root growth within the sampled cylinder, while in the control relatively more extensive root growth may have taken place outside the sampled part of the containers. At harvest 2 root weight per plant was influenced by an interaction between potato cyst nematodes and drought. In the absence of drought nematode infection slightly decreased root weight, while in the drought treatments, nematodes strongly increased the root weight (+ 30% in the late drought) and a decrease (with drought) of the specific root length. Nematodes induced the production of thicker roots under dry conditions but thinner roots under moist conditions. The main effect, however, was an increased root length in the nematode infected late drought plants which might have been a response to the inoculum being depleted.

Nematodes strongly reduced the total tuber dry matter at harvest 1 (Table 4) but only slightly more than proportional to the total plant weight as is shown by the non-significant decrease of the harvest index. Initially the decrease in tuber yield resulted

Table 4. Characteristics of the tubers at the first two harvest on 43 and 70 days after planting. Drought treatments: d1 = control, d2 = early drought, d3 = late drought. Statistical significancies: * $P < 0.1$ ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

Characteristic	Without nematodes			With nematodes			Significancies		
	d1	d2	d3	d1	d2	d3	n	d	d×n
Harvest 1 (43 days)									
Dry weight (g per plant)	42	27		15	13		***	***	**
Dry weight (g per tuber)	1.1	0.8		0.6	0.5		***	*	ns
Harvest index	0.46	0.43		0.43	0.40		ns	ns	ns
Number per plant > 5 mm	30	28		16	16		***	ns	ns
Number per plant < 5 mm	8.5	8.3		12.4	11.7		ns	ns	ns
Number per stolon > 0 mm	1.25	1.07		1.98	1.89		*	ns	ns
Harvest 2 (70 days)									
Dry weight (g per plant)	194	140	93	90	73	100	***	***	*
Dry weight (g per tuber)	5.7	4.5	5.7	3.9	3.4	3.0	***	*	ns
Harvest index	0.80	0.76	0.82	0.73	0.72	0.78	***	**	ns
Number per plant > 5 mm	33	29	33	21	18	27	***	*	ns
Number per plant < 5 mm	1.2	2.6	1.4	2.7	4.4	6.4	**	ns	ns
Number per stolon > 0 mm	0.96	0.83	0.85	1.78	1.80	1.97	***	ns	ns
Harvest 3 (92 days)									
Dry weight (g per plant)	257	237	237	155	150	139	***	*	ns
Dry weight (g per tuber)	10.0	9.8	8.8	9.3	10.8	8.6	ns	ns	ns
Harvest index	0.84	0.85	0.85	0.83	0.84	0.83	*	ns	ns
Number per plant > 0 mm	26	24	28	17	16	17	***	ns	ns

from a decreased individual tuber weight and a reduction of the number of tubers per plant. Towards senescence, at harvest 3, the mean tuber weight was not significantly influenced by the nematode infection but the number of tubers per plant was reduced from about 25 to 17. Nematode infection also reduced the number of stems (Table 3), explaining why the number of tubers per stem (−17%) was less affected. Drought also led to less tubers per plant but the interaction with nematode infection (effects less than additive) illustrate the reduced effect of drought because plants infected with nematodes use less water (Haverkort et al., 1991). Drought only increased the harvest index at harvest 2, because the late drought stress period terminated top growth. Leaf shedding had no influence on the harvest index because the dead fallen leaves were collected and accounted for. The total number of tubers per plant smaller and larger than 5 mm diameter was greater at harvest 2 than at harvest 3 when no more tubers < 5 mm were found. This effect was due to resporption of the little tubers and ranged from 27 to 31% in the nematode control but from 37 to 41% in the infected treatment. This means that infection with nematodes enhances the resorption of small tubers. The number of stolons was also reduced at the final harvest in the nematode infected treatments. This may have been due to resorption along with the small tubers attached to them and to the greater difficulty to identify underground parts as stolons towards senescence. The effect of the reduction of the number of stolons (−55% mean value of the first two harvests) due cyst nematodes on the total number of tubers was almost compensated by the substantial increase of the number of tubers per stolon (+84%).

Discussion

After inoculation, the soil in the containers contained on average 18.5 living juveniles per g. The multiplication rate was low, only about 2 in the containers where the plants were allowed to grow until senescence. Both early drought stress and earlier harvests reduced the multiplication rate of the cyst nematodes. This was likely caused by the same mechanism: removal of infected roots by harvesting and by dying off after the relieval of the early drought stress reduced the formation of cysts.

At the early stages of plant growth, nematodes reduced the weight and area of the leaves more than did the early drought period. Nematode infection and early drought stress increased the total number of leaves produced in the growing season (Table 2), mainly because these plants reached senescence about a week later. Both these stress factors, however, produced smaller and thicker leaves.

Therefore, Wallace (1987) concluded that potato cyst nematodes induced drought stress symptoms in potato plants. Early drought stress has more often been reported to prolong growth (Haverkort et al., 1990b). The control plants grew more vigourously with larger leaves and had earlier exhausted the nutrients especially nitrogen. Under field conditions depletion of the inoculum or nutrients is not likely to occur as rapidly. This may be why nematode infection is generally reported to be associated in field conditions with earlier senescence. This is illustrated by the rapid decline of soil cover with green foliage after potato cyst nematode attack (Evans and Franco, 1979). Our data on the leaf area ratios corroborate those of Fatemy and Evans (1986). Although a harvest at about 25 days after planting in which these authors found lower leaf area ratios associated with nematode infection did not take place in our experiment. Fatemy and Evans (1986) attributed the observed differences to the relative minor contribution of the tubers to total dry matter. As was shown in Table 4, however, the harvest index at maturity was not much affected in our experiment, leading to a reduced influence of potato cyst nematodes on the leaf area ratio towards plant senescence.

At the first harvest, the weight, number and specific weight of the stems were reduced by nematodes but were hardly affected by drought. Similar reductions in stem numbers as we report here, were also reported by Trudgill et al. (1975b). The early drought period led to slightly shorter plants but the late drought period significantly increased the stem length associated with a decrease of the specific stem weight. Both the late drought period and nematode infection increased stem lengths at the later stages of plant growth. The reason for this continued growth was probably the availability of water and nutrients after termination of the drought stress and after depletion of the nematode inoculum.

Potato cyst nematodes had the greatest effect on the shoot weight without affecting the root weight whereas drought affected both. The drought stress periods hardly affected total tuber dry matter production whereas nematode infection reduced total tuber dry matter by 40%. Not all nutrients could have been depleted by the infected plants because they produced substantially less dry matter than the controls. This seems to indicate that the control plants senesced due to nutrient depletion whereas the nematode infected plants senesced resulting from the infection. The mechanism behind this earlier senescence is not clear. The weight and number of stolons were more than halved by the nematode infection. The effects in the plants caused by nematodes such as reduced leaf water potentials may have reduced the number of stolons and tubers in a similar way as low soil water potentials reduced these numbers (Haverkort et al., 1990b).

This study showed that with regard to many plant characteristics, drought and nematodes act similarly, especially at the early stages of plant growth. Both potato cyst nematodes and drought reduced the leaf area and weight per plant, the average leaf size, the specific leaf area, the leaf area ratio and the number of leaves per stem. Both stress factors reduced the stem weight, specific weight and length. At the first two harvests, both stress factors similarly reduced tuber dry matter production, mean tuber weight and harvest index. The drought effects disappeared towards plant senescence, but the effects due to nematode infection remained. The nematode infection in our experiment showed the largest influence on plant organ characteristics in the early stages of growth because later on the inoculum was likely to be depleted. As with the early drought period, it led to later senescing plants. In this experiment this was probably due to nitrogen depletion in the nematode control and drought control treatments. When drought and nematodes apparently did not affect certain plant characteristics in a similar way, this was likely due to the timing of the stress factor. Our early drought treatment did not affect the number of stems, stolons and tubers whereas nematode infection did, because soil water depletion in the droughted containers did not take place until after emergence and tuber formation.

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