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The influence of cyst nematodes and drought on potato growth. 2. Effects on plant water relations under semi-controlled conditions

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Abstract

Potatoes were grown under a permanent rain shelter in mobile containers in soil with and without potato cyst nematodes (*Globodera pallida*). The plants were either subjected to an early drought stress period from planting until 43 days after planting, to a late drought stress period during tuber bulking or to a drought control. Leaf water potentials, stomatal diffusion resistances for water vapour, transpiration rates, dry matter accumulation and water use efficiencies of the plants were determined periodically. Both drought and nematodes decreased leaf water potential and increased stomatal resistance.

Drought led to a higher water use efficiency, cyst nematode infection, however, reduced the water use efficiency at early stages of growth, and increased it at later stages. It is concluded that at least two main growth reducing mechanisms exist of which the relative importance varies with time. Firstly, reduced apparent assimilation rates, which are unrelated to a change in the water balance caused by the initial attack by the cyst nematodes. Secondly, a reduced dry matter accumulation resulting from a decrease of water uptake. Effects of drought and cyst nematode infection on plant growth and water relations were not always additive mainly because infected plants used up less water leading to less drought stress.

Additional keywords: dry matter content, *Globodera pallida*, leaf water potential, *Solanum tuberosum* L., stomatal resistance, water use efficiency.

Introduction

Evans et al. (1975) have reported a decrease of the leaf water potential and an increase of the stomatal resistance of potato leaves infected with *Globodera rostochiensis*. Stomatal closure was thought to be one of the mechanism through which nematodes damage potato plants. Trudgil et al. (1975) concluded from their findings that a reduced uptake of minerals was another component of damage. Seinhorst (1981), however, concluded from his studies with oats infected with *Heterodera avenae* and white clover infected with *H. trifolii* that two mechanisms exist through which nematodes damage plants. One mechanism occurs at nematode densities of about twice the tolerance limit (T) and involves growth reduction without further changes in water uptake and plant dry matter content. The other mechanism, effective at nematode densities of about 30T, leads to a reduced growth rate associated with an increased shoot/root ratio and dry matter content and a decreased water uptake per gram plant per day. The savings in water use were partly explained by the thicker and smaller leaves and the reduced leaf area of the infected plants. For potato, a decrease of the water use per plant after infection with potato cyst nematodes (*G. rostochiensis*) was also reported by Fatemy et al. (1985). They found the increase of the stomatal resistance to be associated with an increase of foliar abscisic acid (ABA). Exogenously applied ABA also increased stomatal resistance. Further study (Fatemy and Evans, 1986ab) included reports on transpiration ratios (i.e., the amount of water used by the plant to form one gram of dry matter). When calculated as the water use efficiency (the amount of plant dry matter produced per liter water used) they reported values of up to 90 g l^{-1} at the first periodic harvest at two weeks after planting, gradually declining to about 8 to 9 g l^{-1} after 5 to 6 weeks. Initially, the infected plants had higher water use efficiencies than the control plants but after 10 weeks they had somewhat lower values.

The objectives of the research presented in this paper are to study the effects of drought and potato cyst nematode infection, separately and in combination, on potato plant growth and water relations. Drought stress was imposed early on in the growing season or during the tuber bulking stage.

Materials and methods

Six potato plants cv. Mentor were grown in containers and subjected to combinations of the following treatments: with and without on average 18.5 juveniles per gram soil and either well watered throughout the season, subjected to drought during the first 43 days after planting or subjected to drought from 43 days after planting until senescence at 92 days after planting. Three periodic harvests were made: on 43, 70 and 92 days after planting.

Two tensiometers with ceramic cups with septum stoppers were placed in each container at 15 and 25 cm depth per container and soil water potential was recorded twice weekly with a digital transducer probe (Tensimeter, Soil Meas. Syst. Inc. Arizona, USA). Stomatal conductance and transpiration were recorded with a LiCor steady state diffusion porometer on a 2 cm^2 area of the abaxial side of the top leaflet of the youngest full-grown leaf. For each series of measurements six readings were taken per treatment at light saturation (photosynthetically active radiation > 300 W m^{-2} between 13:00 and 16:00 h.

Leaf water potential was determined with a Scholander et al. (1965) type pressure chamber (TFDL, Wageningen) at six plants per treatment on the third full-grown leaf from the top. The water use efficiency (dry matter weight produced per litre water used) was calculated at each harvest, based on the total amount of dry matter produced and the amount of water supplied to the container to date. Total dry matter weight at maturity was considered to consist of the total dry weight of the tops at the foliar maximum at the second harvest and the tuber dry matter at maturity. The first of the three periodic harvests, in which all of the six plants per container were lifted, took place at the end of the early drought period (43 days after planting) which was also the start of the late drought stress period. In the middle of the late drought period a second harvest was made at 70 days and the final harvest at maturity was at 92 days after planting. The experiment, of which full details are given by Fasan and Haverkort

(1991) was laid out in a complete bloc design in three replicates in which the containers of the two nematode treatments, the three drought treatments and the three harvest dates were completely randomized.

Results

Soil and leaf water potentials. The effects of nematode infection and drought treatments on soil water potentials are shown in Fig. 1. Soil water potentials most rapidly declined in the treatments in which water was withheld. This effect was continually greater in the uninfected control treatment because these plants grew more vigourously than the infected plants (Fasan and Haverkort, 1991). Once the early drought stress was relieved, soil water potentials in this treatment did not become lower than −0.025 MPa for the remainder of the growing season. The water supply of only 50% to the plants submitted to late drought stress of the amount used by the controls initially also led to a rapid decline of soil water potentials. Later on these increased again because the drought treated plants accommodated for the change in environment by saving water through reduced growth and leaf shedding (Fasan and Haverkort, 1991).

Both drought and nematode infection decreased leaf water potentials (Table 1). The decrease due to drought varied from -1.2×10^4 to -5.2×10^4 Pa and was greater than that due to nematodes only which varied from 0 to -1.3×10^4 Pa. Up to the first harvest, at the end of the first drought period, the effect of drought on leaf water potential was greater than that of nematode infection but nematode infection had the

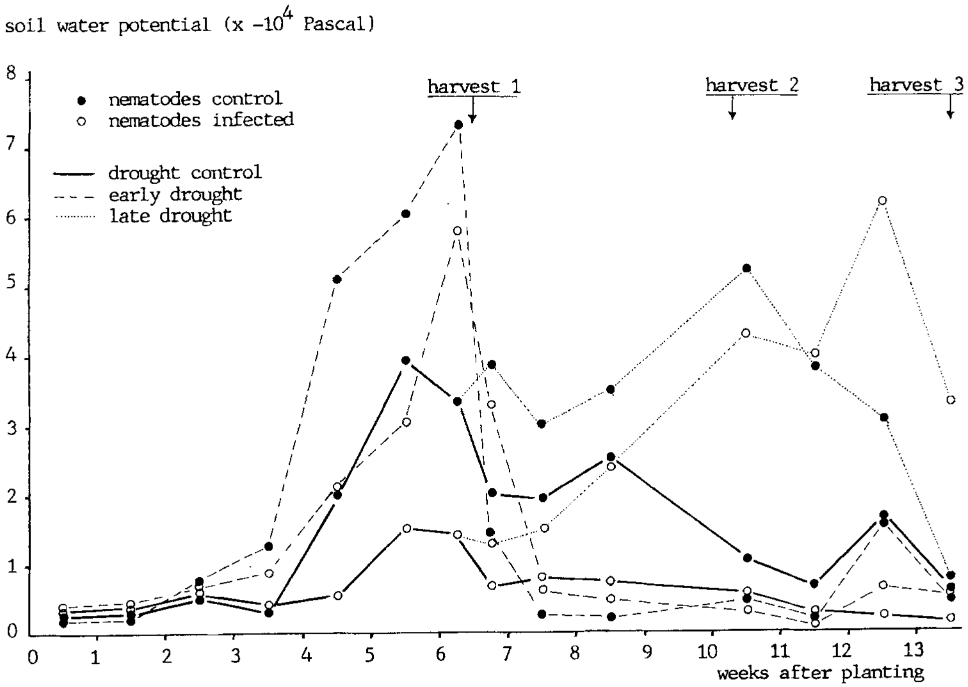

Fig. 1. Soil water potential. Mean values of three replicates per treatment and two soil depths, 15 and 25 cm.

Table 1. Pressure chamber readings ($\times 10^4$ Pa) on four days during the early drought period and on three days during the late drought period.

Drought treatments: d1 = control, de = early drought, d3 = late drought; Nematode treatments: n1 = control, n2 = infected; Significances: ns = not significant, * = $P < 0.1$, ** = $P < 0.01$, *** = $P < 0.001$.

Treatment	Days after planting						
	34	35	37	42	55	57	58
d1; n1	5.37	6.02	6.13	6.92	7.05	6.60	4.17
d1; n2	8.02	10.00	10.82	7.77	9.63	9.45	4.87
d2; n1	7.95	12.03	11.83	13.53			
d2; n2	7.93	10.45	11.52	11.55			
d3; n1					6.93	10.03	4.40
d3; n2					9.32	8.72	5.50
P: d × n	*	***	***	*	ns	*	ns
P: d	*	***	***	***	ns	*	*
P: n	*	*	***	ns	***	*	***

greatest effect on dry matter production. There was a significant interaction between the effects of drought and nematodes because the uninfected plants used up more water because they had higher transpiration rates leading to lower soil water potentials (Fig. 1). The late drought treatment produced little effect (Table 17, partly because the watering took place only one or two days before the pressure chamber observations and because the plant responded by growth reduction and through leaf shedding (Fasan and Haverkort, 1991).

Diffusion resistance and transpiration. Drought and nematodes increased the stomatal resistance and consequently reduced the transpiration rates (Table 2). There was a significant interaction between drought and nematodes with lower diffusion resistances and higher transpiration rates following potato cyst nematode infection in the drought treatment than in the drought treatment without nematodes. This can be explained by the reduction of the total leaf area of the nematode infected plants which was more than halved (Fasan and Haverkort, 1991). Although the transpiration rate per leaf area of the droughted treatment increased if combined with an infection with nematodes because of the greater availability of soil moisture, the total plant transpiration was strongly reduced.

Water use efficiencies. The water use efficiencies calculated from total plant weights at the periodic harvests and the amounts of water used, observed by weekly weighing the containers, are presented in Table 3. From the decreased leaf water potentials (Table 1) and increased diffusion resistances (Table 2) in the drought- and nematode-infected treatments it was to be expected that these treatments would lead to a more efficient use of the available soil moisture. This was indeed observed at the last two harvests (Table 3). The water use efficiency at the final harvest was 7.71 g l^{-1} for the

Table 2. Diffusion resistance (DR; s cm^{-1} and transpiration (TR; μg H_2O cm^{-2} s^{-1}) of the last fully grown leaf on four days during the early drought period. Legend see Table 1.

Treatment	Days after planting								Mean value of DR
	27		35		36		42		
	DR	TR	DR	TR	DR	TR	DR	TR	
d1; n1	1.37	10.23	1.95	8.11	1.36	11.10	0.85	7.27	1.38
d1; n2	1.79	8.59	1.98	8.08	1.51	10.21	0.95	6.87	1.56
d2; n1	1.47	10.31	4.60	4.83	5.11	4.09	0.81	7.67	3.00
d2; n2	1.85	8.58	2.75	6.12	2.77	6.27	1.02	6.65	2.10
d3; n1							2.34	4.58	2.34
d3; n2							0.99	6.90	0.99
P: d × n	ns	ns	**	ns	**	*	*	***	***
P: d	na	ns	***	***	***	***	*	**	**
P: n	***	***	*	ns	*	ns	ns	ns	*

Table 3. Water use efficiency for total dry matter production (g l^{-1} for each periodic harvest (H1, H2, H3 respectively at 43, 70 and 92 days after planting) and between the first two (H1–2) and last two (H2–3) harvests. Legend see Table 1.

Treatment	H1	H2	H3	H1–2	H2–3
d1; n1	7.34	8.35	7.71	9.06	5.90
d1; n2	6.43	8.59	9.38	10.20	10.98
d2; n1	9.19	8.96	8.40	8.86	7.52
d2; n2	7.17	9.39	9.26	10.76	9.24
d3; n1		9.09	9.41	10.62	11.78
d3; n2		9.06	10.07	10.84	15.68
P: d × n	*	ns	ns	*	ns
P: d	***	***	**	**	**
P: n	***	*	***	***	**

control plants wheras nematode infection had increased this to 9.38 g l^{-1} (+22%). The late drought treatment even further increased the water use efficiency to 10.07 g l^{-1} (+30% over the control). In contrast, at the first harvest nematode infection had decreased water use efficiency from a mean of 8.27 g l^{-1} (control) to 6.80 g l^{-1} (infected) an 18% decrease, whereas the early drought treatment led to an increase from a mean of 6.89 to 8.18 g l^{-1}. The reduction in efficiency at the first harvest due to nematodes from 7.34 to 6.43 g l^{-1} (−13%) in the undroughted treatment and from 9.19 to 7.17 g l^{-1} (−22%) in the droughted treatment was not associated with decreased leaf water potentials (Table 1) nor increased stomatal resistances (Table 2).

Table 4. Percentage of dry matter in the plant organs at the three harvest dates. Legend see Table 1.

Treatment	Harvest 1					Harvest 2						Harvest 3
	leaves	stems	stolons	roots	tubers	green leaves	yellow leaves	stems	stolon	roots	tubers	tubers
d1; n1	8.5	6.51	17.9	12.3	15.0	8.9	6.52	7.11	11.0	11.5	22.3	24.7
d1; n2	10.5	7.96	17.3	11.4	15.2	11.2	9.68	9.83	14.2	13.1	20.7	26.9
d2; n1	12.3	8.03	14.7	14.8	21.7	9.3	5.56	7.93	12.0	10.4	20.4	25.4
d2; n2	12.4	9.22	17.6	10.9	17.1	11.7	7.72	10.31	13.7	12.3	20.8	27.0
d3; n1						9.6	8.44	7.26	7.8	9.7	23.4	25.6
d3; n2						11.2	10.30	8.78	12.1	12.2	23.6	28.4
P: d × n	***	ns	**	**	***	**	ns	*	*	ns	*	ns
P: d	***	**	**	ns	***	**	***	**	***	**	***	*
P: n	***	**	*	**	***	***	***	***	***	***	ns	***

Dry matter contents. Drought and nematode infection both led to higher dry matter contents in most plant organs (Table 4). At the first harvest drought increased the dry matter content of all plant parts, but nematode infection decreased the root and tuber dry matter contents. Potato cyst nematodes tend to retard the growth of tubers and the tuber dry matter content increases with tuber age and size. Tuber dry matter content of the nematode infected plants increased faster than that of the control plants, exceeding 27% at the final harvest. Nematode-infected roots initially had a low dry matter content because they grew relatively excessively causing a decreased shoot/root ratio (Fasan and Haverkort, 1991) and a higher proportion of fresh root tissue than in the control. At the time of the second harvest, the capability to form fresh root tissue may have been lost. The late drought treatment in the second harvest may have shown low root dry matter contents because plants subjected to drought form more fresh roots. Drought, contrary to what was to be expected, also led to significantly lower dry matter contents in the stolons at the first two harvests. Drought may have enhanced dry matter transfer from the stolons to the tubers which also becomes apparent from the decrease of the stolon dry matter content from about 17% at the first harvest to about 12% at the second harvest.

Discussion

Beside effects of nematodes on nutrient uptake (Trudgill et al., 1975) and consequently on light use efficiency and plant growth, the observed differences may be partly accounted for in terms of the water relations in the various treatments. These plant water relations are shown in the leaf water potentials (Table 1), the stomatal diffusion resistance for water vapour and leaf transpiration (Table 2), the water use efficiencies as calculated at each periodic harvest (Table 3) and in the dry matter contents of the plant organs (Table 4). Our finding of an initial reduction of the water use efficiency associated with potato cyst nematode infection at first sight does not seem to agree with that of Fatemy and Evans (1986a), who initially observed higher values. Their unexplicable, extremely high initial water use efficiencies (up to 90 g^{-1}), however, declined with time to values comparable to ours and after about 8 weeks nematode infection in their experiment also led to reduced water use efficiencies. Our findings, however, do corroborate those of J. Schans (personal communication 1991) who found decreased water use efficiencies of individual leaves until 60 days after planting. Later on these differences disappeared in their experiment as they did in ours. J. Schans did not continue measurements until senescence but we expect him to have found higher water use efficiencies in leaves of infected plants than in the controls at later stages of plant growth, as we did in our experiment.

Our results indicate that at all stages of growth in infected plants, water uptake is impaired resulting in decreased leaf water potentials and increased stomatal resistances but that at the early stages of growth plant dry matter production is reduced more than was to be expected on the basis of impaired water relations alone. A direct effect of nematode infection on the dry matter production must exist. This direct effect may be the result of the combination of the following processes: a reduced assimilation rate (more than expected from stomatal regulation caused by intoxication and/or nutrient deficiency), an increased respiration rate needed to heal the damage inflicted by infecting juveniles and an allocation of carbon to the nematodes and to the soil (leaking). A reduction in top size and hence light interception does not account for the observed differences because, in fact, the leaf area ratio (LAR i.e. the leaf area per plant weight) at the first harvest was affected more by drought than by nematodes (Fasan and Haverkort, 1991). Later on in the season when the inoculum is depleted and most juveniles had developed into cysts the direct effect of nematodes on dry matter production ceased but the water-regulated (and/or nutrient deficiency) effects remained. These results are consistent with those of Evans et al. (1977) and Trudgill (1987). They reported a decreased efficiency of the potato root system leading to a diminished top growth as a consequence of a chronic deficiency of one or more nutrients, which beside the water limitation caused by nematodes, contributed to a decrease in the light use efficiency of the canopy.

These findings may also explain how Seinhorst (1981) most likely wrongly concluded that, at low nematode densities of about twice the tolerance limit, yield reduction was not brought about by a reduction of water uptake by the plant. He may have observed with low nematode densities a situation we observed at the second harvest where the two mechanisms (yield reduction associated without and with an influence on water uptake) cancelled out the effect on water use efficiency. In our new view, the time of cancelling out is later at low densities than at high densities. Seinhorst (1981) did not include an early harvest so he could not have observed an earlier reduced water use efficiency.

With the high nematode densities of about thirty times the tolerance limit, which was in the order of magnitude of the nematode density we used in our experiment, Seinhorst observed a situation (with regard to water use efficiency) at his final harvest as we did at ours (Table 3). The effect of growth reduction, which was not related with water uptake, on water use efficiency was more than cancelled out by the growth reduction caused by the disruption of the water relations. Seinhorst then, rightly suggested two different mechanisms of damage but wrongly concluded that they depend on nematode density. No, we found them to appear simultaneously but they have a varying influence on dry matter accumulation with time. One mechanism (which does not influence water use efficiency) is of relatively greater importance at the beginning of crop growth and the other (which does influence water use efficiency) is more important later on in crop growth.

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