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Photosynthesis, transpiration and plant growth characters of different potato cultivars at various densities of Globodera pallida

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Abstract

Plants of four potato (*Solanum tuberosum* L.) cultivars were grown in pots in a greenhouse at five densities of *Globodera pallida* between 0 and 300 eggs per gram of soil. Photosynthesis and transpiration of selected leaves were measured at 30, 37, 49 and 60 days after planting. Stem length was recorded at weekly intervals. Plants were harvested 70 days after planting and various plant variables were determined.

At 30 days after planting, when second and third stage juveniles were present in roots, both photosynthesis and transpiration rates were severely reduced by *G. pallida*. In the course of time these effects became less pronounced. Water use efficiency was reduced by *G. pallida* between 30 and 49 days, but not at 60 days after planting. The results suggest independent effects of *G. pallida* on stomatal opening and on photosynthesis reactions. There were no consistent differences among cultivars in the response of leaf gas exchange rates and water use efficiency to nematode infection. Reduction of photosynthesis by *G. pallida* appeared additive to photosynthesis reduction due to leaf senescence.

Total dry weight was reduced by 60 % at the highest *G. pallida* density. Weights of all plant organs were about proportionally affected. Shoot/root ratio was not affected and dry matter content was reduced. Stem length and leaf area were most strongly reduced during early stages of plant-nematode interaction. The number of leaves formed was only slightly reduced by *G. pallida*, but flowering was delayed or inhibited. Reduction of total dry weight correlated with reduction of both leaf area and photosynthesis rate. Leaf area reduction seems the main cause of reduction of dry matter production. Tolerance differences among cultivars were evident at 100 eggs per gram of soil only, where total dry weight of the intolerant partially resistant cv. Darwina was lower than that of the tolerant partially resistant cv. Elles and of the tolerant susceptible cv. Multa. The tolerance differences were not correlated with leaf photosynthesis and transpiration. Apparently these processes are not part of tolerance of plants.

Additional keywords: potato cyst nematodes, *Solanum tuberosum* L., host-parasite interaction, damage mechanism, tolerance, gas exchange, stomata, water use efficiency, total dry weight, leaf area, stem length.

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Introduction

Potato cyst nematodes (PCN), *Globodera rostochiensis* (Woll.) Skarbilovich and *G. pallida* Stone, cause reduction of growth rate and tuber yield of potato plants. Under the same environmental conditions, the amount of damage due to PCN varies among susceptible as well as among resistant cultivars (Huijsman et al., 1969; Dale et al., 1988). The term 'tolerance' has been used for several aspects of this phenomenon. Here tolerance is defined as the complex of 'physiological mechanisms that enable the plant, passively or actively, to counteract the stresses caused by environmental constraints including parasitic nematodes' (Wallace, 1987). Although effects of PCN on plant growth characteristics have been shown in many studies (summarized by Trudgill, 1986), the causal mechanisms of damage and the nature of tolerance remain largely unclear. Insight in these phenomena can be gained from the effects of PCN on the physiological processes that determine plant growth and yield, e.g. photosynthesis and dry matter distribution. This may identify the key factors of tolerance and improve selection methods for higher tolerance levels.

Plant growth reduction due to nematode infection was associated with reduction of photosynthesis rate for *Phaseolus* bean infected with *Meloidogyne incognita* (Melakeberhan et al., 1985) and for soybean infected with *Heterodera glycines* (Poskuta et al., 1986). Schans (1991) reported a strong reduction of photosynthesis and transpiration rates of potato plants, due to invasion into roots by second stage juveniles of *G. pallida*, but effects of nematodes on plant growth were not investigated.

In order to investigate whether the photosynthesis response of different potato cultivars to infection by *G. pallida* contributes to their tolerance of damage by *G. pallida*, measurements of leaf gas exchange rates at several times after plant emergence and at several densities of *G. pallida* were combined with measurements of plant growth rate. The experiment was carried out in pots in a greenhouse, where PCN-free treatments could be included as the control series and where root weights could be measured accurately.

Materials and methods

Plants and nematodes. Eye scoops of potato tubers with one sprout were planted on 7 July 1987 in pots containing 4 kg of fertilized sandy loam soil to which 15 mass % water was added (pF = 2). Pots were watered twice a day to keep soil moisture approximately at this level. At planting, an egg suspension of *G. pallida*, pathotype Pa3, was added to the pots as described by Schans (1991). Five density levels were established: 0, 10, 30, 100 and 300 eggs per gram of soil (e/g_s). Four potato cultivars were used. Two, 'Darwina' and 'Elles', are partially resistant to Pa3, but 'Elles' has a higher tolerance level (Boerma and Velema, 1987). The other two cultivars, 'Multa' and 'Eba', are susceptible to PCN. The high tolerance level of 'Multa' is well documented (Huijsman et al., 1969) and 'Eba' is relatively intolerant (Ir. A. Mulder, pers. comm.). The experiment was done in a randomized block design with seven replicates. The pots were kept in a naturally lit glasshouse at 18 °C for 10 hours and 12 °C for 14 hours per day. Relative air humidity was kept at 80 %. Plants emerged on average 10 days after planting. Analysis of root samples indicated that at 30 days after planting numerous nematodes, mainly second and third stage juveniles, were present in the roots. Tubers were not yet present at that time.

Photosynthesis and transpiration rates. Photosynthesis rate (PHOT; expressed in μg CO_2 m^{-2} s^{-1}) and transpiration rate (TRANS; expressed in mg H_2O m^{-2} s^{-1}) of terminal leaflets of leaves were measured with the LCA-2 gas analysis system (The Analytical Development Company Ltd., Hoddesdon, England). Air was supplied from a gas cylinder at a rate of 400 ml/minute and contained approximately 585 mg m^{-3} CO_2. Air temperature in the leaf chamber varied between 20 and 24 °C. The relative humidity of the air was 40-50 %. The halogen light source delivered 360 J m^{-2} s^{-1} (1800 μEinstein m^{-2} s^{-1}) photosynthetically active radiation at the leaf surface. Water use efficiency (WUE) was calculated as PHOT/TRANS.

At 30 days after planting, the first leaf from the plant top with length > 2.5 cm was labeled A. The leaves, which developed subsequently above leaf A, were labeled B through E respectively. The position of the leaves on the plant at the time of measurement are presented in Table 1. At 30, 37, 49 and 60 days after planting gas exchange rates of selected leaves were measured in light. At 30 and 49 days after planting gas exchange rates were also measured in darkness.

Plant growth. Stem length was recorded at weekly intervals during plant growth. The plants were harvested 70 days after planting, and the number of leaves formed was counted. The highest leaf with a length > 2.5 cm was regarded as leaf 1. Three groups of leaves were distinguished. They are referred to as young (leaf 1-5), intermediate (leaf 6-10) and old leaves (leaf 11-15). Leaf area and length of the stem parts for these groups were recorded. Also, the diameter of the stem 30 cm under the top was measured. Fresh and dry weight of leaves, stems, stolons, roots and tubers were determined. Shoot/root ratio's were calculated on dry weight basis. Dry matter content was calculated as total dry weight / total fresh weight. Specific leaf area was calculated as leaf area/dry weight of leaves and specific stem length as stem length/dry weight of stem. Finally, cysts were extracted and counted. Tolerance differences among cultivars were examined as differences in final total dry weight per nematode density level. Correlations between various characteristics were calculated, based on means per cultivar and density.

Table 1. Position of leaves used for gas exchange measurements at each observation date (days after planting). The leaf label indicates the relative position of the measured leaf. Leaf A is the first leaf from the plant top with length > 2.5 cm at 30 days after planting, leaves B through E have developed subsequently above leaf A. The leaf number indicates the actual position of the leaf, relative to the plant top, at the time of measurement.

Observation date	Leaf label	Leaf number at measurement time
30	A	5
37	A	7
	B	6
	C	5
49	C	7-8
	D	6-7
60	E	8-10

Results

Photosynthesis and transpiration rates. Significant differences in gas exchange rates among cultivars were found on each observation date, but these were neither consistent with nematode density nor with time. On each observation date, the relative reduction of photosynthesis and transpiration rates due to *G. pallida* was not different among cultivars. Therefore no correlation between effects of *G. pallida* on leaf gas exchange and known tolerance or resistance characteristics of the four potato cultivars to *G. pallida* was apparent.

Respiration in darkness at 30 days after planting was not affected by *G. pallida*, but TRANS in darkness was strongly reduced at 30 or more e/g_s (Fig. 1). In darkness no photosynthesis occurs, therefore these results suggest a direct reduction of stomatal opening by *G. pallida*. Gas exchange measurements at 49 days after planting revealed no effects of nematode density.

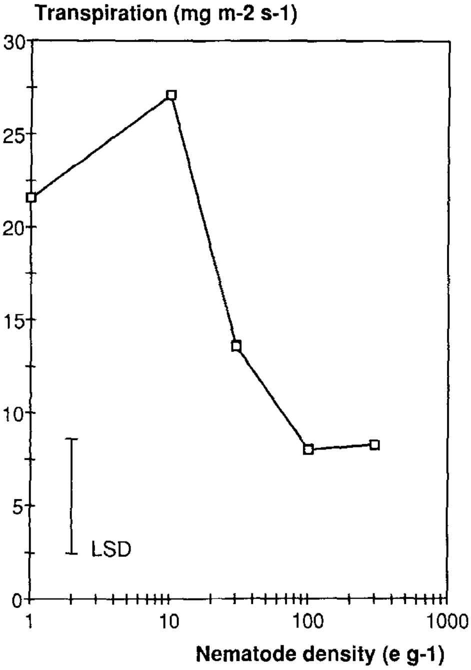


Fig. 1. Transpiration rate (TRANS, mg H_2O m^{-2} s^{-1}) of leaf A in darkness, averaged over four potato cultivars at various densities of *G. pallida* (eggs per gram of soil), at 30 days after planting. The vertical bar indicates the least significant difference (LSD, P = 0.05).

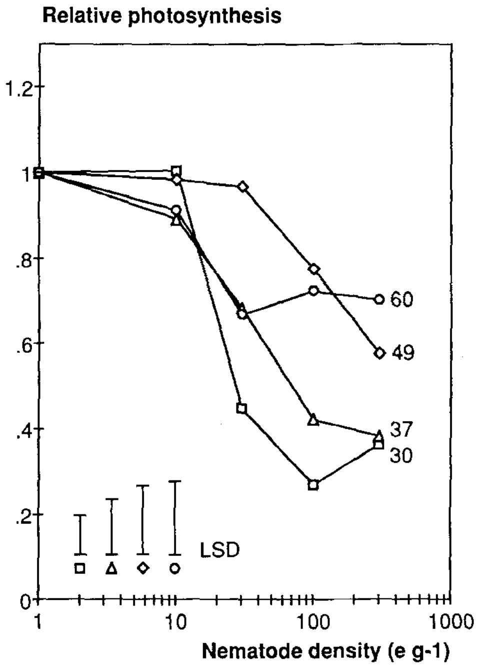


Fig. 2. Photosynthesis rate in light (PHOT) at each observation date, averaged over four potato cultivars, at various densities of *G. pallida* (eggs per gram of soil), relative to control plants. Symbols: (□) leaf A; 30 days after planting. (△) leaf C; 37 days after planting. (◇) leaf D; 49 days after planting. (○) leaf E; 60 days after planting. The vertical bars indicate the least significant difference (LSD, P = 0.05) for each observation date.

At 30 days after planting, *G. pallida* infection reduced PHOT of irradiated leaves to about 45 % of control values at 30 e/g_s, and to about 30 % of control values at 100 and 300 e/g_s (Fig. 2). In the course of time, the reduction of PHOT by *G. pallida* became less pronounced. At 37 days after planting, PHOT of plants infected with *G. pallida* at 30 e/g_s was still about 70 % of control values and only at 300 e/g_s a reduction to 30 % of control values was observed. At 49 days after planting, PHOT was reduced to about 80 % and 60 % of control values at 100 and 300 e/g_s, respectively. The trend of diminishing effects of *G. pallida* with time was not continued at 60 days after planting, when PHOT was reduced by *G. pallida* at 30 or more e/g_s to about 70 % of control values. The absolute values of PHOT of control plants are presented in Table 2.

Infection by *G. pallida* reduced TRANS of irradiated leaves along with, but not

Table 2. Absolute values of PHOT ($\mu g\ CO_2\ m^{-2}\ s^{-1}$) and WUE (1000 × PHOT/TRANS) of indicated leaves of control plants (0 e/g_s) in Figures 2 and 3, at each observation date (days after planting). The values are averages of the four cultivars.

Observation date	Leaf measured	PHOT	WUE
30	A	532.2	9.1
37	C	605.2	10.1
49	D	457.4	9.4
60	E	490.9	7.2

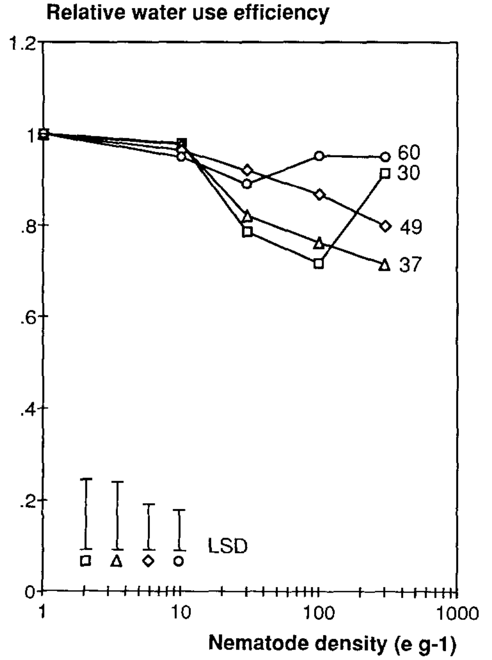
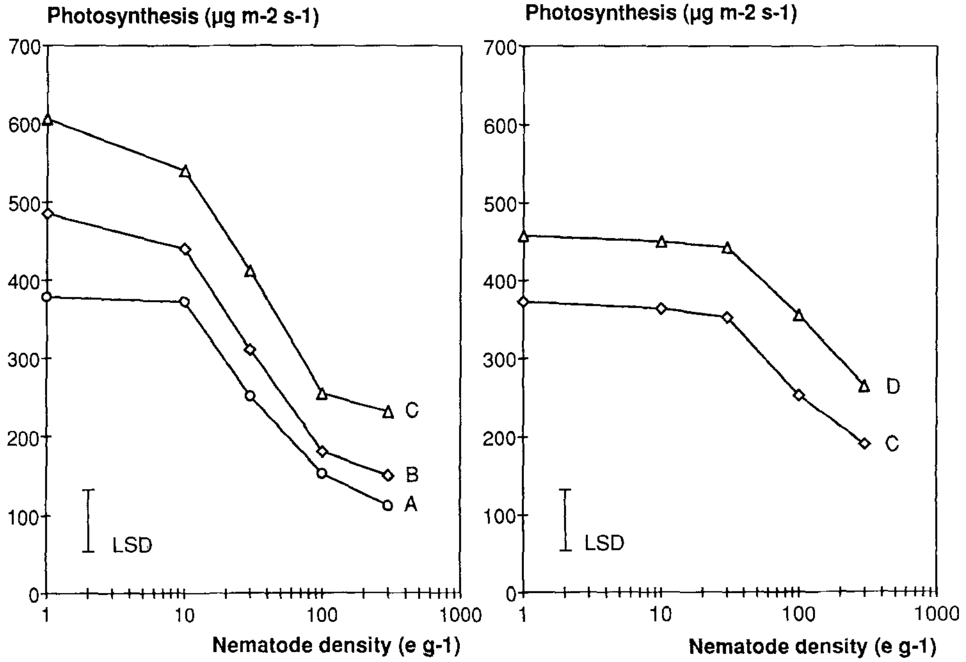


Fig. 3. Water use efficiency (WUE) at each observation date, averaged over four potato cultivars, in light at various densities of *G. pallida* (eggs per gram of soil), relative to control plants. Symbols: (□) leaf A; 30 days after planting. (△) leaf C; 37 days after planting. (◇) leaf D; 49 days after planting. (○) leaf E; 60 days after planting. The vertical bars indicate the least significant difference (LSD, $P = 0.05$) for each observation date.

always proportional to the reduction of PHOT. At 30, 37 and 49 days after planting, WUE (= PHOT/TRANS) was increasingly reduced with increasing *G. pallida* densities (Fig. 3), indicating that PHOT was more reduced than TRANS by *G. pallida*. This suggests that gas exchange rates of infected plants were reduced mainly by limitations on photochemical or biochemical processes of photosynthesis rather than on stomatal functioning. The high WUE 30 days after planting at 300 e/g_s is an inexplicable exception. At 60 days after planting, WUE was not affected by nematodes. The absolute values of WUE of control plants are presented in Table 2.

The interference of effects of *G. pallida* with ageing of leaves was analysed by comparing PHOT of leaves A, B and C at 37 days after planting (Fig. 4), and PHOT of leaves C and D at 49 days after planting (Fig. 5). At 37 days after planting, PHOT of leaves A and B was significantly lower than PHOT of leaf C, at all *G. pallida* densities. PHOT of leaf A was significantly lower than that of leaf B only at 0 and 10 e/g_s. At 49 days after planting, PHOT of leaf C was significantly lower than that of leaf D, irrespective of nematode density. Interaction between the effects of leaf age and nematode density on PHOT was absent (F-probability = 0.59 and 0.99, respectively). This indicates that *G. pallida* did not affect senescence processes in potato leaves in this period.



Figs 4-5. Effect of leaf position on photosynthesis rate (PHOT; µg CO_2 m^{-2} s^{-1}) of potato leaves in light at various densities of *G. pallida* (eggs per gram of soil). Average of four cultivars. The vertical bar indicates the least significant difference (LSD, P = 0.05).

Fig. 4. (Left). 37 days after planting. Symbols: (○) leaf A, (◇) leaf B and (△) leaf C .

Fig. 5. (Right). 49 days after planting. Symbols: (◇) leaf C and (△) leaf D.

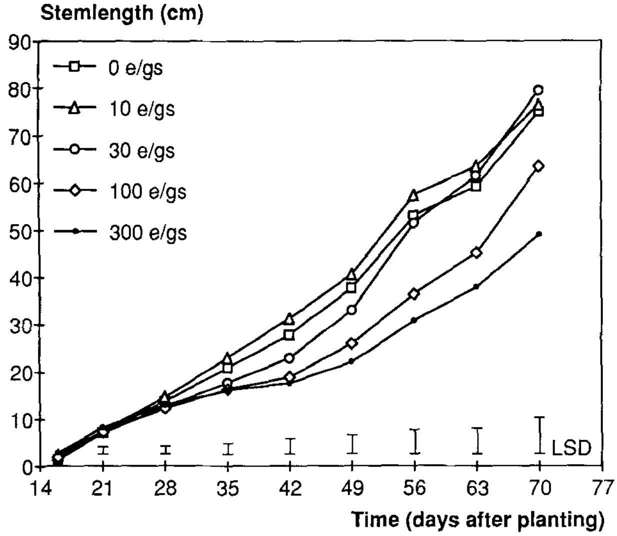


Fig. 6. Stem length of potato plants (cm), averaged over four cultivars, at weekly intervals for five *G. pallida* densities (eggs per gram of soil). The vertical bars indicate the least significant difference (LSD, $P = 0.05$) for each observation date.

Plant growth. Significant interaction between cultivars and density of *G. pallida* was observed only for dry weight of roots and tubers, total stem length at 50 days after planting and the length of the stem section carrying the oldest leaves at 70 days after planting. The correlation of these characters with total dry weight at 70 days after planting (TDW) was high. Cultivar effects for the other measured plant characters were not important when compared with effects of nematode density.

Stem length was reduced by *G. pallida* from 28 days after planting onwards (Fig. 6). Between 21 and 42 days after planting, the growth rate of stem length was significantly reduced at 30 and more e/g_s. From 42 to 56 days after planting, reduction of stem length growth rate occurred at 100 and 300 e/g_s. Between 63 and 70 days after planting, stem length growth rate was reduced at 300 e/g_s only.

Total dry weight at 70 days after planting (TDW), averaged over cultivars, was significantly reduced by *G. pallida* at 100 and 300 e/g_s (Fig. 7). At 300 e/g_s, average TDW was about 40% of that of control plants. The reduction of TDW was about proportionally distributed over root, sprout and tuber weights. The correlation of root, sprout and tuber weights with TDW was 0.85, 0.95, and 0.79, respectively. Similarly, the decrease in sprout weight due to *G. pallida* infection was caused by about proportionally decreased weights of leaves, stems and stolons. A significant difference in tolerance was observed at 100 e/g_s only, where TDW of 'Darwina' was lower than that of 'Multa' and 'Elles'.

The shoot/root ratio, whether calculated with shoot weight including or excluding stolons and tubers, was not affected by *G. pallida* (Table 3; F-probability = 0.15, for both computations). Dry matter content was reduced at 100 e/g_s. The total leaf area per plant was strongly reduced at 100 and 300 e/g_s and was highly correlated with TDW (Table 3). The number of leaves longer than 2.5 cm was only slightly decreased

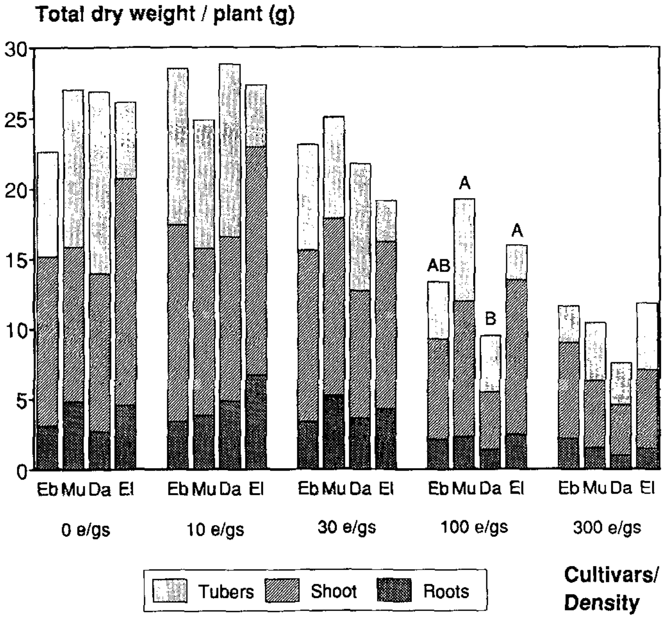


Fig. 7. Total dry weight (g) and dry weight of roots, sprouts and tubers (g) 70 days after planting for four cultivars at five *G. pallida* densities (eggs per gram of soil). Different letters indicate significant differences ($P = 0.05$) in total dry weight between cultivars per density level.

at 100 and 300 e/g_s (Table 3). Hence, total leaf area was reduced because of smaller size of individual leaves. Specific leaf area was not influenced by *G. pallida* (Table 3). Specific stem length increased at 100 and 300 e/g_s, indicating that stems of infected plants were thinner, and had a highly negative correlation with TDW (Table 3). The stem diameter 30 cm under the top highly correlated with specific stem length ($r = 0.79$). The number of plants flowering 70 days after planting was significantly lower at 100 and 300 e/g_s (Table 3). 'Darwina' was excluded from these data, because this cultivar seldomly flowers.

The decrease of total leaf area was mainly attributed to leaf area reduction of the old leaves (Table 4), which were formed during early stages of nematode infection. The leaf area of the old leaves at 300 e/g_s was less than half of that of the control, whereas the leaf area of young leaves was not reduced at all (Table 4). However, the young leaves were not yet full-grown at harvest time. The correlation between leaf area and TDW increased with age of leaves. The same effects were found for length of different stem parts, but length of young stem parts was still reduced at 300 e/g_s (Table 4).

The correlation between PHOT of various leaves at various dates and TDW was quite high (Table 5). At 60 days after planting correlation was lowest, but still significant.

There was no correlation between the number of cysts and TDW ($r = 0.04$).

Table 3. Means per density and correlation with TDW for several plant growth characteristics. Different letters indicate significant differences (P = 0.05) of characteristics between densities. Significance of the correlation at the 5 % and 1 % level is indicated by (*) and (**), respectively.

Characteristic	Density					Correlation with TDW
	0	10	30	100	300	
shoot/root ratio (tubers and stolons excluded)	3.1	3.0	2.7	4.4	3.9	-0.36
shoot/root ratio (tubers and stolons included)	6.3	6.2	5.2	7.9	7.2	-0.23
dry matter content (%)	11.3a	11.3a	10.6ab	10.4b	10.7ab	0.32
number of leaves formed	18.9ab	19.4a	19.3a	18.2b	17.2c	0.72**
leaf area plant $^{-1}$ (cm^2)	2160a	2427a	2215a	1558b	1069c	0.92**
specific leaf area ($\mathrm{cm}^2\ \mathrm{g}^{-1}$)	291	323	308	317	318	-0.19
specific stem length ($\mathrm{cm}^2\ \mathrm{g}^{-1}$)	24a	24a	28a	42b	46b	-0.81**
frequency of flowering	0.60a	0.55a	0.64a	0.29b	0.32b	0.67**

Table 4. Means per density and correlation with TDW for area leaf $^{-1}$ plant $^{-1}$ (cm^2) and for length of stem parts (cm) in young, intermediate and old leaf layers. Different letters indicate significant differences (P = 0.05) of traits between densities. Significance of the correlation at the 5 % and 1 % level is indicated by (*) and (**), respectively.

Trait	Density					Correlation with TDW
	0	10	30	100	300	
area young leaves	63	73	66	65	61	0.36
area interm. leaves	152a	164a	161a	134b	97c	0.71**
area old leaves	144a	150a	139a	92b	65c	0.95**
length young stem part	18a	19a	20a	19a	14b	0.48*
length interm. stem part	26a	26a	28a	22b	16c	0.64**
length old stem part	17a	19a	17a	12b	10b	0.64**

Table 5. Correlation of photosynthesis measurements with total dry weight (TDW). Significance of the correlation at the 5 % and 1 % level is indicated by (*) and (**), respectively.

Days after planting	Leaf label	Leaf number at measurement time	Correlation with TDW
30	A	5	0.72**
37	A	7	0.73**
37	B	6	0.78**
37	C	5	0.81**
49	C	7-8	0.78**
49	D	6-7	0.67**
60	E	8-10	0.58**

Discussion

Photosynthesis and transpiration rates. PHOT and TRANS of potato leaves were strongly reduced by *G. pallida* at 30 or more e/g_s, at 30 days after planting. The reduction of gas exchange rates persisted throughout the experiment, but its severity decreased with time. Schans (1991) reported a reduction of leaf gas exchange rates of potato, three days after inoculation with freshly hatched second stage juveniles of *G. pallida*. The prolonged reduction of gas exchange rates by *G. pallida* reported here can be explained by the continuous presence of second stage juveniles in roots, because emergence of second stage juveniles from eggs and subsequent penetration of roots is dispersed over time. The dispersion varies from six weeks in small pots (Forrest and Phillips, 1984) to three months in the field (Storey, 1982). The decreasing severity of the nematode effects with time, up to 49 days after planting, reflects the gradual increase of the fraction of non-infected root tips, due to growth of new roots and diminishing numbers of infective second stage juveniles. The turn of this trend at 60 days after planting might have been caused by second stage juveniles of a second generation of the nematodes, as observed by Evans (1969).

The reduction of PHOT due to *G. pallida* might also be explained by a decrease of sink strength of the tubers (Dwelle, 1985), because *G. rostochiensis* at 189 e/g_s reduced the number of tubers per plant (Trudgill & Cotes, 1983). However, the strongest reduction of PHOT and TRANS occurred at 30 days after planting, before the start of tuber growth. Therefore, it is more likely that the reduction of tuber number due to PCN is caused by lower PHOT or by the factors, responsible for the reduction of PHOT.

The reduction of WUE by *G. pallida* in this experiment is different from the observations by Schans (1991), where WUE of potato plants was increased by *G. pallida*, three days after inoculation with freshly hatched second stage juveniles. The increased WUE indicated that PHOT was less inhibited than TRANS, which implies that limitation of gas exchange was due to stomatal closure. The decreased WUE indicated that non-stomatal processes (i.e. photochemical or biochemical processes of photosynthesis) were involved in the reduction of PHOT and TRANS. However, a simultaneous direct reduction of stomatal conductance may have been masked because of feedback of these processes on stomatal opening. Apparently, infection by *G. pallida* reduced gas exchange rates initially by stomatal closure and later on by non-stomatal processes, as observed between 30 and 49 days after planting. Possibly the prolonged release of stomatal inhibitors by infected roots (as discussed by Schans, 1991) not only reduces stomatal conductance, but affects the Calvin cycle or the photochemical reactions as well. Schapendonk et al. (1989) reported analogous effects of water stress on photosynthesis of potato plants. Photosynthesis rate was reduced by water stress initially as a consequence of stomatal closure, but after three days increasingly by non-stomatal processes. These results support the hypothesis of Seemann and Sharkey (1987), that initial plant reaction to stress in the root environment, resulting in stomatal closure, is independent of the nature of the stress. The effects of *G. pallida* on the WUE of individual leaves agree with effects of *G. rostochiensis* on the transpiration ratio (i.e. water consumption/dry matter growth per period of 7 days) of whole potato plants (Evans, 1982). Initially the transpiration ratio was decreased (WUE increased) by *G. rostochiensis*, but from 32 days onwards the transpiration ratio was increased in the presence of nematodes.

The reduction of leaf photosynthesis by *G. pallida* was additive to the reduction of leaf photosynthesis due to senescence. In ageing potato leaves, photosynthesis reduction is closely correlated with the reduction of leaf nitrogen content due to breakdown of proteins (Vos and Oyarzun, 1987; Thimann, 1980). However, the reduction of nitrogen content of haulms or leaves by PCN is unimportant, when compared with the reduction of potassium content (Trudgill et al., 1975; Trudgill and Cotes, 1983; Trudgill, 1987). Leaf potassium content of infected plants is reduced by 75 % of control plant values to about 1 % of leaf dry matter, depending on cultivar and fertilizer level. This is below the potassium levels that reduced photosynthesis rates of sugar-beet and alfalfa because of increased mesophyll resistance (Terry and Ulrich, 1973; Peoples and Koch, 1979). The results suggest that the reduction of photosynthesis by *G. pallida* is not mediated by processes of leaf senescence, but by the release of stomatal inhibitors in infected roots, probably in combination with reduced potassium uptake rate.

Plant growth. Total dry weight of potato plants was strongly reduced by *G. pallida*. The weight reduction was proportionally distributed over all plant organs and was associated with reduction of leaf area, stem length and stem diameter. The number of leaves longer than 2.5 cm at 10 weeks after planting was only slightly reduced by *G. pallida*. Hence, dry matter production was reduced primarily by equal growth reduction of all plant organs, and only little by reduction of vegetative development rate as concluded by Seinhorst (1986). The reduced frequency of flowering at 70 days after planting due to *G. pallida* may indicate interference of the nematodes with reproductive development of potato plants.

Dry matter content of plants was reduced by *G. pallida*. In most reports dry matter content is increased by PCN, but Fatemy and Evans (1986) showed that the effect depends on the time of measurement: up to 51 days after planting infected plants had greater dry matter contents than uninfected plants, and smaller dry matter contents at 71 days after planting. Shoot/root ratio was not affected by *G. pallida*. Sometimes a reduction of shoot/root ratio due to PCN infection is observed. This may also depend upon the time of measurement (Trudgill and Cotes, 1983).

The expected tolerance differences among cultivars were confirmed significantly for 'Darwina', 'Multa' and 'Elles' at 100 e/gs only. At lower densities tolerance could not be expressed because TDW was not reduced. TDW of 'Darwina' tended to be lower than that of the other cultivars at 300 e/gs as well, but this was not significant. The intolerance of 'Eba' was not observed in this experiment. However, the experiment was ended when plants were still growing, whereas tolerance differences are usually based on tuber yield of fully matured plants. Possibly final tuber yield of the cultivars is affected differently by nematodes than TDW at 70 days after planting.

The reduction of TDW was not related to the number of cysts formed on the plants, hence resistance to PCN did not influence damage in this experiment. Resistance acts upon the development of third and later juvenile stages, therefore damage was brought about before the third juvenile stage. Apparently feeding on plant roots by third and later juvenile stages and adults has no implication for the expression of damage.

Gas exchange rates related to plant growth. The strong reductions of PHOT and leaf area may both have been caused by stress-induced elevated ABA levels in leaves (Watts et al., 1981). Leaf area and PHOT were both highly correlated with TDW, but this does not necessarily imply causal relationships between TDW and these factors. In several studies, differences among cultivars in dry matter production are highly correlated with leaf area, but not with leaf photosynthesis rate (Dwelle et al., 1981; Shimshi and Susnoschi, 1985; Prange, 1987). This indicates that leaf area is the most important factor in light capture and plant growth. Based on these findings, the reduction of leaf area by *G. pallida* is most likely the causal factor of plant growth reduction, with reduction of gas exchange rates being a parallel effect of the underlying mechanism, i.e. the presumed elevated levels of ABA in leaves.

Apparently damage was caused in the early stages of plant-nematode interaction: the strongest reduction of gas exchange rates was observed 30 days after planting, the strongest reduction of leaf area occurred for the oldest leaves and the increase of stem length was most strongly reduced during 28-42 days after planting. The intensity of the damage effects probably depends on the proportion of root tips invaded by second stage juveniles to nematode-free root tips. In this experiment root weight, stem length, leaf area and leaf gas exchange rates were good indicators of PCN damage. Tolerance differences were significant only at 100 e/g_s and were correlated with root weight, stem length and leaf area, but not with leaf gas exchange rates. Nematodes strongly reduced photosynthesis and transpiration rates, but apparently these processes are not part of the tolerance of plants, as defined by Wallace (1987). Further research using a wider range of cultivars should be carried out to identify tolerance mechanisms, especially in *G. pallida* resistant material, and to find a more simple *G. pallida* tolerance test.

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