Growth, water uptake and calcium content of potato cultivars in relation to tolerance of cyst nematodes

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SUMMARY

The growth of early maturing potato cultivars was more affected by nematode infection than that of late maturing cultivars and all infected plants contained a greater proportion of dry matter than uninfected plants, possibly because they have a smaller ratio of cell contents to cell wall materials. Initially, infected plants used water more efficiently i.e. they used less water than uninfected plants to produce unit dry matter. Later on, accumulation of dry matter was much reduced in infected plants and water use efficiency decreased. The degree of reduction depended on the cultivar and the severity of nematode damage but it was not possible to use water use efficiency as a measure of tolerance of potatoes to cyst nematodes. Despite a highly significant correlation between total water used and total calcium content in the plants there was no correlation between transpiration ratio and calcium concentration, whether plants were infected or not. All infected plants took up more calcium per unit water transpired and per unit dry matter produced than uninfected plants, the effect being more pronounced for " Cara " and " Maris Anchor " when they were infected with *Globodera pallida* rather than *G. rostochiensis*. Resistance may, therefore, contribute to tolerance of cyst nematodes by potatoes. Leaf area, root weight and shoot/root ratios of these two cultivars were also decreased more when grown in soil infested with *G. pallida* than with *G. rostochiensis*. Although total water uptake was reduced by nematode infection, there was little change in total calcium uptake : water fluxes into roots of " Arran Banner " decreased whereas calcium uptake rates increased as nematode density increased. This increased calcium uptake may be a result of disruption of the endodermis by nematodes. The potassium/calcium ratio decreased with increasing nematode density but much less in the resistant-tolerant cultivar Cara than other cultivars.

RÉSUMÉ

Croissance, absorption d'eau et contenu en calcium de différents cultivars de pomme de terre en relation avec leur tolérance aux nématodes kystogènes

La croissance des cultivars hâtifs de pomme de terre est plus affectée par une infestation due aux nématodes que celle des cultivars tardifs, tous les plants infestés présentant une plus grande proportion de matière sèche que les plants sains; la raison en est peut-être que les premiers montrent un plus faible contenu cellulaire par rapport aux matières constituant les parois de ces cellules. En début d'expérience, les plantes infestées utilisent l'eau d'une manière plus efficace, c'est-à-dire qu'elles utilisent moins d'eau que les plantes saines pour constituer la même quantité de matière sèche. Par la suite, l'accumulation de matière sèche se réduit très sensiblement chez les plantes infestées et l'efficacité dans l'utilisation de l'eau décroît. La valeur de cette décroissance dépend du cultivar lui-même et de la gravité des dégâts causés par le nématode, mais il n'a pas été possible de se servir de cette utilisation de l'eau comme mesure de la tolérance des pommes de terre aux nématodes kystogènes. Malgré une corrélation hautement significative entre la quantité totale d'eau utilisée et le contenu total en calcium dans les plantes, aucune corrélation n'apparaît entre le quotient respiratoire et la concentration en calcium, que les plantes soient infestées ou saines. Par rapport aux plantes saines, toutes les plantes infestées prélèvent une plus grande quantité de calcium par unité d'eau transpirée et par unité de matière sèche produite, ce phénomène étant plus prononcé pour les cultivars Cara et Maris Anchor s'ils sont infestés par *Globodera pallida* plutôt que par *G. rostochiensis*. La résistance peut, par conséquent, contribuer à la tolérance des pommes de terre envers les nématodes kystogènes. Si ces deux cultivars sont cultivés dans un sol infesté, la surface foliaire, le poids des racines et le rapport parties aériennes/parties souterraines décroissent plus s'il s'agit de *G. pallida* que de *G. rostochiensis*. Bien que l'absorption totale d'eau soit réduite par l'infestation en nématodes, la teneur totale en calcium est peu modifiée : l'absorption d'eau par les racines du cv. Arran Banner décroît tandis que l'absorption de calcium croît lorsque le taux des nématodes augmente. Cette augmentation dans l'absorption de calcium pourrait résulter de la rupture de l'endoderme par les nématodes. Le rapport potassium/calcium décroît lorsque le taux de nématodes augmente, mais moins sensiblement chez le cv. Cara, tolérant/résistant, que chez les autres cultivars testés.

The ability of a plant to tolerate adverse conditions depends on the interaction of its genotype with the environment (Bell, 1966). Thus, to improve the performance of potato crops under attack by nematodes we need to understand the fundamental mechanisms of nematode damage but we must also understand the factors which lead to high yield, whether or not they are affected by nematode attack.

Trials in fields heavily infested with *Globodera rostochiensis* (Wollenweber) have shown marked differences in yield loss between cultivars (Huijsman, Klinkenberg & Den Ouden, 1969; Oydvin, 1977; De Scurrah, 1977; Evans & Franco, 1979; Trudgill & Cotes, 1983) and these differences have been attributed to variation between cultivars in ability to tolerate nematode attack. Little is understood about the mechanisms which confer tolerance. Early maturing potato cultivars seem to be less tolerant of damage by cyst nematodes than late maturing cultivars (Meinl & Stelter, 1963; Evans & Franco, 1979; Trudgill & Cotes, 1983) and differences in yield loss between resistant and non-resistant cultivars grown in heavily infested soil have also been observed (Trudgill *et al.*, 1978; Evans & Franco, 1979). Four experiments, therefore, were done to study the growth of potato cultivars under attack by *Globodera* spp. Potato cultivars with different maturity dates were used in the first and resistant and non-resistant cultivars were grown in the second, in order to study the effects of maturity date and resistance on tolerance. Because Evans and Franco (1979) suggested that water use efficiency might be important in determining a cultivar's tolerance of nematode attack and Evans (1982) showed that it might be possible to use calcium (Ca) uptake as an indicator for water use, water and Ca uptake were monitored in both experiments. Two additional experiments were done to monitor water and Ca uptake in potato plants infected with a range of densities of the nematodes.

Materials and methods

All the experiments used similar basic methods, which are therefore described first. The detailed differences between experiments are described separately. Five hundred grammes of sterilised Kettering sandy loam was put in plastic pots (12.5 cm diam.) and a tuber piece with a single sprout along with the number of cysts to give the required egg population density were added. The pot was then filled with a further 500 g of soil. Eight grammes of 18:11:10 ($N:P_2O_5:K_2O$) slow-release fertiliser were added to each pot and, to minimise evaporation from the soil surface, 100 g of polyethylene granules were spread on top of the soil. Each pot was weighed and watered to a constant weight, corresponding to about 21 % moisture content, and three additional pots with no plants were used to estimate evaporative water loss. The constant weight to which pots were made up was increased periodically to compensate for the increase in weight of the plants. At first, pots were watered every two days, increasing to every day and eventually twice per day when plants became very large.

Three replicates were allowed per treatment in all experiments. The amount of water transpired and plant dry weights were used to calculate transpiration ratios (TR, the amount of water transpired to produce unit dry matter). Plant material was dried for 48 hr at 80° and Ca content was measured by standard procedures (Cosimini & Talibudeen, 1978).

Experiment 1

In order to study the effects of maturity date, three non-resistant cultivars of different maturity date viz Catriona (second early), Arran Banner (early main) and Golden Wonder (late main) were selected. Cysts of *G. rostochiensis* Ro 1 were added to half the pots to give a density of 100 eggs/g soil. Water use was recorded beginning seven days after planting and three plants of each treatment were harvested at weekly intervals from fifteen days up to ten weeks from planting.

Experiment 2

In the experiment to study the effects of resistance on tolerance, four cultivars were chosen, two resistant and two non-resistant, with one of each pair early maturing and the other late maturing. The four cultivars were Cara (late main crop) and Maris Anchor (first early) both with the H_1 gene for resistance effective against *G. rostochiensis* Ro 1, and Pentland Crown (main crop) and Maris Peer (second early) both non-resistant. They were grown in soil with or without *G. rostochiensis* Rol or *G. pallida* (Stone) Pa 2/3 at 80 eggs/g soil. Water use was recorded from nine days after planting and harvests were made 23, 43, 63 and 83 days after planting.

Experiment 3

Plants of the non-resistant cultivar Arran Banner were grown in soil with four densities of *G. pallida* Pa 2/3 : 0, 10, 50 or 250 eggs/g soil. Water use was recorded from seven days after planting and plants were harvested at weekly intervals for ten weeks starting at day 17.

Experiment 4

Four cultivars which had shown differences in tolerance in the field were chosen : Cara (resistant and tolerant), Pentland Crown (non-resistant and tolerant), Pentland Dell and Arran Banner (both non-resistant and intolerant). The soil contained cysts of *G. rostochiensis* Ro 1 at densities of 0, 25 and 250 eggs/g soil. From day 30 onwards plants were watered with deionised water instead of tap water to avoid adding large amounts of Ca. Plants were harvested at ten day intervals, from 20 to 70 days after planting.

The concentration of nutrients in the soil solution is a reflection of the total uptake by plants and of the soil buffer capacity. In order to compare soil solution concentration measurements they must be based on an equivalent soil moisture level, which is usually field capacity (Adams, 1974). The procedure of Hodgson, Geering and Norvell (1965) was adopted to obtain samples of soil solution : at each harvest date the above ground plant parts were cut off near the soil surface, and the polyethylene granules covering the soil surface discarded. Each pot, containing soil and underground plant parts, was placed in the top of a funnel and 5 ml of deionised water was poured evenly onto the soil every ten minutes until the soil solution started to run out of the pot (i.e. the soil was saturated with water). The first 10 ml of this solution was discarded and the next 30 ml collected, after filtration (Whatman filter paper No. 40), in a bottle.

Results

Experiment 1

The rate of dry matter production was similar in uninfected plants of all three cultivars throughout the experiment (Fig. 1) and all grew more slowly when infected by nematodes. The dry weights of infected plants were significantly less than those of uninfected plants from day 29 and this difference became greater in Catriona from day 43 onward. By the end of the experiment infected plants of Catriona weighed less than half as much as infected plants of Arran Banner and Golden Wonder ($P < 0.01$).

Table 1 shows that infected plants had greater dry matter contents than uninfected plants up to 51 days from planting, and smaller dry matter contents by day 71.

Measurements of leaf area ratio (total leaf area divided by total plant dry weight) showed that all infected plants initially had smaller leaf areas per unit dry weight (Fig. 2) than uninfected plants. However, the ratios changed with time and by the end of the experiment ratios were larger for infected than for uninfected plants.

Transpiration ratio (TR) is a measure of water use efficiency (water transpired per unit dry weight produced) and increased with time for both uninfected and infected plants (Tab. 2). Water use efficiency of infected plants increased relative to that of uninfected plants (i.e. their TR's were decreased) from day 22 for Catriona ($P < 0.05$) and from day 29 for the other two cultivars. Later on, the TR's of infected Arran Banner became greater than those of uninfected plants (from

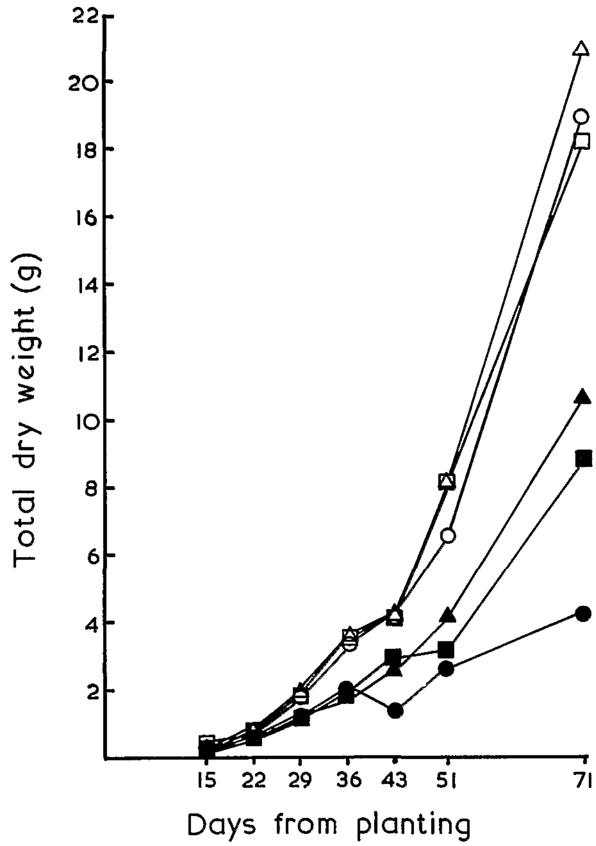

Fig. 1. Total dry weights (g) of Catriona, Arran Banner and Golden Wonder potato plants grown at 0 or 100 eggs/g soil of *G. rostochiensis* : Catriona (○ = — Nem, ● = + Nem), Arran Banner (△ = — Nem, ▲ = + Nem) and Golden Wonder (□ = — Nem, ■ = + Nem).

Table 1

Percentage dry matter of potato plants (means of three cultivars) grown in uninfested soil (—) or soil infested (+) with 100 eggs/g of *G. rostochiensis* Ro 1, at 7 harvests

Days from planting	*— Nem*	*+ Nem*	*Ratio —/+*
15	6.3	6.9	0.9
22	6.1	7.1	0.9
29	6.2	8.1	0.8
36	7.7	9.1	0.8
43	8.1	9.1	0.9
51	9.4	9.5	1.0
71	14.4	10.7	1.3

Table 2

Transpiration ratios [Total water used (g)/total dry matter (g)] of three potato cultivars grown in uninfested (—) soil or soil infested (+) with 100 eggs/g of *G. rostochiensis* Ro 1 at 7 harvests

Days from planting	*Catriona*		*Arran Banner*		*Golden Wonder*		*SED* (df)*
	—	+	—	+	—	+	
15	19.8	17.6	24.9	14.7	11.6	10.8	5.7 (12)
22	77.4	57.0	92.0	81.5	46.7	39.6	8.9 (12)
29	104.7	84.8	113.6	92.1	97.9	64.0	4.6 (12)
36	113.7	97.6	131.7	101.7	111.0	85.3	8.2 (12)
43	130.2	100.8	128.0	107.6	118.4	91.4	3.8 (11)
51	131.9	100.2	128.2	142.4	—	109.3	13.0 (7)
71	122.6	109.2	113.1	140.6	116.8	120.8	6.3 (9)

* Standard error of the difference between means.

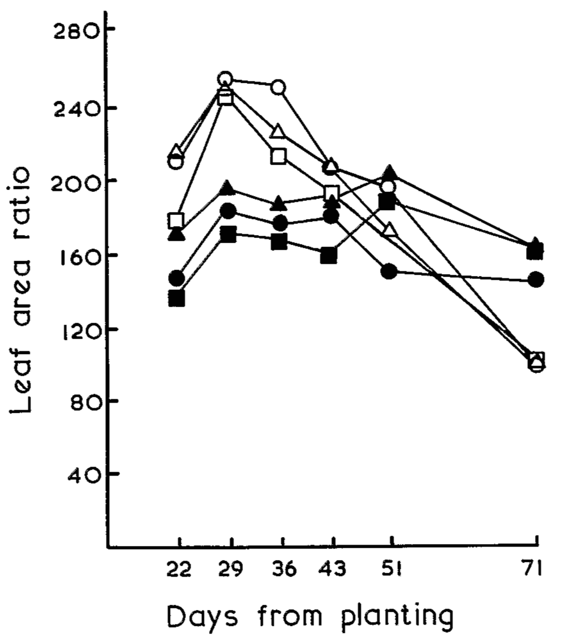

Fig. 2. Leaf area ratio (leaf area per unit dry weight) of three potato cultivars growing at 0 or 100 eggs/g soil of *G. rostochiensis* : Catriona (○ = — Nem, ● = + Nem), Arran Banner (△ = — Nem, ▲ = + Nem) and Golden Wonder (□ = — Nem, ■ = + Nem).

day 51) whilst those of infected Catriona remained smaller ($P < 0.01$); although TR's for infected Golden Wonder plants were greater than those for uninfected at day 71, the differences were not significant.

EXPERIMENT 2

Leaf area, root weight and total water uptake were all decreased as a result of nematode infection (Tab. 3), the effect being more marked with *G. pallida* than with *G. rostochiensis* on Cara and Maris Anchor (the cultivars with H_1 resistance) and also Maris Peer. By the end of the experiment, infected plants of the main crop cultivars (Cara and Pentland Crown) produced over twice as much root as the early cultivar Maris Anchor and slightly more than Maris Peer. Calcium concentrations in plant dry matter were higher in nematode infected plants of all cultivars, but for the resistant cultivars Cara and Maris Anchor, the effect of *G. pallida* was greater than that of *G. rostochiensis* at all harvests.

Total Ca uptake was a good indicator of total water used but infected plants took up more Ca per unit water transpired (Tab. 4) and the H_1 resistant cultivars Cara and Maris Anchor took up more Ca per unit water when infected by *G. pallida* than by *G. rostochiensis.*

EXPERIMENT 3

The water consumption of plants in soil infested with 10 or 50 eggs/g was significantly reduced only during the first 38 days of growth (Tab. 5); later they consumed as much water as uninfected plants. Heavily infected plants (250 eggs/g soil) had used significantly less water than all other plants at all harvests except the first.

Total Ca content was similar for all plants at each harvest, with a highly significant correlation between total Ca uptake and total water used within nematode treatments (Tab. 6). Nematode damage caused plants to take up more Ca per unit water transpired and this effect

Table 3

Leaf area, root fresh weight, shoot/root ratios (fresh weight), total water use (g) and percentage Ca in dry matter of four potato cultivars grown at 0 or 80 eggs/g soil of *G. rostochiensis* (Gr) or *G. pallida* (Gp)
Data are for plants at 63 days from planting

Cultivar		*Leaf area*	*Root fresh weight*	*Shoot/root ratio*	*Water used*	*% Ca*
Cara	0	1 180	7.3	10.0	799	2.5
	Gr	933	7.3	7.4	648	3.7
	Gp	568	5.0	6.5	444	4.2
M. Anchor	0	1 232	4.0	14.5	937	1.6
	Gr	641	3.2	9.6	382	2.4
	Gp	535	2.5	9.9	258	3.1
P. Crown	0	781	5.9	9.5	603	2.1
	Gr	756	8.1	6.7	689	2.8
	Gp	821	9.0	6.4	696	3.1
M. Peer	0	1 684	8.1	10.8	1 065	2.2
	Gr	1 324	7.1	10.0	758	3.1
	Gp	683	3.9	9.8	391	3.7
SED (df 24)		187.0	1.4	0.53	150.2	0.24

Table 4

Linear regression analysis of total Ca uptake versus total water used for four potato cultivars grown in uninfested (0) soil or soil infested with *G. rostochiensis* (Gr) or *G. pallida* (Gp)

Cultivar		*Slope (± SE)*	*Correlation coefficient*
Cara	0	0.176 (0.005)	0.992
	Gr	0.178 (0.018)	0.885
	Gp	0.192 (0.016)	0.921
M. Anchor	0	0.144 (0.006)	0.975
	Gr	0.181 (0.010)	0.963
	Gp	0.222 (0.021)	0.882
P. Crown	0	0.179 (0.010)	0.944
	Gr	0.218 (0.007)	0.986
	Gp	0.229 (0.012)	0.972
M. Peer	0	0.169 (0.007)	0.970
	Gr	0.251 (0.007)	0.987
	Gp	0.180 (0.021)	0.860

All Correlation coefficients significant at $P < 0.001$.

Table 5

Total water use (g) of Arran Banner plants grown in uninfested soil (0) or in soil infested with 10, 50 or 250 eggs/g of *G. pallida* at 10 harvests

Days from planting	*Eggs/g soil* 0	10	50	250	*SED (df)*
17	50	21	27	29	11.6 (8)
24	201	108	104	51	18.9 (8)
31	319	196	139	76	75.1 (8)
38	507	435	218	93	39.0 (8)
45	627	541	485	90	77.0 (8)
52	826	904	633	412	117.0 (8)
59	1 059	993	967	469	76.2 (8)
66	1 151	1 236	1 193	512	122.0 (8)
73	1 472	1 407	1 380	487	139.6 (8)
80	1 764	1 628	1 648	626	141.1 (5)

was greater as nematode density increased. Consequently, the greater the nematode density the greater the Ca concentration in plant dry matter : 1.3, 1.7, 2.1 and 4.6 % for 80 day old plants in soil containing 0, 10, 50 and 250 eggs/g soil respectively. Despite large differences in plant weight at different densities of

Table 6

Correlation coefficients and slopes from linear regression analyses of total calcium uptake versus total water used for Arran Banner plants grown in uninfested soil (0) or in soil infested with 10, 50 or 250 eggs/g of *G. pallida*

Eggs/g soil	*Slope (± SE)*	*Correlation* coefficient*
0	0.148 (0.004)	0.966
10	0.171 (0.005)	0.973
50	0.218 (0.007)	0.977
250	0.454 (0.016)	0.965

* All correlation coefficients significant at $P < 0.001$.

nematodes, the effect on Ca concentration was so great that the total amount of Ca per plant did not differ significantly between nematode densities.

The rates of Ca and water uptake were examined by calculating total Ca or water uptake per unit fresh weight of root per day, as outlined by Mengel and Barber (1974). Uptake rates for weekly periods were estimated by subtracting the amounts of Ca present in, or water used by, the plants harvested at the beginning of the week from the values for plants harvested at the end of the week, and dividing this amount by the average root fresh weight during the week. The results were variable but the overall mean Ca uptake rate increased with increasing nematode density whilst the overall mean rate of water uptake decreased (Tab. 7).

Initially, plants growing in soil infested with 10 or 50 eggs/g had smaller TR's than uninfected plants; later on TR's of these infected plants became as large as those of uninfected plants. The return to values similar to those of uninfected plants occurred earlier for plants grown in soil infested with 10 eggs/g than for plants in soil with 50 eggs/g. Heavily infected plants (250 eggs/g soil) had smaller TR's than all other plants during the first 52 days but even these eventually became similar to uninfected plants.

Table 7

Water (g) and Ca (mg) uptake per g fresh roots per day of Arran Banner plants grown in uninfested soil (0) or in soil infested with 10, 50 or 250 eggs/g of *G. pallida*
Means of 9 harvests

	Eggs/g soil			
	0	*10*	*50*	*250*
mg Ca/g root/day	0.76	0.82	0.99	1.3
g water/g root/day	6.1	5.2	4.9	1.7

EXPERIMENT 4

Total Ca uptake was a good indicator of total water used, all correlations between them being highly significant ($P < 0.001$, Tab. 8). Infected plants took up more Ca per unit water transpired as nematode density increased but the slopes of the regression lines for Pentland Dell and Pentland Crown were increased much more by the high density of nematodes than were the equivalent slopes for Cara or Arran Banner.

Table 8

Slopes and correlation coefficients from linear regression analysis of total Ca uptake against total water used for 4 potato cultivars grown in soil infested with 0,25 or 250 eggs/g of *G. rostochiensis*

Cultivar	*Eggs/g soil*	*Slope (SE)*	*Correlation coefficient*
Cara	0	0.173 (0.012)	0.963
	25	0.224 (0.012)	0.979
	250	0.380 (0.031)	0.954
P. Crown	0	0.192 (0.012)	0.972
	25	0.255 (0.013)	0.981
	250	0.671 (0.069)	0.925
A. Banner	0	0.177 (0.013)	0.957
	25	0.174 (0.013)	0.959
	250	0.225 (0.018)	0.955
P. Dell	0	0.232 (0.010)	0.985
	25	0.238 (0.010)	0.989
	250	0.827 (0.089)	0.919

All correlation coefficients were significant at $P < 0.001$.

The K/Ca ratios, based on the total K and total Ca content of plants, were very similar for uninfected plants of all cultivars but were decreased slightly at the low nematode density and rather more in heavily infected plants of all cultivars (Tab. 9). Effects on the K/Ca ratio of Cara were generally less than for other cultivars.

The P content of the soil solution remained constant during the experiment. The concentrations of K (and those of Mg and Na) decreased with time and were much depleted by day 70 in soil containing uninfected plants (Tab. 10). The concentration of Ca, which was present in a much higher concentration than other nutrients, also decreased but by the last harvest the heavily infested soil planted with Cara or Pentland Dell still had a high concentration; this was not so for Pentland Crown and Arran Banner.

Table 9

K/Ca ratio at 3 plant ages of Cara, Pentland Crown, Arran Banner and Pentland Dell grown in soil infested with 0, 25 or 250 eggs/g of *G. rostochiensis*

Days from planting	*Cultivar*	*Eggs/g soil* 0	25	250	*SED (df)*
20	Cara	2.2	1.8	1.8	
	P. Crown	2.1	1.6	1.3	0.26
	A. Banner	2.3	2.2	1.3	(24)
	P. Dell	2.3	1.6	1.5	
30	Cara	1.7	1.3	1.1	
	P. Crown	2.0	1.8	0.89	0.14
	A. Banner	2.5	1.9	0.85	(24)
	P. Dell	2.1	1.5	0.95	
60	Cara	1.2	1.3	0.99	
	P. Crown	1.6	1.5	0.53	0.17
	A. Banner	1.1	1.2	0.99	(23)
	P. Dell	1.1	1.1	0.52	

Discussion

These results suggest that both maturity date and resistance may influence the tolerance of some cultivars but that water use efficiency, measured in pots with plentiful water supply, is not a sensitive measure of tolerance. Figure 2 shows that Catriona and Arran Banner had greater leaf area ratios than the late-maturing cultivar Golden Wonder during the first 45 days (with or without nematodes) and that Catriona had the smallest leaf area ratio of infected plants from day 45 onwards. Early maturing potato cultivars have a faster relative leaf growth rate (increase in leaf area per unit leaf weight per unit time) than late maturing cultivars (Cotes, 1983), with a shorter period of leaf growth. The recovery of normal growth rates by infected Arran Banner and Golden Wonder therefore appears partly to be due to their maturity class, i.e. the ability to maintain vegetative growth beyond the period of maximum nematode damage and their later diversion of assimilates to tuber production compared with early cultivars; this is consistent with results reported from field trials (Cotes, 1983). The leaf area ratios were higher in infected than uninfected plants after 51 days but this was due to the relatively larger weight of tubers produced by uninfected plants (tubers can account for up to 70 % of total plant weight).

Although percentage dry matter was increased by nematode infection (Tab. 1), the infected plants were small and probably had smaller cells with a higher ratio of structural materials (cell walls) to cell contents. Trudgill, Evans and Parrott (1975) found that percentage dry matter in the haulm increased in plants stunted by nematodes and also suggested that this increase came from an increase in the proportion of cell wall materials due to differences in the size of cells.

Water use efficiency was increased in infected plants but only significantly for Catriona and Arran Banner and only in the period up to day 22 (Tab. 2). After this period, water use efficiency frequently decreased in infected plants because dry matter production was greatly decreased, to an extent depending on the severity of nematode attack. The effects of nematode infection on the water use of young plants are probably the result of reduced stomatal apertures; this results in smaller transpiration ratios with only a small decrease in total dry weight because partial stomatal closure reduces transpiration more than dry matter production (Raschke, 1976). Transpiration ratios of Catriona were

Table 10

K and Ca content (ppm) of soil solution 70 days after planting Cara, Pentland Crown, Arran Banner and Pentland Dell with population densities of 0,25 or 250 eggs/g of *G. rostochiensis*

Eggs/g soil	*Cara* K	Ca	*P. Crown* K	Ca	*A. Banner* K	Ca	*P. Dell* K	Ca
0	0.2	572	0.2	477	0.4	711	0.5	587
25	0.6	936	0.4	711	0.5	786	0.4	499
250	15.4	2 860	159.1	587	0.8	768	49.6	2 464

SED 32.9 (for K)
(df = 20) 255.3 (for Ca)

decreased more than those of Arran Banner and Golden Wonder, perhaps because the lowering of TR's depends on continued invasion of roots; if this is so infected Arran Banner and Golden Wonder plants, with bigger root systems than Catriona, probably outgrew the effects of nematode invasion so that their TR's rose to values more closely resembling those of uninfected plants.

Total Ca uptake was well correlated with total water uptake for all cultivars so should be a good indicator of total water used (Tabs 4, 6 and 8). However, infected plants took up less water than uninfected plants but took up similar amounts of Ca, so must have taken up more Ca per unit water transpired. In fact, water fluxes (rate of uptake per unit root weight per day) into roots of Arran Banner decreased whereas Ca uptake rates increased as nematode density increased (Tab. 7). When infected with *G. pallida* the H_1 resistant cultivars Cara and Maris Anchor took up more Ca per unit water transpired than when infected with *G. rostochiensis.* The continuation of this effect throughout the experiment supports the suggestion by Seinhorst and Den Ouden (1971) that, although most damage is caused by the invading juveniles, some damage is also associated with the development of female cyst nematodes and their syncytia.

Two hypotheses can be advanced to explain why infected plants took up more Ca per unit water transpired :

(i) Nematode invasion damaged the endodermis and maintained an apoplastic pathway for the uptake of Ca in regions of the root where such a pathway is normally inoperative (i.e. where Casparian bands and secondary endodermal thickening are present). This suggestion was made by Price and Sanderson (1984), when they found the amount of Ca translocated from lengths of oat root containing third stage juveniles of *Heterodera avenae* was over eleven times that of control roots.

(ii) Infected plants may have taken up more Ca to maintain their ionic balance because nematode infection reduced uptake of the cations (eg. K) which are taken up actively (Mengel & Kirkby, 1978).

Infected plants had lower concentrations of K and Mg in their total dry matter, the effect being greater as nematode density increased in the soil. The K/Ca ratios indicate the degree of nematode damage (Tab. 9) : the ratio was decreased in all infected plants but less in the tolerant cultivar Cara than other infected cultivars. Franco (1977) suggested that transfer cells initiated by cyst nematodes are partly responsible for the large decreases in K content in plant dry matter; in resistant plants, where nematodes do not cause formation of long lasting transfer cells, the K content (and the K/Ca ratio) is little affected but in non-resistant plants it is possible that K ions involved in phloem transport may pass out of roots via the transfer cells rather than returning to the leaves in the xylem.

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