The uptake of potassium and phosphorus in oats infested with the cereal cyst nematode, *Heterodera avenae* Woll.

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SUMMARY

The uptake of phosphorus and potassium by the roots of oats infested by the cereal cyst nematode, *H. avenae*, was studied using radio-labelling. The presence of nematodes in the roots did not impede uptake or transport of nutrients and roots compensated for reduced and altered root growth by increasing rates of uptake of phosphorus and potassium.

RÉSUMÉ

Absorption du potassium et du phosphore par l'avoine infestée par Heterodera avenae *Woll.*

L'absorption du phosphore et du potassium par les racines d'avoine infestées par *Heterodera avenae* a été étudiée par marquage des éléments. La présence de nématodes dans les racines ne gêne pas l'absorption ni le transport d'éléments nutritifs et les racines compensent les effets de la réduction et de l'altération de leur croissance en augmentant le taux d'absorption du potassium et du phosphore.

Symptoms of nutrient deficiency are a common feature of nematode parasitized plants. Endoparasitic nematodes usually develop giant cells or syncytia in close association with the vascular tissues and there is an implied, if rarely stated, assumption that nematodes "block" the "uptake" of nutrients by the plant (Shepherd, 1965 ; Seinhorst & Den Ouden, 1971). However experimental details are contradictory ; Shaffie and Jenkins (1963) reported increased concentrations of potassium and phosphorus in the roots of *Capsicum frutescens* infected by *Meloidogyne incognita acrita* but there were no significant differences in the amounts of the two chemicals in shoots of infested and uninfested plants. Jenkins and Malek (1966) testing four nematode species, including *Meloidogyne hapla* on vetch (*Vicia villosa* Roth.) concluded "that nematodes in some way alter the plant mechanisms of absorption, translocation and accumulation of mineral constituents". Slightly greater amounts of ^{32}P were taken up by tomato infected by *Meloidogyne javanica* (Oteifa, Barrada & Elgindi, 1958) but Hunter (1958) suggested that *Meloidogyne incognita acrita* caused no interference with the absorption or translocation of minerals including phosphorus labelled with ^{32}P, in tomato.

This paper presents two experiments in which the absorption and transport of potassium and phosphorus by oat plants (*Avena sativa)* infested with the cereal cyst nematode (*Heterodera avenae* Woll.) was investigated using radioactive tracers in hydroponic culture.

Materials and methods

PREPARATION OF INFESTED PLANTS

Cysts of *H. avenae* extracted from infested field soil were placed on a Whitehead tray (Whitehead & Hemming, 1965) and the hatched second stage juveniles added to pots containing oat plants growing in sand.

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In the first experiment 30 oat seeds of the susceptible cultivar Maris Osprey were sown individually into 7.5 cm pots filled with sand. After germination three days later, fifteen pots received a total of 1100 juveniles per pot over five days. On the eighth day all seedlings were washed from the sand and transferred to hydroponic culture. Three infested seedlings were retained, stained in lactophenol acid fuchsin and the number of nematodes invading the roots counted.

In the second experiment oat seeds of the susceptible cultivar Maris Tabard, were germinated on damp tissue and 24 newly germinated seeds with similar primordial roots were selected and planted individually in 12.5 cm pots filled with sand. Nylon gauze was placed in the base of the pot to prevent sand being washed out during watering. Twelve plants remained uninfested, the other twelve pots having juveniles of *H. avenae* added 24 hours after seeds were sown and on nine further occasions, receiving a total of approximately 3000 juveniles per pot, over a period of four weeks. Plants were watered with nutrient solutions on four occasions.

RADIO-ACTIVE LABELLING, SAMPLING AND COUNTING

In both experiments plants were left in hydroponic culture for 24 hours before being radio-labelled.

In the first experiment, five uninfested and five infested plants, six days after germination, were selected and placed together in a 5 l beaker. $^{86}RbCl$ was added to the culture solution to give an activity of 10 μ Ci l^{-1}, Rb^+ being a mimic for K^+ (Smith & Epstein, 1964).

After 24 h plants were removed from the beaker, shoots and roots separated at the base of the seed, dried lightly with tissue and fresh weights recorded. The lengths of seminal root axes and the number of laterals on each axis was recorded.

Root and shoot samples were packed into the bases of 10 ml polypropylene vials and the γ emission of ^{86} Rb^+ was counted directly in the well of a NaI Crystal Detector using a γ spectrometer (Nuclear Data).

In the second experiment, all 24 seedlings had their nodal roots removed prior to labelling, leaving only the seminal root system. Plants were then put in three 5 l beakers containing nutrient solution labelled with $KH_2\ ^{32}PO_4$ to an activity of 10 μ Ci l^{-1}. After 24 h plants were removed and lightly dried ; the shoots and roots were separated and their fresh weights recorded.

Since estimates of dry weight, radio-labelling or examination of roots for nematodes were destructive, samples were randomly assigned to a particular procedure. Six shoot samples were dried and weighed and six shoots processed to assess radio-labelling. Four root samples were dried and weighed, four processed to assess radio-labelling and four preserved in F.A. 4 : 1 (Southey, 1970) for estimating nematode invasion.

Dry weights of shoots and roots were done after oven drying for a minimum of 48 hours. Samples to be counted for $^{32}P^-$ were wet-ashed which involves dissolving the plant material in nitric acid and reducing the volume of this solution by evaporation on a hotplate. Concentrated solutions were transferred to planchettes (aluminium saucers approximately 2 cm in diameter) and counted in a Beckman Low Beta 2 Planchette Counter.

Preserved roots were spread out on wet black paper and numbers and lengths of axes and primary laterals were measured. Root systems were then divided into "upper" and "lower" portions by cutting axes 3 cm from the seed : these samples were stained in lactophenol acid fuchsin and the number of nematodes in the roots counted. The stage of development of each nematode was ascertained and its position in either the root axis or lateral roots was recorded.

Results

In the first experiment 9, 11 and 30 second stage juveniles were found in the three root systems, equivalent to an invasion of 150-500 juveniles g^{-1} of root.

Results from the first experiment are presented in Table 1. There were no significant differences in the fresh weight of shoots between infested and uninfested plants but the fresh weight of infested roots was reduced ($p < 0.001$). Both uninfested and infested plants had similar numbers of lateral roots but infested root axes were significantly shorter ($p < 0.001$) : thus there were significantly ($p < 0.001$) greater numbers of laterals cm^{-1} of root axes on infested plants.

Potassium uptake was calculated from the radioactive rubidium found. Shoots of infested plants had significantly lower concentrations of labelled potassium (μ mole g^{-1} fresh weight of shoot, $p > 0.001$) than in uninfested plants though there were no significant differences in the concentrations of labelled potassium in the roots (μ mole gm^{-1} fresh weight of roots). Total uptake of potassium however, relative to the size of the root system was significantly greater ($p < 0.005$) in infested plants (total K^+, μ mole g^{-1} fresh weight of roots).

In experiment 2 the number and distribution of nematodes within the root systems of infested plants is presented in Table 2. Third and fourth stage juveniles tended to occur in root axes in the "upper"

Table 1

First Experiment : The effect of *H. avenae* on growth and potassium uptake in young oat seedlings, cv. Maris Osprey (± S.E.)

	Uninfested	*Infested*	*Significance*
Fresh Weight of Shoot (mg)	127 ± 10	117 ± 3	N.S.
Fresh Weight of Root (mg)	131 ± 12	62 ± 6	< 0.001
Ratio : shoot/root	0.96	1.89	
Mean length of seminal axes (cm)	10.23 ± 0.48	2.72 ± 0.21	< 0.001
Number of Laterals cm^{-1} axis	0.42 ± 0.05	1.26 ± 0.08	< 0.001
Potassium ($^{86}Rb^+$) uptake			
Concentration of potassium in shoots (μ mole $K^+ g^{-1}$ F.W.)	23.02 ± 1.02	16.01 ± 0.05	< 0.001
Concentration of potassium in roots (μ mole $K^+ g^{-1}$ F.W.)	25.00 ± 1.04	27.00 ± 0.04	N.S.
Total uptake of potassium (μ mole $K^+ g^{-1}$ F.W. Root)	47.08 ± 2.09	58.03 ± 2.00	< 0.005

Table 2

Second Experiment : Distribution within the root system, and development stage of, *H. avenae* in four-week old oat plants cv. Maris Tabard (± S.E.)

	Root axes		*Laterals*	
	j 2	*j 3/4*	*j 2*	*j 3/4*
Upper part of root	7.7 ± 1.6	15.5 ± 1.5	9.2 ± 2.7	8.2 ± 2.2
Lower part of root	3.5 ± 1.0	8.2 ± 0.7	21.7 ± 5.9	4.5 ± 1.2

part of the root system with second stage juveniles most abundant in the "lower" laterals. Changes in root morphology brought about by nematode infestation are shown in Table 3. Root axes were significantly ($p < 0.001$) reduced in length on infested plants, with significantly fewer primary laterals present ($p < 0.001$) ; the total lengths of infested root systems was significantly ($p < 0.001$) shorter. (This ignores however, the development of secondary laterals which occured only on infested roots, and were not measured).

The effect of *H. avenae* on plant weight and uptake of phosphorus is shown in Table 3. The weights of uninfested and infested root systems did not differ significantly though the dry weight of infested roots was slightly greater than the uninfested roots : fresh and dry weights of infested shoots were reduced (dry weight significant at $p < 0.05$). Total uptake of phosphorus in shoots differed little between infested and uninfested plants but total uptake of phosphorus in roots was greater in the infested plants (but not significantly).

There was no significant difference in the concentration of labelled phosphorus in the shoots (μ mole g^{-1} fresh weight of shoot) although the increased uptake by the roots of infested plants is reflected in a significantly ($p < 0.05$) greater concentration of labelled phosphorus being present (μ mole g^{-1} fresh weight of root).

Discussion

In both experiments the presence of *H. avenae* in the roots did not impede the absorption or transport of either potassium or phosphorus.

Table 3
Second Experiment : The effect of *H. avenae* on plant weight, root system morphology and phosphorus uptake in four week old Maris Tabard oats (± S.E.)

	Uninfested	*Infested*	*Significance*
Plant Weight (gms)			
Fresh Weight of Shoots	1.7 ± 0.1	1.4 ± 0.1	N.S.
Dry Weight of Shoots	0.2 ± 0.01	0.13 ± 0.01	< 0.05
Fresh Weight of Roots	1.9 ± 0.13	1.7 ± 0.13	N.S.
Dry Weight of Roots	0.13 ± 0.01	0.16 ± 0.03	N.S.
Mean length of root axes	18.3 ± 1.4	9.7 ± 0.8	< 0.001
Mean length of primary laterals	2.5 ± 0.2	2.9 ± 0.5	N.S.
Mean no. laterals per plant	207.0 ± 7.7	83.2 ± 11.0	< 0.001
Mean no. of laterals cm^{-1} root axis	1.8 ± 0.1	1.8 ± 0.2	N.S.
Mean total length (axes + laterals) per plant	640.4 + 17.4	310.7 ± 53.0	< 0.001
Total uptake $H_2 PO_4$ (μ moles)			
Shoots	4.3 ± 0.8	4.0 ± 0.6	N.S.
Roots	3.2 ± 0.5	5.9 ± 1.7	N.S.
Conc. $H_2 PO_4$ (μ moles g^{-1} F.W.)			
Shoots	2.8 ± 0.5	2.6 ± 0.2	N.S.
Roots	1.9 ± 0.1	3.5 ± 0.7	< 0.05

The total amount of potassium taken up by the infested plants (Experiment 1) was reduced, but this was due to the reduced size of the root system. Potassium uptake (total K^+ μ moles gm^{-1} fresh weight of root, Tabl. 1) was increased which is in agreement with other research (Drew & Nye, 1969 ; Drew, Nye & Vaidyanathan, 1969).

In the second experiment the amounts and the total concentration of labelled phosphorus in shoots in both uninfested and infested plants was similar (Tab. 3).

Though nematode invasion caused only a slight, non-significant, decrease in the fresh weight of roots it will be noted (Tab. 2) that labelled phosphorus in the shoots, absorbed by the roots will have been transported along root axes containing mature third and fourth stage nematodes.

In the first experiment there were no differences in the concentration of potassium in uninfested and infested plants, but in the conditions of the second experiment the concentration of labelled phosphorus in infected roots was significantly greater ($p > 0.05$), reflecting a greater total uptake of phosphorus similar to that described by Oteifa, Barrada and Elgindi (1958) for tomatoes infested with *Meloidogyne javanica*.

Other work suggests that root absorption and transport is unimpaired by root-knot and cyst nematode parasitism. O'Bannon and Reynolds (1965) found that roots of cotton severely damaged by *Meloidogyne incognita acrita* could transmit sufficient water when water was available, and Hanounik and Osborne (1975) found no impedence in nicotine (synthesized near the root tip) translocation to the leaves of tobacco infested with *Meloidogyne incognita*. Evans, Trudgill and Brown (1977) concluded that the primary cause of poor nutrient uptake (and reduced growth) in the early stages of the growth of potatoes infested with *Globodera rostochiensis* was the reduced root system.

It is concluded that the presence of nematodes in the root is of minor importance in affecting root function compared to morphological alterations brought about by invasion. It has been demonstrated that nematodes incorporate photosynthates (Bird & Loveys (1975) but the significance to the whole plant of nematodes acting as "metabolic sinks" has not been established (Wallace, 1974). Consequently we suggest a major degree of tolerance could be achieved by producing plant varieties capable of developing adequate root systems in the presence of plant parasitic nematodes.

ACKNOWLEDGEMENT

The authors wish to acknowledge the support of the Agricultural Research Council who financed the project.

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Accepté pour publication le 8 mars 1982.

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