Water Transport Through Tomato Roots Infected with *Meloidogyne incognita*

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ABSTRACT

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The effect of *Meloidogyne incognita* on water flow in tomato roots was investigated in rooted split-stem cuttings. Total water flow through infected root parts was significantly lower than through comparable uninfected parts. Total water uptake was correlated with total length of the root system. In a root system severed from its stem and placed under a partial vacuum applied at the stem stump, the infected half transported significantly less water than its corresponding uninfected half. In perfusion chambers, infected apical, but not basal, root segments transported less water than adjacent uninfected segments. Axial resistance to water movement in galls at the root apex, but not at the base, increased. Cross sections of galls at the root base showed little effect on vascular continuity, but in terminal galls the number and diameter of xylem vessels were reduced.

Plants infected with *Meloidogyne* spp. often show signs of water stress. The sedentary endoparasites induce giant cells in the stele, hyperplasia, and hypertrophy of cortical cells (gall formation) and disturb normal development of root anatomy (6,9,14,15). The particular responses to nematode infection are influenced by plant species and cultivar, nematode species and population, and environmental conditions during the year. In snap bean, cultivar tolerance appears to be related to the effects of nematodes on plant water relations (31). Wilting occurs when water lost during transpiration is not replaced sufficiently from the soil. Cotton plants, heavily infected with *M. incognita acrita*, grow as well as uninfected plants under autonomous irrigation (water is not limiting), whereas under allonomous irrigation (water content of the soil is brought to field capacity at intervals), growth is significantly suppressed (24). These experiments indicate that water uptake by infected plants is a limiting factor when soil moisture content drops below a certain threshold level. Reduced water uptake also has been found in potato plants infected with the cyst nematode, *Globodera rostochiensis* (10). However, Meon et al (18) and Rahi et al (25) found that infection by *Meloidogyne* species had no effect on the transpiration rate of tomato and tobacco plants, respectively.

Several investigators compared root and leaf characteristics that are important for water transport in uninfected and nematode-infected plants. Leaf water potential was lower in tomato plants infected with *M. javanica* (18) and in tobacco plants harboring *M. incognita* or *M. javanica* (25). Increased leaf diffusive resistance, probably as a result of reduced stomatal apertures, has been observed in tomato (18) and potato plants (11) infected with *M. javanica* and *G. rostochiensis*, respectively. The negative xylem hydrostatic pressure in tomato roots infected with *M. javanica* is lower than that in uninfected roots (18). Bloom and Burpee (3) measured a decreased root pressure in tomato plants infected with *M. incognita*. Kotcon and Loria (16) showed that the root hydraulic conductivity of susceptible potato cultivars was adversely affected by infection with *Pratylenchus penetrans*. This was also the case for a susceptible snap bean cultivar infected with *M. hapla* (31). The withdrawal of cell sap by the nematodes contributes little to wilting (20).

Most of the results of the previous studies were obtained by comparing water relations in infected plants with those in uninfected plants. However, growth of infected susceptible plants is strongly suppressed, and senescence is accelerated (10). Therefore, the observed differences possibly could be attributed to the different developmental stages of the plants compared. Furthermore, changes in transpiration rates induce alterations in the hydraulic conductivity of the root system (4,19).

The purpose of the present study was to determine the effect of an infection with *M. incognita* (Kofoid & White) Chitwood on the hydraulic conductivity of tomato root systems in relation to morphological and histological changes of the root. We used rooted split-stem cuttings, in which one half of the root system was infected and the other one remained uninfected. In this way we were able to measure primary effects of an infection on root function, without interference of secondary effects due to suppressed shoot growth or accelerated senescence.

MATERIALS AND METHODS

Plant materials. Tomato plants (*Lycopersicon esculentum* 'Moneymaker') were grown from seeds in potting compost in a greenhouse with temperature varying from 18 to 25 C. Shoot cuttings were taken and allowed to develop a split-root system as described previously (8). Each of the two parts of the split-root system, consisting of a stem half with adventitious roots, was grown in a separate pot in silver sand and watered daily. The shoot cuttings together with their adventitious roots are termed "shoot-root systems." After 1 wk, one part of a root system of each plant was inoculated with about 1,500 freshly hatched second-stage juveniles of *M. incognita* (singly infected shoot-root system) (Fig. 1B). Other shoot-root systems were inoculated on both root parts (doubly infected shoot-root systems) (Fig. 1C). Uninoculated shoot-root systems served as controls (Fig. 1A). Once a week the plants were watered with a soluble fertilizer concentrate (Plant-Prod. 20-20-20, obtained from Maasmond Co., de Lier, The Netherlands).

Water uptake by singly infected shoot-root systems. After 12 wk of growth, the roots of 10 singly infected shoot-root systems were washed carefully. Discolored roots were removed. The shoot-root systems were incubated for 1 wk on a flowing 50% Hoagland nutrient solution. Each part of the root system then was immersed separately in 2 L of aerated Hoagland's solution in a beaker maintained in the greenhouse with a foil cover to prevent evaporation. Water uptake of the root parts was measured twice a day. After 3 days, each root part was weighed, and its total length was measured with a Comair root length scanner (Commonwealth Aircraft Corp. Ltd., Melbourne, Australia) (21). The paired *t* test was used to determine whether there were significant differences between the treatments.

Hydraulic conductivity of root systems. After 8 wk of growth, 10 each of control, singly infected, and doubly infected shoot-root systems were prepared as in the water uptake experiments. At the time of transfer from flowing Hoagland's solution, shoots were excised just below the original incision sites (Fig. 1A), and the root systems were placed in an aerated Hoagland's solution held at 22 ± 2 C to measure their hydraulic conductivity. A tube slipped over the stem stump and sealed with polysiloxane dental impression material was held under a partial vacuum of 9.4 kPa for 16 hr. Collected xylem suction fluid was removed, and its weight was determined. Root systems with the shoots removed did not exude xylem sap under atmospheric pressure. Significant differences between the treatments were determined with the paired *t* test.

Perfusion of root segments. In these experiments, an infected basal root segment (a segment taken from near the split stem and containing numerous nematodes in different developmental stages) and an adjacent uninfected one of the same length (2–4 cm, free of visible lateral roots) were selected from the same adventitious root. Segments from a comparable uninfected adventitious root were used as controls. Similar experiments were done with apical root segments (about 0.5 cm from the root apex). The segments were sealed with polysiloxane in a Perspex perfusion chamber (Technical and Physical Engineering Research Service,

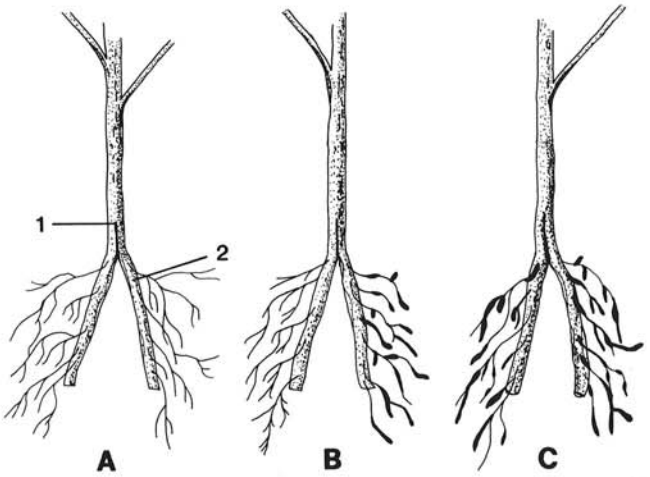


Fig. 1. Rooted split-stem cuttings of tomato plants infected with *Meloidogyne incognita*. **A,** Control shoot-root system. **B,** Singly infected shoot-root system, consisting of an infected root part and an uninfected one. **C,** Doubly infected shoot-root system. 1 = incision site; 2 = stem half.

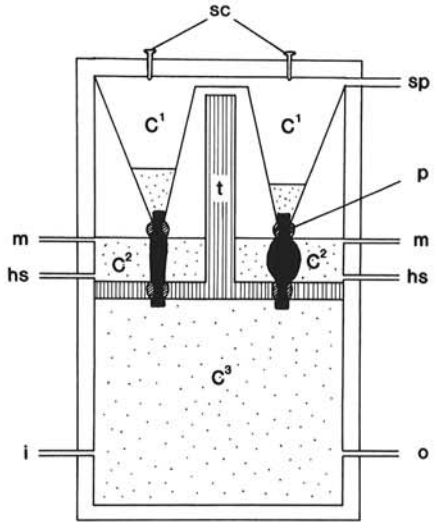


Fig. 2. The perfusion chamber used to simultaneously measure axial and radial water flow through root segments (black). C^1 = upper compartments. C^2 = middle compartments. C^3 = lower space. sp = suction pump. t = mobile T-piece. p = polysiloxane. m = connection for microcapillary. hs = connection for hypodermic syringe. i = water inlet lower space. o = water outlet lower space. sc = stop-cock by which perfused fluid can be collected.

Wageningen, The Netherlands) consisting of three subdivisions (Fig. 2). Aerated tap water was flowing through the lowest one. The upper space was subdivided by a septum into two compartments connected via air. A partial vacuum of 9.4 kPa was applied on the upper space. The middle space also was subdivided into two compartments by a mobile T-piece. The size of this space could be adapted to the length of the root segments by moving the T-piece. Each middle compartment was connected with a microcapillary and a 2-ml hypodermic syringe. The position of the microcapillaries was adjusted to the top level of the water surface in the middle compartment. The syringe was used to control the position of the meniscus in the microcapillary. Before measuring, there was an equilibration period of about 30 min. The radial water flow through the segment was determined by measuring the displacement of the meniscus in the microcapillary under a binocular microscope. The total water flow through the root segment was measured by weighing the solution collected in the upper compartment. The axial water flow could be calculated by deducting the measured radial water flow (from the middle compartment) from the volume sap collected in the upper compartment. After each experiment, the total length and the length of the root segment in the middle compartment were measured. The mean diameter of the root segments in the middle compartments also was determined. The seals were tested afterward. The lower one was tested by lowering the water level in the lower space until the root segments were just in contact with the water. Leakage would result in an enhanced water uptake from the microcapillary. Afterward the upper compartments were filled with water and the middle compartments were filled with air. The suction pressure on the upper space was maintained. If no air bubbles were observed in the upper compartments, it was concluded that there was no leak in the upper seals. The experiments were done at 22 ± 2 C and did not last longer than 8 hr.

Axial resistance to water flow. Axial resistance to water flow was measured by a pressure-flow method (27). The experiments were done in a constant-temperature room at 22 ± 2 C. One day before starting an experiment, 10-wk-old singly infected shoot-root systems were placed in aerated tap water. Segments (2–3 cm) without visible lateral roots were cut from infected adventitious roots. The basal end of each root segment was connected with silicone rubber tubing filled with tap water (Fig. 3). The surface of the root segment was dried gently with tissue paper. The juncture between the root segment and silicone rubber tubing was consolidated with polysiloxane. The root segment surface then was rubbed with grease (high-vacuum grease obtained from Dow Corning S.A. Co., Seneffe, Belgium) to prevent radial entry of water. The rubber tubing was connected with a 2-ml hypodermic syringe and with a microcapillary. The apical end of the root segment was placed in aerated tap water; then about 0.5 cm of this end was removed. A partial vacuum of 9.4 kPa was applied on the microcapillary, resulting in a displacement of the meniscus. The meniscus in the microcapillary could be controlled by the syringe so that it was visible in the microcapillary. Measurements were made after an equilibration period of about 30 min. The movement of the meniscus could be determined under a binocular microscope. In experiments with basal root segments, movement of the meniscus could be determined with the unaided eye.

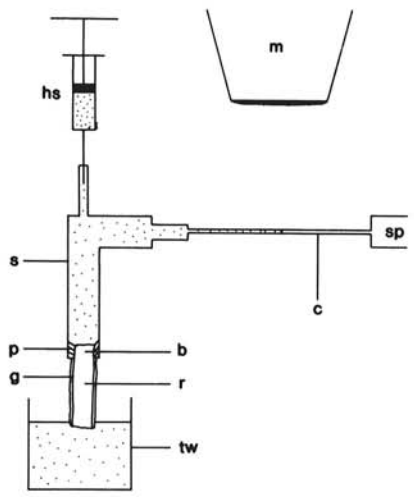


Fig. 3. Apparatus for measuring the axial resistance to water flow in root segments. m = binocular microscope. hs = hypodermic syringe. s = silicone rubber tubing. c = microcapillary. sp = suction pump. p = polysiloxane. b = basal root end. g = grease layer. r = root segment. tw = beaker filled with tap water/Tinopal CBS solution.

Axial resistance per unit root length was calculated by the following equation:

$$R^a = \Delta P/q \cdot l \text{ kPa} \cdot \text{mm}^{-4} \cdot s$$

where l = length of the root segment (mm), q = water flow through the root segment (mm^3/s), and ΔP = partial vacuum applied on the root segment (kPa).

To reveal conductive xylem vessels, the root segments were perfused with a 0.01% (w/v) aqueous solution of Tinopal CBS (a gift of CIBA-Geigy A.G., Basel, Switzerland) (26), an apoplastic fluorescent dye that binds to cell walls. After perfusion, the root segments were rinsed in tap water for 1 hr to release unbound dye, and their length was measured. Free-hand cross sections were made over the entire length of the root segment. Photographs and Kodak Ektachrome slides were made with a Leitz fluorescence microscope (Filterblock A: BP 340–380 + RKP 400 and filter LP 430, E. Leitz, Inc., Rockleigh, NJ). Diameters of the stained xylem vessels were measured from slides.

Axial resistance per unit root length also was calculated from the Poiseuille equation:

$$R^a = 8 \cdot \eta/\pi \cdot \Sigma\, r^4 \text{ kPa} \cdot \text{mm}^{-4} \cdot s$$

where r = radius of the conductive xylem vessels (mm), and η = viscosity of water (10^{-6} kPa · s).

Radial resistance to water flow. To measure radial resistance to water flow, basal root segments that showed relatively little axial resistance were used. Uninfected and infected (galls with a maximum diameter up to 6.9 mm) basal root segments with a length of 3–4 cm were dried gently with tissue paper. Silicone rubber tubing filled with tap water, supplied with hypodermic syringes and capillaries (Fig. 4), was connected to both cut ends. The distance between the rubber tubing was small compared with the length of the segments. The root segments were placed in aerated tap water. A partial vacuum of 9.4 kPa was applied on both microcapillaries. After an equilibration period of about 30 min, the displacement of the menisci was measured.

The radial resistance per unit root length was calculated by the following equation:

$$R^r = \Delta P \cdot l/q \text{ kPa} \cdot \text{mm}^{-2} \cdot s$$

where l = length of the root segment between tubing (mm), q = radial flow (mm^3/s), and ΔP = partial vacuum applied on the root segment (kPa).

Sectioning and staining. Root material was fixed for 18 hr in FAA (50% ethanol, 5% formaldehyde, 5% acetic acid, v/v/v), washed in 96% ethanol, and dried gently with tissue paper. Infiltration and embedding were with an LKB 22180-500 Historesin Embedding Kit (LKB-Products Co., Zoetermeer, The Netherlands). Sections of 5–10 μm were cut on a microtome and stained with periodic acid/Schiff's reagent or with 0.5% toluidine blue for light and fluorescence microscopy. Photographs were made with a Leitz fluorescence microscope equipped with a polarization filter block.

RESULTS

Water uptake by singly infected shoot-root systems. The infected parts of the shoot-root systems had generally fewer

branches than the uninfected ones. Infected roots were generally thicker and significantly shorter (total root length = 36.4 ± 10.6 m) than corresponding uninfected roots (56.0 ± 12.1 m) ($P < 0.005$). The wet weight of both root parts did not differ significantly. In these experiments, water uptake is linearly related to the total root length (Fig. 5). The total water uptake of infected root parts was significantly lower ($P < 0.025$) than that of corresponding uninfected parts. However, their water uptake per unit root length was significantly higher ($P < 0.005$). Water uptake of infected as well as uninfected root parts was fivefold higher during the day than at night.

Hydraulic conductivity of root systems. Water flow through infected root parts with the shoots removed, measured by applying a partial vacuum of 9.4 kPa on the stem stump, was lower (0.22 ± 0.13 ml/hr/root part) than that through the corresponding uninfected root part (0.54 ± 0.19 ml/hr/root part). The values are significantly different ($P < 0.01$). Maximal measured reduction equaled 90% of the flow through the corresponding uninfected root part. Water flow through the parts of control root systems (0.67 ± 0.16 ml/hr/root part) was significantly higher ($P < 0.005$) than that through doubly infected shoot-root systems (0.29 ± 0.19 ml/hr/root part). Differences in water flow between two corresponding root parts of the controls or between the parts of doubly infected shoot-root systems were not significant. Removal of the adventitious roots resulted in a 100-fold increase of the water flow, indicating that the hydraulic conductivity of the stem was of minor importance for the total water flow.

Perfusion of root segments. Water flow through a root has both a radial and an axial component. Both components were measured simultaneously using a segment perfusion technique. The flow rates through segments taken from different roots varied greatly. Therefore, the results of two representative experiments (out of 29) are shown in Figure 6, where the axial and radial flows of adjacent basal and adjacent apical root segments are presented.

At the root base, the axial and radial water flow through the infected root segment differs relatively slightly from the adjacent uninfected root segment, as was the case for basal root segments of the uninfected root. In contrast, the infected root segment from the root apex shows a strong decreased axial flow compared with the uninfected adjacent segment. This tendency was observed in all experiments with apical galls. Such a strong decrease was not observed in uninfected apical root segments (Fig. 6).

Axial resistance to water flow. Water flow through a root system is inversely proportional to the resistance encountered. The resistance to water movement thus also has a radial and an axial component. In the experimental design as described above, it was not possible to determine the axial and radial resistances because radial water movement will result in a nonlinear pressure drop within the xylem vessels. This is particularly the case for apical root segments with a relatively high axial resistance to water movement. The axial resistance therefore was measured by perfusing root segments, without interference of radial water uptake (Fig. 3). The measured values are compared with calculated values, obtained by applying the Poiseuille equation for water transport through vessels. The water-conductive xylem elements were traced by perfusing the segments with a Tinopal-CBS solution (Fig. 7D, E, and F), after which their diameters were measured. The results of a representative experiment (out of 36) are presented in Figure 8.

At the root base, the axial resistance per unit root length of an infected root segment is slightly higher than that of an adjacent uninfected root segment. At the root apex, however, infection increased the axial resistance considerably, compared with more basal adjacent uninfected root segments. Similar experiments with uninfected roots showed a more gradual increase of the axial resistance from root base to root apex. The calculated axial resistance was always lower than the measured one. In apical galled root segments, the increased resistance was due to a reduction of the xylem vessel diameter and the number of xylem vessels involved in the transport of Tinopal-CBS (Fig. 8).

Radial resistance to water flow. Radial resistances of infected and uninfected basal root segments, as measured by applying a partial vacuum on both cut ends of the root segments (Fig. 4), did not differ significantly, even in experiments with galls with a maximum diameter up to 6.9 mm. The radial resistance per unit root length of uninfected root segments and galls (out of 32 experiments) varied between 1.5 and 7.6 10^5 kPa · mm^{-2} · s.

Sectioning and staining. Cross sections of basal galls showed that giant cells were generally located in the ray parenchyma

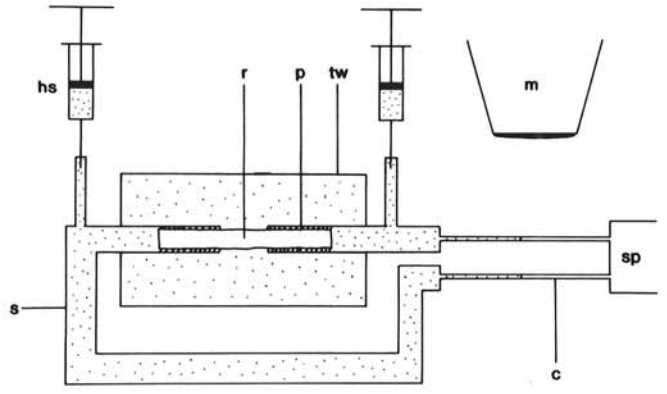


Fig. 4. Apparatus for measuring the radial resistance to water flow in root segments. hs = hypodermic syringe. r = root segment. p = polysiloxane. tw = beaker filled with tap water/Tinopal CBS solution. m = binocular microscope. s = silicone rubber tubing. c = microcapillary. sp = suction pump.

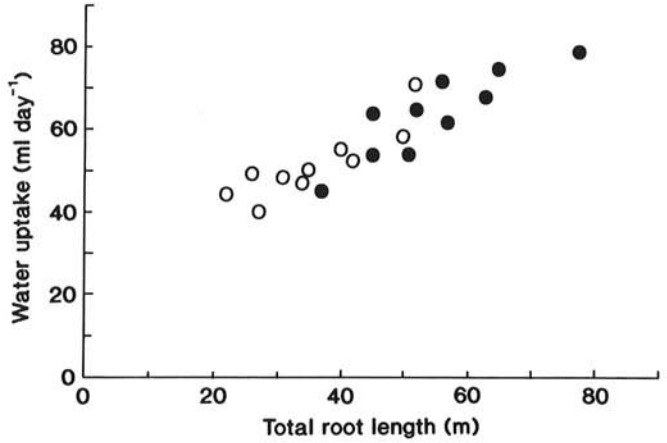


Fig. 5. Water uptake by infected (○) and uninfected (●) root parts of singly infected shoot-root systems in relation to their total root length.

Size		Waterflow		Size		Waterflow	
l (mm)	d (mm)	q^a ($mm^3\ s^{-1}$)	q^r (10^{-3} $mm^3\ s^{-1}$)	l (mm)	d (mm)	q^a ($mm^3\ s^{-1}$)	q^r (10^{-3} $mm^3\ s^{-1}$)
basal							
15	1.6	3.0	0.4	15	1.5	1.5	0.6
15	1.4	1.0	0.3	15	5.3	0.5	0.7
apical							
5	0.6	0.13	3.6	5	0.9	0.60	3.0
5	0.4	0.07	6.9	5	2.3	0.01	10.6

Fig. 6. Axial (q^a) and radial (q^r) water flow of basal and apical root segments measured in a perfusion chamber. The length of the basal root segments was 25 mm; length of the apical root segments was 15 mm. l = length of the segment in the middle chamber. d = mean diameter of the root segment in the middle compartment.

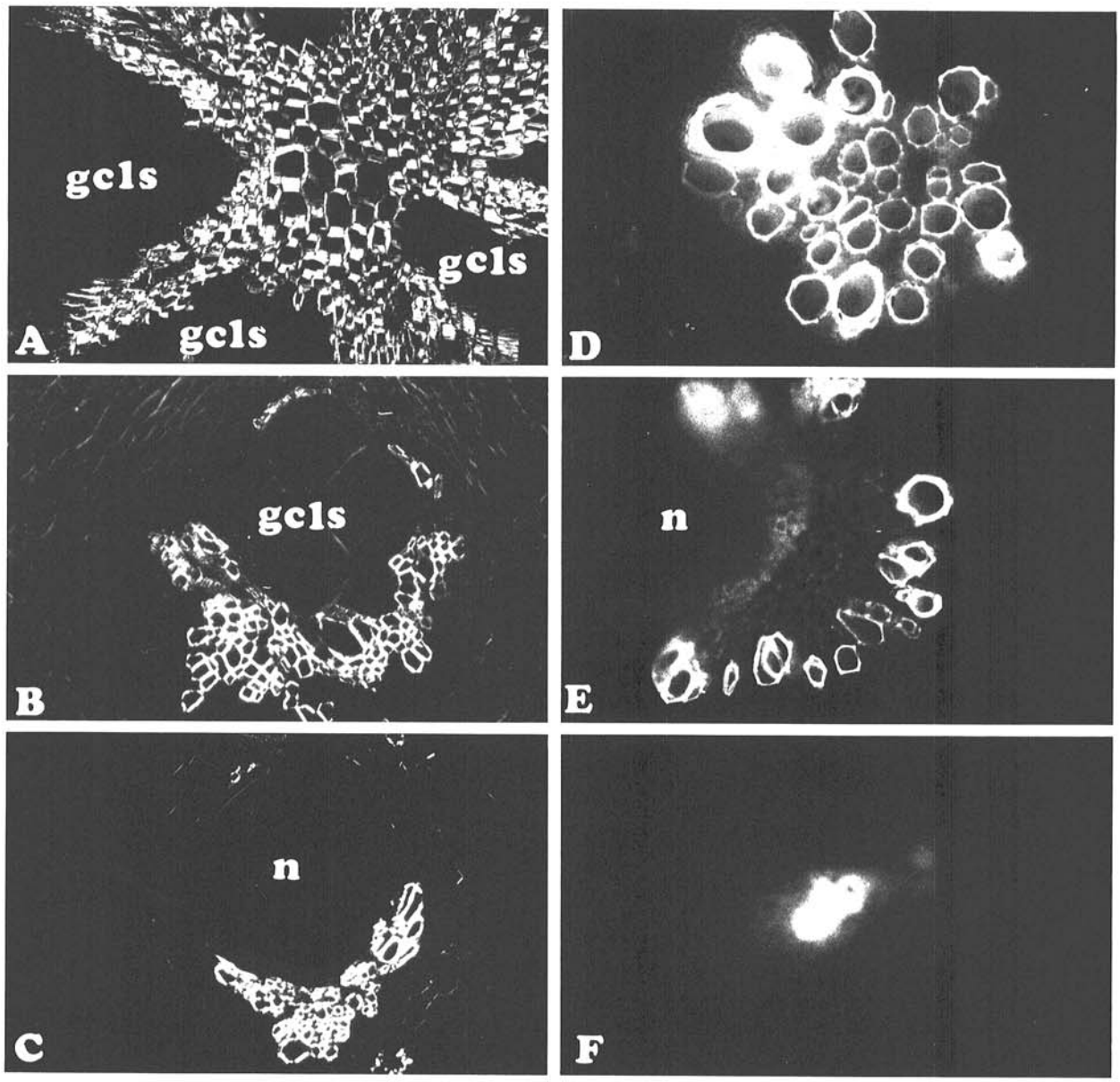
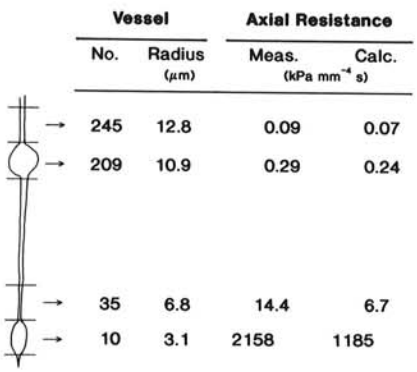


Fig. 7. A–C, Microtome cross sections of an infected root viewed with a fluorescence microscope equipped with a polarization filter block. **A,** An infected section taken from the root base showing the lignified xylem vessels. The giant cells are located in the ray parenchyma, resulting in dilated rays. **B,** In infected apical sections, the giant cells often are located in the xylem, resulting in a reduced cross-sectional area of the xylem. **C,** The body of the nematode sometimes disturbs xylem formation in apical root regions. **D–F,** Hand-cut cross sections of root segments perfused with a Tinopal CBS solution. The conductive xylem vessels fluoresce brightly. **D,** Cross section of an uninfected basal root segment. **E,** Section of an infected basal root segment. A part of the body of the nematode (n) is located in the xylem. There are some large metaxylem vessels, which are involved in the transport of Tinopal CBS. **F,** Infection at the root apex disturbs the continuity of the xylem vessels. There are a few small xylem vessels, which are involved in the transport of Tinopal CBS. gcls = cluster of giant cells.



	Vessel		Axial Resistance	
	No.	Radius (μm)	Meas. (kPa mm^{-4} s)	Calc.
→	245	12.8	0.09	0.07
→	209	10.9	0.29	0.24
→	35	6.8	14.4	6.7
→	10	3.1	2158	1185

Fig. 8. Measured and calculated axial resistance per unit root length of an infected root. No. = number of xylem vessels transporting Tinopal CBS.

(Fig. 7A). The rays were dilated, but the broad secondary xylem vessels in the center of the root were mostly present. At the root apex, xylem development was disturbed either by the formation of giant cells (Fig. 7B) or sometimes also by the body of the nematode (Fig. 7C). As a result, the cross-sectional area of the xylem was reduced.

DISCUSSION

In the present study, rooted split-stem cuttings were used to investigate the effect of an infection with *M. incognita* on water relations in tomato plants. The total root length of an infected part of a root system was reduced compared with that of an uninfected part. Infected root parts transported less water to the shoot than corresponding uninfected ones (Fig. 5). This cannot be attributed to an increased suction pressure of the shoot on the uninfected root part (or a reduced suction pressure on the

infected root part) because the negative xylem hydrostatic pressure in the stem at the point where both root parts are connected is the same for each part. A reduced water flow through infected roots (decreased hydraulic conductivity) also was found when roots with their shoots removed were exposed to a partial vacuum applied on the stem stump. The maximal decrease of water flow through an infected root part was then up to one tenth of that through the corresponding uninfected one, indicating that the resistance (reciprocal of the flow) to water movement was increased about 10-fold. These results are similar to those obtained with snap bean infected with *M. hapla* (31). The measured values of the hydraulic conductivities of the root systems are similar to those reported for tomato (22).

One of the major resistances to water movement through the plant is located in the roots (4,17,23,30). Resistance to water flow through roots has both an axial and a radial component. Because the resistance to water movement is sensitive to environmental factors (23) and is increased by metabolic inhibitors (13), it was concluded that the main resistance is not located in the walls of the cortical cells or in the xylem vessels but in the symplasm of the endodermis. The Casparian strip in the walls of endodermal cells interrupts apoplastic water flow from the cortex into the stele (7). However, recent studies by Bacic and Ratcovic (1) using nuclear magnetic resonance techniques to estimate water flow showed that a significant proportion of the water flow passes the symplasm of the cortical cells. Steudle et al (28,29) concluded that under an osmotic gradient the symplasm is the main pathway for water movement across the cortex, whereas under a hydrostatic pressure gradient the apoplast is the preferred cortical pathway. The endodermis is then the main barrier.

The axial and radial resistances were determined separately under a hydrostatic pressure gradient (Figs. 3 and 4). The axial resistance in apical galled segments is considerably higher than in uninfected adjacent root segments taken from just above the gall. In basal galls, this effect was much less. Nonlinear flow as a result of rough elliptical patches on the walls of the xylem vessels may account for the differences obtained between measured and calculated resistances (26).

Gall formation at the root base has no detectable effect on the radial resistance, which is in accordance with previous suggestions (28,29) that under a hydrostatic pressure gradient the suberized walls of the endodermal cells are the main barrier for the radial water movement across the root. The negative hydrostatic pressure inside the stem is the driving force for water transport through the root system in strongly transpiring plants. Although the nematode pierces the endodermis, there is no bulk flow of water and solutes from the cortex into the stele along the body of the nematode (8).

Light and fluorescence microscopic studies of cross sections showed that the cross-sectional area of the xylem was reduced in infected apical root segments (Fig. 7B and C). Byrne et al (5) also found a reduction of the xylem cross-sectional area between the triarch lateral roots of *Glycine max* infected with *M. incognita* and the uninfected tetrarch lateral roots. In the present study, generally a small reduction of the cross-sectional area of the xylem was found in basal root segments. The large metaxylem vessels in basal sections of uninfected regions were also present in adjacent infected regions (Fig. 7A). These vessels contribute much to the total axial water flow. According to the Poiseuille equation, doubling the radius of a vessel increases the flow by a factor of 16. Secondary infections at the root base will have little effect on axial water flow because the large water-conducting metaxylem vessels already have been formed.

Root-knot nematodes usually do not infect the basal regions of roots but mostly penetrate just behind the root cap. After an apical infection, root growth may continue or stop. In the former case, this will result in a more basal gall; in the latter case, the gall becomes terminal. In the present study, it was found that galls were located at the apex and also in more basal regions of the root. It is tempting to speculate about the factors that determine whether, following infection at the apex, root growth will continue or cease. It has been argued (17) that the ratio of axial to radial resistance determines the optimum length of a root. A disturbed R^a/R^r in the root apex thus might be the cause of infected roots that are significantly shorter, as was found (Fig. 5). When the formation of giant cells has no profound effects on xylem vessel development, the root apex is able to grow further, and a more basal gall will be the result. It is obvious that the degree of xylem disruption in the root tip is related to the number of nematode infections. Byrne et al (5) also found that, even in uninfected parts located apical from infection sites, the cross-sectional area of the xylem is reduced.

Inhibited growth of the root apex also can be caused by a disturbed phloem or an enhanced phloem unloading at infection sites (2), reducing nutrient flow to the apex. Because nutrient transport via the phloem depends on the sink strength and is less dependent on its cross-sectional area as is water transport through the xylem, a disturbed phloem seems to be of minor importance. Although a withdrawal of nutrients from the phloem at basal infection sites probably will occur, this does not necessarily result in a complete inhibition of root growth.

Water supply to shoots depends on the geometry and hydraulic properties of the root system. Heavily infected plants usually have a less extensive root system than uninfected plants (10). This can result in a depletion of water just along the root surface of a strongly transpiring plant. Water supply will then depend on water transport within the soil from more remote places. The resistance to water flow within the soil then will become a limiting factor.

It is generally accepted that the axial resistance to water flow is small compared with the radial resistance, except in the root apex where the metaxylem vessels have not yet developed (12). The present results show that infection does not change the radial resistance per unit root length in more basal root regions. Because, however, root systems of infected plants are shorter, their total radial resistance will be higher than that of uninfected plants. This increased total resistance may be a major factor contributing to wilting of infected plants, even in situations where soil moisture is adequate (14).

Effects of nematodes on plants often have been studied in relation to a root-knot index (amount of knotting). Such a relation, however, is not obvious. The present results show that, at basal infection sites, the resistance to axial water movement is much less reduced than in apical galls. Thus, it is not only the number of infection sites but also their location along the root that account for the deleterious effects on water relations in an infected plant.

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