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THE INFLUENCE OF LESION NEMATODE INFECTION ON PLANT
WATER RELATIONS AND ROOT TISSUE INTEGRITY

A Thesis Presented

By

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And to my wife, Lynne, for her patience, understanding and love throughout this endeavor.

PREFACE

This thesis is presented in two sections. Each is written in manuscript form for publication in Phytopathology. Experiments performed to support each hypothesis deal with the effects of Pratylenchus penetrans (Cobb) Filip. and Stek. on host metabolism. It was not the intention of this study to correlate the phenomena observed in the two studies with each other, although, further experimentation would probably do so.

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THE INFLUENCE OF THE LESION NEMATODE, PRATYLENCHUS
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INTERNAL WATER RELATIONS IN SUNFLOWERS INFECTED BY THE
LESION NEMATODE, PRATYLENCHUS PENETRANS AS DETERMINED
BY DIFFUSIVE RESISTANCE

ABSTRACT

Diffusive resistance measurements of leaves of sunflowers whose roots are infected with small populations of Pratylenchus penetrans indicate that the internal water status of otherwise symptomless infected plants is lower than that of healthy plants. Such moisture stress may induce the stunting commonly associated with lesion nematode infection. It is probable that the extent to which damage to plants occurs is influenced by physiological age, the degree to which water stress develops, and the host species concerned. Younger plants experience greater deficits than do older plants; however, regardless of age, infected plants experienced internal water deficits in advance of healthy plants growing under similar conditions.

INTRODUCTION

All plant physiological processes depend on water and if growth and development are to proceed normally, internal water stresses must not develop within plant tissues (Gates, 1968; Gardner, 1965). Relatively low leaf moisture stress inhibits such processes as photosynthesis (Kozlowski, 1964; Boyer, 1970; Boyer and Bowen, 1970) and as water deficits intensify, organelles (Todd, 1972) and other cell components become disrupted. This causes further reductions in metabolic activity, which ultimately result in lower yield (Kozlowski, 1964; Black, 1965; Bushnell and Rowell, 1968; Duniway, 1973; Gates, 1968).

Yield reductions of forage legumes (Willis and Thompson, 1969a,b), tobacco (Olthof, Marks, and Elliot, 1973) and other crops also result from root infestations by the lesion nematode, Pratylenchus penetrans (Mountain and Patrick, 1959; Odhirin and Jenkins, 1965; Townshend, 1962a,b). Stunting resulting from lesion nematode infection often occurs in the absence of extensive root tissue damage. Such plants have been reported to appear to be more susceptible to wilt than healthy plants during periods of slight water stress (Society of Nematologists, Committee on Crop Losses), although the effect of P. penetrans on

host-water relations has never been quantitatively estimated. Because yield reduction and wilting can result from both lesion nematode infection and water stress, it was of interest to determine if a significant water deficit exists in nematode-infected plants.

The purpose of this investigation was to determine the effect of P. penetrans on host-water relations. Measurement of water vapor loss from leaves with a diffusive resistance porometer was selected as an accurate means of determining the internal water status of healthy and diseased plants (Duniway, 1971; Kassam, 1973).

MATERIALS AND METHODS

Sunflower seedlings, (Helianthus annuus var. Mammoth) were grown singly in equal quantities of loam:sand (1:1) in standard four inch diameter plastic pots at 25 C in a growth chamber. Plants were maintained under a twelve hour light period throughout the experiment. Light intensity was measured with a spectroradiometer Isco Model SR and is presented in Table I.

Upon cotyledonary expansion, each of 50% of the seedlings was inoculated with approximately 2000 Pratylenchus penetrans (Cobb) Filip. and Stek. larvae and adults. Inoculum was obtained from alfalfa callus grown aseptically on nutrient medium containing 2,4-D according to the method established by Krusberg (1961).

Determination of internal water status of healthy and nematode infected sunflowers was accomplished through the use of a diffusive resistance porometer (Lambda, Model LI-60) of the type described by Kanemasu et al., 1969. The horizontal diffusive resistance sensor, after being dried with a hand-pumped aspirator, was stored in a closed position at 25 C in a desiccator containing silica gel. Diffusive resistance of abaxial leaf surface (r_1) was

measured at eight hour intervals commencing twelve hours after saturation of the rooting medium with water, and ending upon the first signs of leaf flaccidity. This technique involves the use of a dehydrated cup containing a humidity sensor which is placed over the leaf surface. As transpiration proceeds, the humidity in the cup increases, and the time required for the sensor to respond over a prescribed range is determined as a measure of resistance to water vapor diffusion (Morrow and Slatyer, 1971).

Raw data in seconds, collected from diffusive resistance measurements of the first and third pairs of true leaves at similar physiological ages was converted to sec cm^{-1} through the use of a calibration curve developed at 25 C based on the findings of Morrow and Slatyer (1970, 1971). In initial experiments, growth chamber humidity was monitored with a thermal hygrometer and was found to range from 40%-60%. In agreement with the findings of Davies and Kozlowski (1973), diffusive resistance measurements taken during light hours did not appear to be dependent on air moisture at the high light intensity (Table I) under which the plants were grown. Growth chamber humidity was $60 \pm 5\%$ throughout all diffusive resistance measurements taken in the dark. Consequently, humidity was not regulated in these experiments.

RESULTS

The data obtained from measurement of the diffusive resistance of first and third true leaf pairs of healthy plants and plants whose roots were infected by P. penetrans were converted to indicate absolute differences (Figs. 1 and 2). As soil moisture was reduced, the diffusive resistance (r_1) of nematode-infected plants, taken in the dark, increased before that of healthy plants. Furthermore, younger nematode-infected plants (Fig. 1) appeared to experience significant internal water deficits at higher soil moisture levels than did diseased plants which were approximately three weeks older (Fig. 2). These older plants experienced significant internal water deficits 58 hours after initial readings (Fig. 2) while younger plants experienced water deficits 40 hours after initial measurements (Fig. 1).

Inoculation of sunflower seedlings with 2000 lesion nematodes did not produce stunting or other foliar symptoms at the time of measurement of diffusive resistance. However, the roots, particularly the tap root, exhibited extensive lesion formation and browning due to phenol accumulation (Acedo and Rohde, 1971; Dickerson et al., 1964;

Mountain and Patrick, 1959; Odhirin and Jenkins, 1965; Rohde, 1963; and Townshend, 1962a,b, 1963a,b). Upon staining parasitized roots (Dropkin, 1969), nematodes were observed in cortical tissues behind differentiating meristem regions and many eggs were seen throughout the cortex.

An attempt was made to study the effect of 12,000 lesion nematodes/plant on host-water relations. However, leaf surface areas of inoculated plants were too small to be measurable by the sensor aperture of the diffusive resistance porometer. Many of the plants inoculated with high population levels of nematodes died after two weeks and those which survived had very few roots.

DISCUSSION

P. penetrans is pathogenic to H. annuus var. Mammoth. Low population levels (2000 nematode/plant) cause damage to sunflower roots which is similar to that observed in other hosts as a result of P. penetrans infection (Acedo and Rohde, 1971; Dickerson et al., 1964; Mountain and Patrick, 1959; Odhirin and Jenkins, 1965; Rohde, 1963). Large lesion nematode populations greatly reduced host root systems. When a pathogen causes extensive root damage, distribution of roots must play a key role in the ability of such plants to attain water (Duniway, 1973). However, when roots of plants infected with low population levels of P. penetrans and roots of healthy plants were placed side by side, they appeared to have root systems of equal size. Yet, internal water status of infected plants declined in advance of healthy plants as soil moisture became limited. It would appear that root tissue integrity and distribution are essential for efficient soil moisture utilization.

Due to the high light intensity under which plants were measured (Table I), it is probable that internal water deficits were not detectable during light hours. When stomatal response to light is saturated, leaf water deficits

have little effect on stomatal movement until extreme internal water deficits exist (Kassam, 1973). However, dark hour measurements should be highly sensitive to changes in internal water status as light, an experimental artifact, is eliminated. Although stomata are closed, the rate of cuticular water loss is also dependent upon internal water status and is measurable as diffusive resistance (Duniway, 1973). In spite of oscillations in transpiration (Cowan, 1973) which are probably responsible for the variability in diffusive resistance measurements, dark hour measurements of the first set of true leaves (Figure 1) indicate water deficits developed in diseased plants when soil moisture was abundant. This difference between the internal water status of healthy and diseased plants became substantial between 16 and 40 hours after initial measurements (Fig. 1). Plants which were approximately three weeks older and were infected with P. penetrans did not appear to differ from healthy plants with regard to utilization of soil moisture until 58 hours after initial readings (Fig. 2) when the soil surface appeared dry.

In summary, experimental data indicate that leaves of nematode-infected plants, when compared with those of healthy plants, experience premature water deficits as determined by diffusive resistance measurements. Although

healthy plants probably experience short term water deficits whenever transpiration exceeds absorption by the roots, such deficits are normally reported to be restored at night (Livne and Vaadia, 1972). In this experiment, significant internal water deficits in nematode-infected plants were determined to occur during the night. Perhaps such deficits reduce or stop restoration of normal internal water deficits. Such stresses could account, in part, for the stunting that is often associated with the attack of lesion nematodes.

Table I. Spectral intensity of the twelve hour light period under which sunflowers were grown.

wave length (nm)	intensity (uw/cm^{-2})
380	0
400	.7
425	2.3
430	6.2
450	3.3
475	3.9
500	4.7
525	5.6
550	>10.0
575	>10.0
600	>10.0
625	>10.0
650	7.1
675	4.1
700	2.9
725	2.5
750	2.5

Fig. 1 Absolute differences in diffusive resistance (sec cm^{-1}) of the first true leaf pairs of three week old healthy plants (0) and lesion nematode-infected plants which arose as soil moisture decreased.

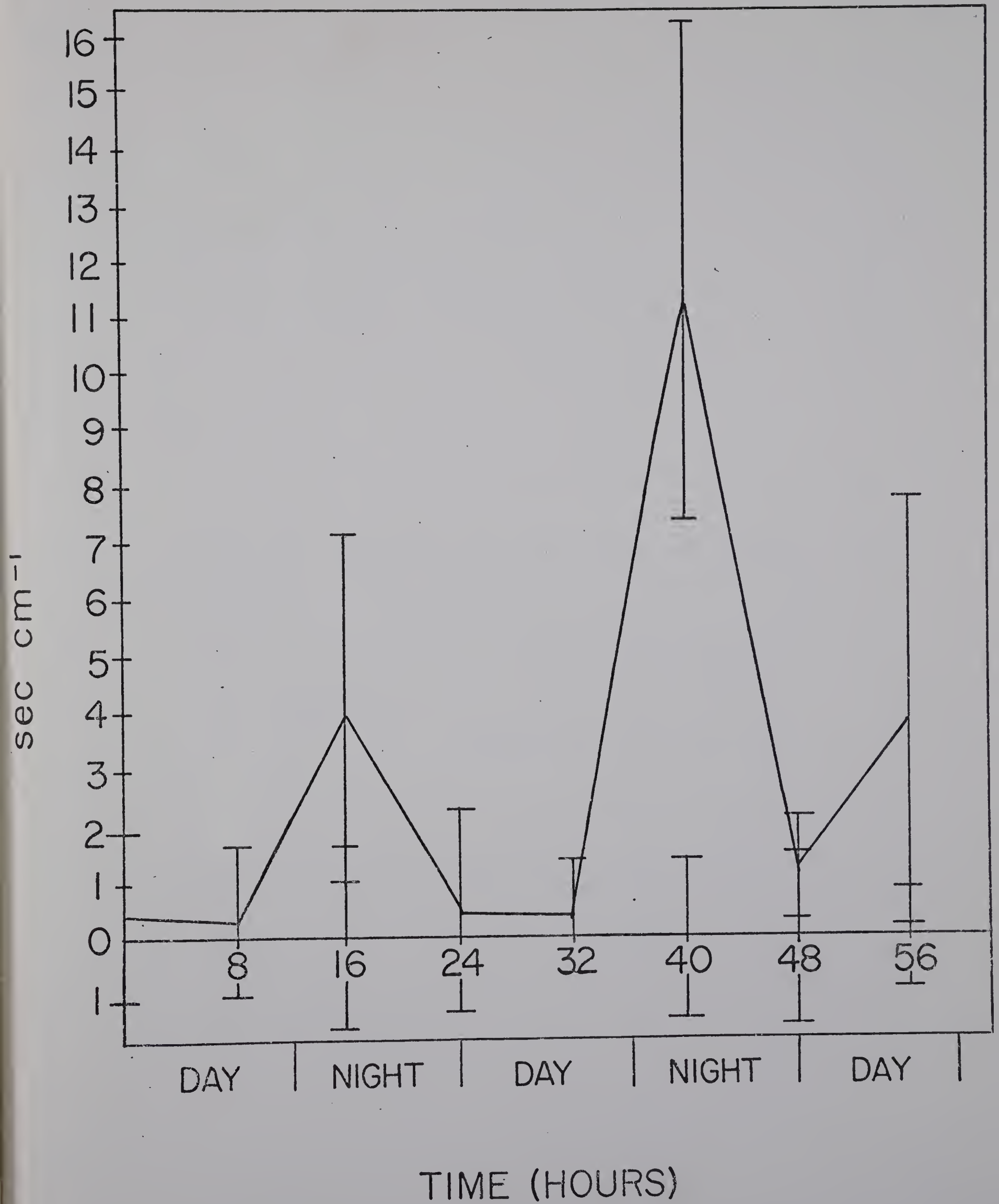
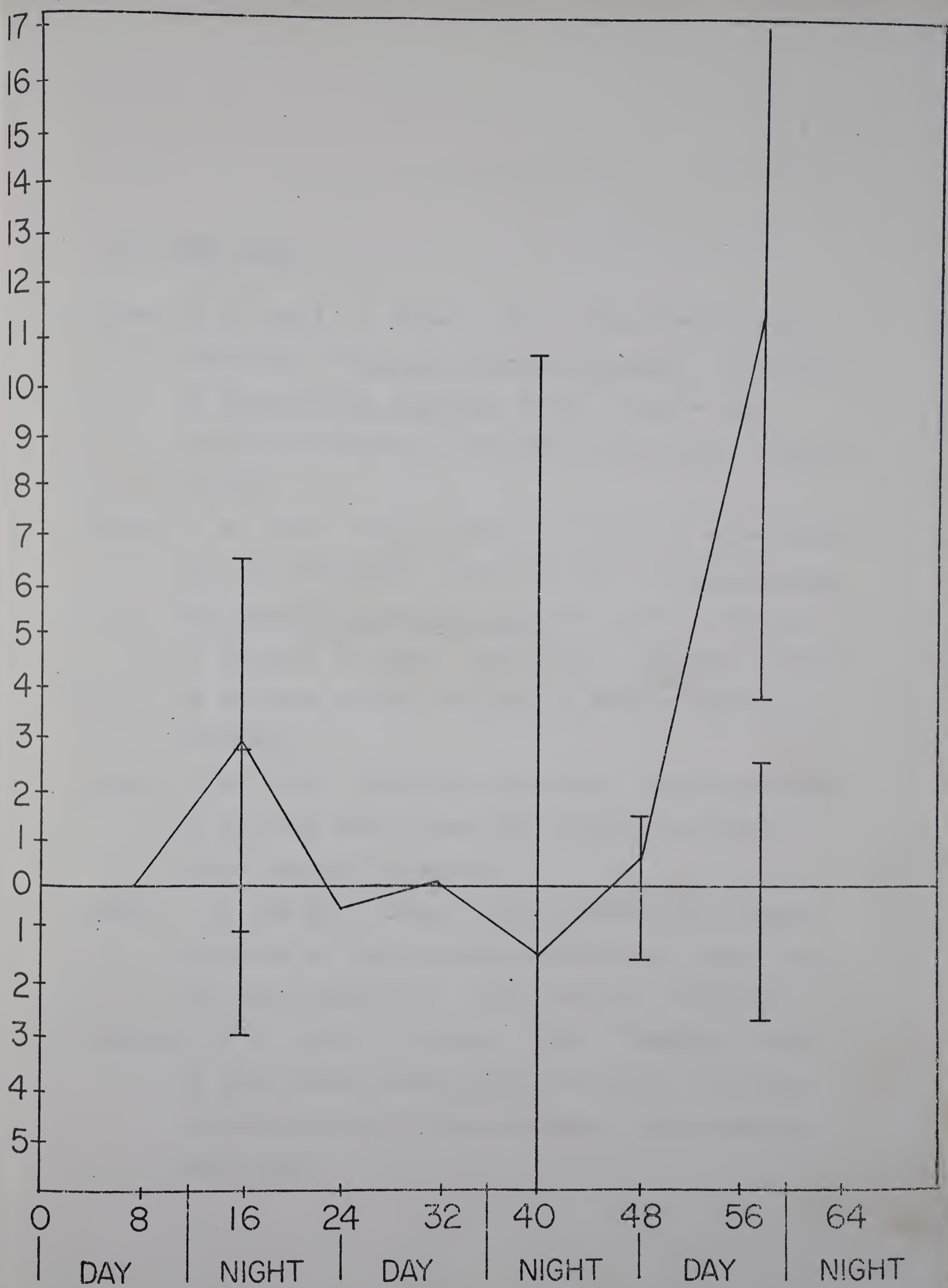


Fig. 2 Absolute differences in diffusive resistance (sec cm^{-1}) of the third true leaf pairs of six week old healthy plants (0) and lesion nematode-infected plants which arose as soil moisture decreased.



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THE INFLUENCE OF THE LESION NEMATODE, PRATYLENCHUS PENETRANS
ON ELECTRICAL RESISTANCE OF CORN AND SUNFLOWER ROOTS

ABSTRACT

Decreases in the electrical resistance (ER) of sunflower root tissue infected with Pratylenchus penetrans indicated that changes in integrity occurred in infested tissues within 3-6 hours while lesion formation did not occur until 16-24 hours after inoculation. Similar changes in ER were not detected in lesion nematode infected corn root tissue. This difference may be correlated with varying host phenol accumulation and tends to emphasize the importance of enzymatic activity in pathogenesis associated with lesion nematodes. Changes in ER could not be detected in parasitized root tissue 2 cm from the inoculation site of either of the species tested. A technique to determine accurately the ER of vegetative tissue is described.

INTRODUCTION

As soil moisture becomes limiting internal water deficits develop sooner in nematode-infected plants than in healthy plants (Kaplan et al., 1975, unpublished data). Stresses of this type may contribute to the stunting of many hosts in response to lesion nematode attack.

Pratylenchus penetrans causes lesions on roots at feeding sites as well as phenol accumulation in cells adjacent to feeding sites and in the endodermis (Acedo and Rohde, 1971; Dickerson et al., 1964; Mountain and Patrick, 1959; Odhirin and Jenkins, 1965; Rohde, 1963; and Townshend, 1962a,b, 1963a,b). Since P. penetrans feeds in tissues associated with water and nutrient absorption, and since stunting often occurs in the absence of extensive root-tissue damage, it was of interest to determine the effect of infection on root tissue integrity.

A method for detecting changes in the integrity of woody tissues using resistance to a pulsed electric current was described by Skutt et al., 1972. Using this technique, measurements of electrical resistance have been related to studies of wood deterioration (Tattar et al., 1972, 1974; Tattar and Saufley, 1973; Tattar, 1974;

Skutt et al., 1972), host response to fungal infection (Friedman and Jaffe, 1960) and to the extent of injury resulting from enzymatic activity (Caruso et al., 1975; Friedman and Jaffe, 1960) and the rough handling of fruit (Greenham, 1966). The aim of this study was to determine the effect of lesion nematode infection on the integrity of host root tissue as measured by electrical resistance (ER).

MATERIALS AND METHODS

Seeds of sunflower, Helianthus annuus cultivar "Mammoth," and sweet corn, Zea mays cultivar "I O Chief," were treated with captan-pentochloronitrobenzene and captan respectively, placed on germination paper which was rolled into cylinders, and left standing upright in a germination chamber (30 C day, 20 C night) for five days. The cylinders were then unrolled and seedlings with roots of similar length and diameter were selected. One miracloth (Chicopee Mills, Inc., New York) disc (0.5 cm diameter) was placed on each root, approximately 0.5 cm from the root tip.

Lesion nematodes, Pratylenchus penetrans, were raised axenically in alfalfa callus growing on a nutrient medium containing 2,4-D (Krusberg, 1961). Adults and larvae were extracted with a Baerman funnel, collected in distilled water, and 0.2 ml of the nematode-distilled water suspension containing 2500 nematodes/ml was placed on the miracloth disc of each of 50% of the test plants. Miracloth discs on control plants were treated with .02 ml of distilled water only.

The integrity of lesion nematode-infected, non-infected adjacent tissues and control root tissue was

estimated with a shigometer (Northeast Electronics Co., Concord, N. H.), a device which measures electrical resistance to a pulsed current. Seedlings were placed individually on a platform composed of nylon mesh stretched over an open glass petri dish which was secured to a glass block (Fig. 1). The miracloth disc was removed and a single layer of nylon mesh stretched across a plastic hoop was lowered over the seedling. Two subdermal platinum needle electrodes, 10 mm long with a diameter of 0.5 mm (Grass Instrument Co., Quincy, Ma.), were previously fixed in position, 0.5 cm apart, on a lucite block which was supported by a micromanipulator (Fig. 2). By using the fine adjustment of the micromanipulator, the electrodes were inserted completely through the root in the area of inoculation. ER measurements were recorded in Kilo (K) ohms immediately after insertion of the electrodes. This technique serves to minimize extensive root tissue damage which occurred in preliminary experiments from hand directed electrode insertion. These procedures also allowed for standardization of the age of the tissue measured, the extent of electrode-root surface contact, and the types of tissue that the electrodes came in contact with.

After each measurement around the inoculation site the electrodes were immediately inserted again at a distance

of 1 and 2 cm from the inoculation site. Data were collected from 8-10 seedlings for each treatment at each sampling time.

RESULTS AND DISCUSSION

The presence of lesion nematodes in the cortex of sunflower roots, three to six hours following inoculation, was correlated with decreases in ER (Figure 3). Lesions, however, were not observed until 16 to 24 hours after inoculation. Similar drops in ER, in advance of symptom expression in other disease progressions, have also been reported (Friedman, 1960; Caruso et al., 1975; Greenham and Muller, 1956).

The path of small, direct current pulses at low frequencies of the type used in this experiment, is reported to almost entirely follow the channels of the cell walls in healthy tissue (Fensom, 1966). ER of plant tissue has been related to the number of electrolytes or mobile ions (Fensom, 1966; Tattar et al., 1972). Injury and/or cellular death result in electrolyte loss from cells and subsequent decreases in the ER of affected tissues (Greenham and Muller, 1956; Greenham, 1966). ER also decreases when cell wall destruction occurs (Tattar, 1974). In tissue infected by lesion nematodes, movement of the nematodes throughout the root cortex has been observed to cause mechanical and enzymatic disruption of cell walls and of

the living protoplast within (Acedo and Rohde, 1971; Rohde, 1963; Townshend, 1962a,b, 1963a,b).

Alterations in host tissue have also been observed in intact cells adjacent to parasitized cells as well as in the endodermis (Acedo and Rohde, 1971; Ogiga and Estey, 1975). Sixteen hours after inoculation, intact cortical cells in sunflower roots which were adjacent to nematode-infected cells exhibited browning. The mechanical and enzymatic destruction of parasitized cells was postulated to induce changes in adjacent uninfected tissues (Acedo and Rohde, 1971). Such changes may be the result of enzymes liberated from parasitized cells or from enzymes of nematode origin. In a study using similar techniques to determine ER in plant tissue, pectolytic enzymes were thought to increase electrical conductivity in advance of the pathogen (Friedman, 1960). However, in the present experiment, when electrodes were inserted into uninfected cells, 1-2 cm away from the inoculation site, a slight decrease in ER was detected in only one of three replicates.

No changes in ER or corn root tissue were detected at either the inoculation site or in adjacent intact cells. Measurements were made at intervals for a period of 43 hours following inoculation. Although nematodes were found to be in the root cortex, none of the cells in infected

areas turned brown. This is in accordance with previous findings that P. penetrans moves through the root cortex of gramineae species by tearing cross walls and yet, no discoloration occurs (Troll and Rohde, 1966). However, it was recently observed that phenolic accumulation does occur in lesion nematode-infected roots of several corn varieties (Ogiga and Estey, 1975). In this experiment, brown lesions did not appear in roots of the corn cultivar "I O Chief" although the presence of P. penetrans in the cortex and cell wall breakage were confirmed by staining.

Despite partial digestion of cell walls by lesion nematodes as they move through corn roots, ER is unaltered. The cell walls of sunflower are also digested by lesion nematodes; however, the ER of parasitized tissue is reduced. The reason for this differential response of corn and sunflower to lesion nematode attack is unknown; perhaps it may be correlated with effects on host tissue resulting from enzyme activity or the number of cells that are killed. Enzymatic changes in host tissue may result in more extensive root tissue alteration than does mechanical injury resulting from nematode movement.

Fig. 1 ER of roots was determined with two subdermal platinum needle electrodes attached to a lucite block which was supported by a micromanipulator. Roots were supported between two layers of nylon mesh and a shigometer was used to measure ER to a pulsed current.

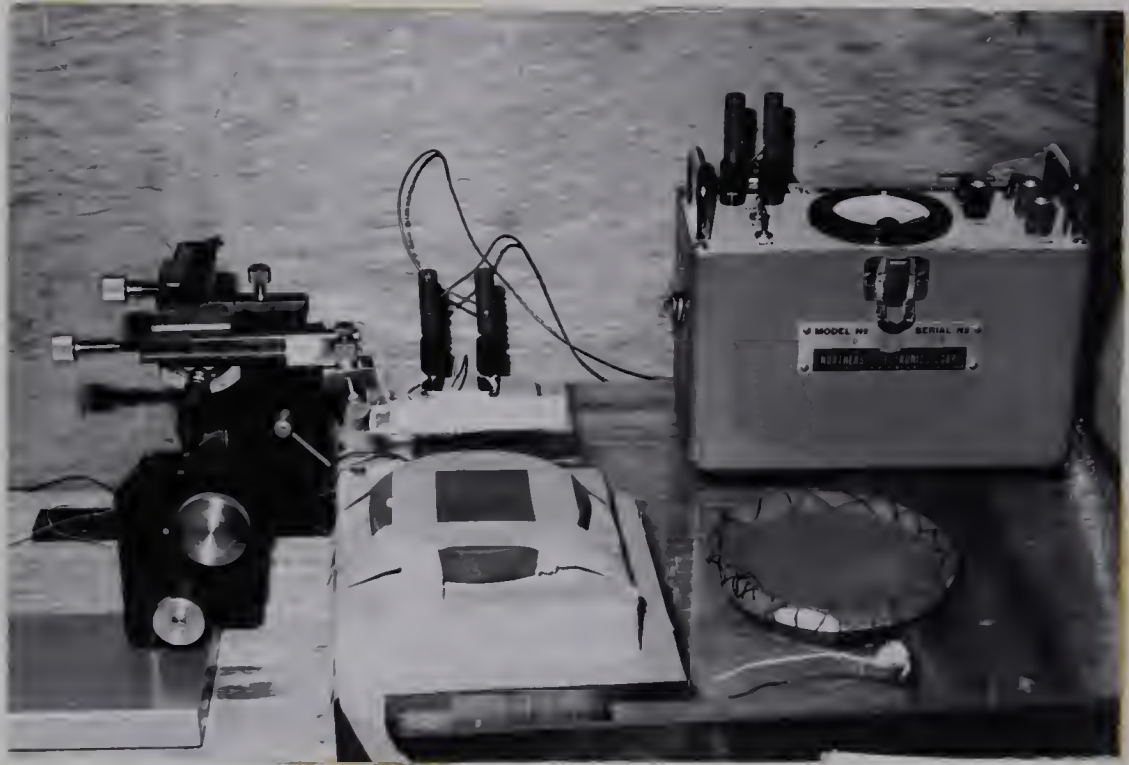


Fig. 2 Two subdermal platinum electrodes were inserted through roots which were supported between two layers of nylon mesh.

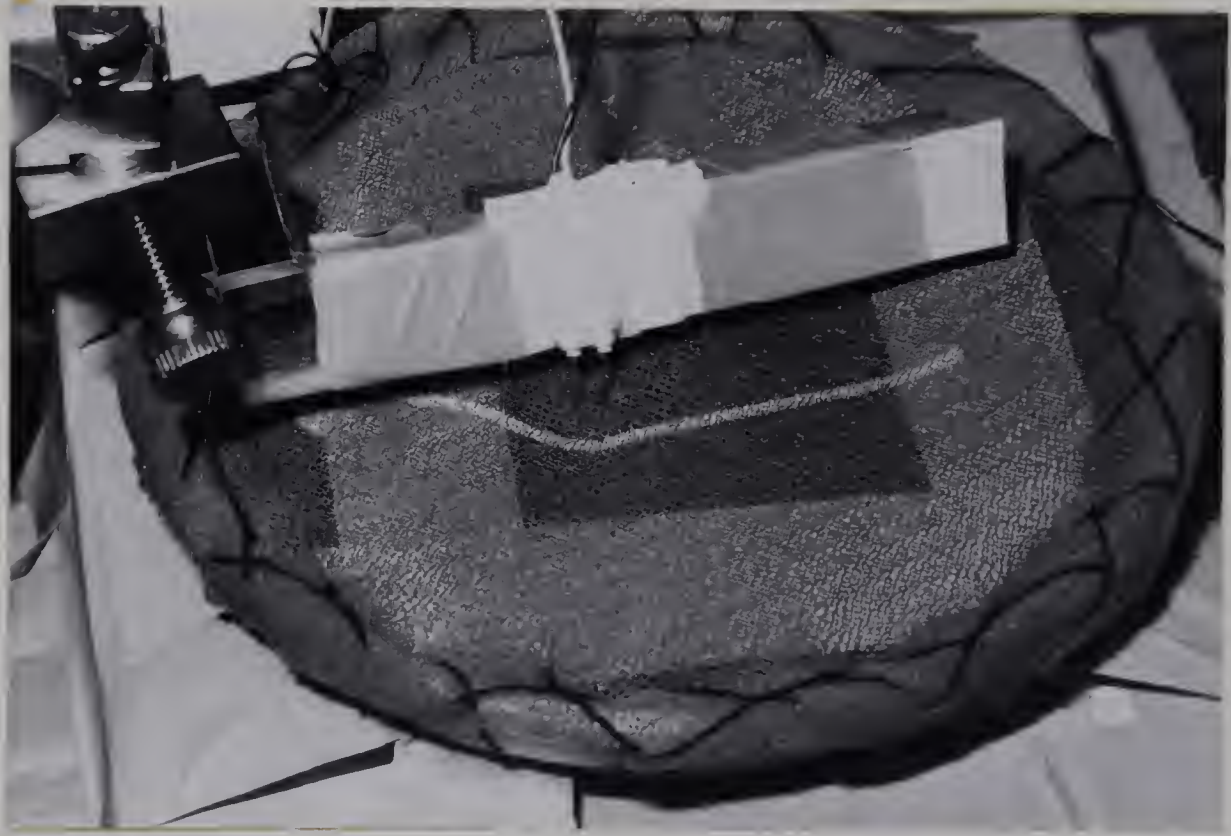
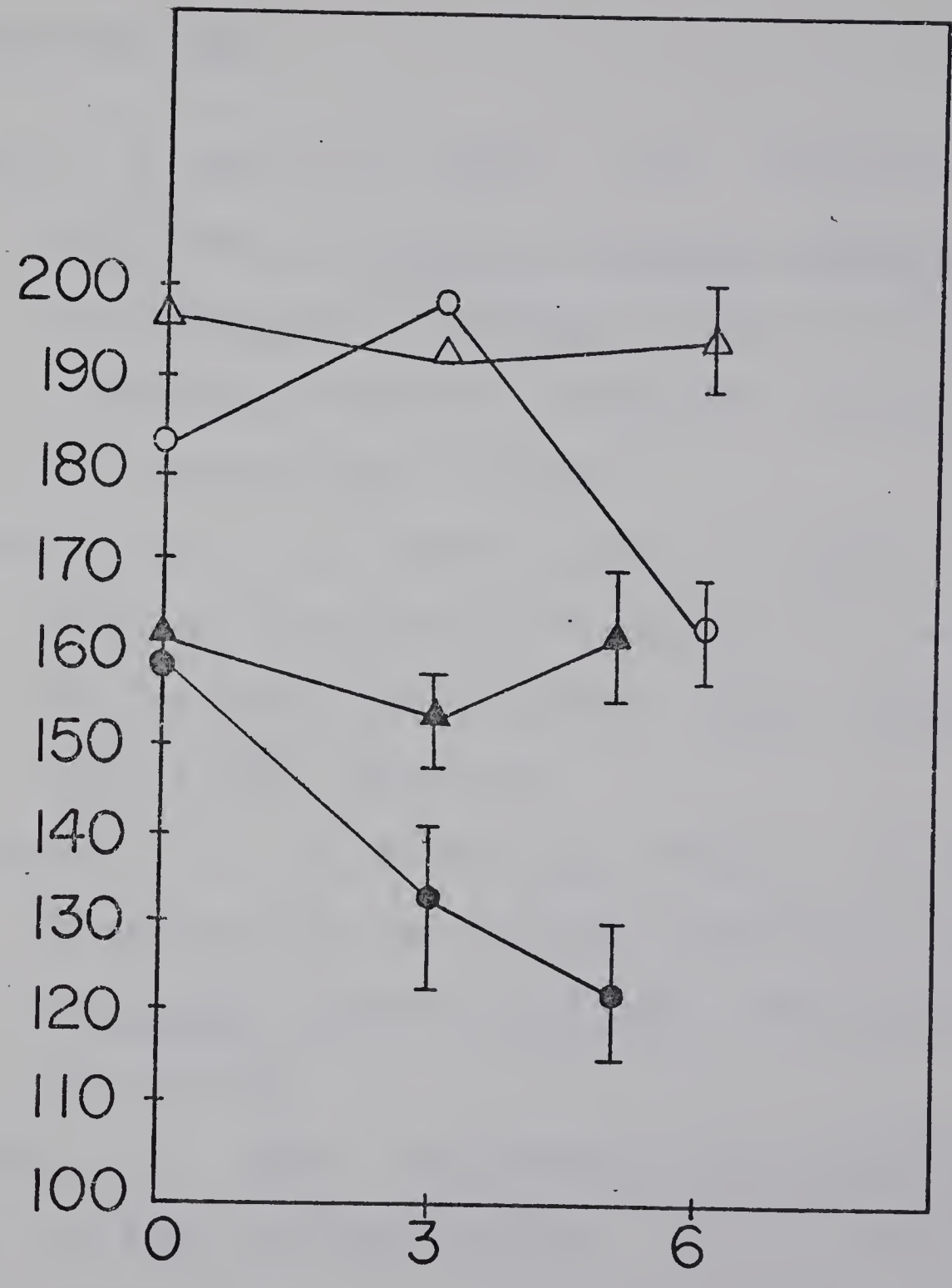


Fig. 3 ER of nematode-infected sunflower root tissue decreased between 3 and 6 hours after inoculation. (Electrodes were 5 mm apart in healthy (Δ) and diseased (0) root tissue and 3 mm apart in healthy \blacktriangle and diseased (\bullet) root tissue.)

ELECTRICAL RESISTANCE

k ohms



TIME (HOURS)

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