The relationship between development of the citrus root system and infestation by *Tylenchulus semipenetrans*

Larry W. Duncan and Joe W. Noling

University of Florida, IFAS, Citrus Research and Education Center, 700 Experiment Station Road, Lake Alfred, FL 33850, USA.

Summary

Fibrous root growth and *Tylenchulus semipenetrans* population development were monitored monthly on 100 citrus trees in a bedded grove on the Florida coast. Fibrous root weights in individual samples were related ($p = 0.01$) to visual estimates of tree vigor. Nematode infestation levels (number of free living nematodes/g root) were inversely related to tree vigor ($p = 0.01$). Proportional growth of fibrous roots of individual root systems was also inversely related ($p = 0.05$) to tree vigor. The mean proportion of young roots to total roots in a sample was 44 % in healthy trees compared with 72 % ($p = 0.05$) in decline trees during the January sample period. In the present study, mature, vigorous citrus trees were less susceptible to population development by *T. semipenetrans* which only infect young roots.

Résumé

Relations entre le développement du système radiculaire des citrus et de l'infestation par Tylenchulus semipenetrans

La croissance des racines fibreuses et le développement des populations de *Tylenchulus semipenetrans* ont été mesurés chaque mois sur 100 pieds de citrus dans un verger situé sur la côte de la Floride. Le poids des racines fibreuses dans les échantillons individuels est correlé ($p = 0{,}01$) à l'estimation visuelle de la vigueur de l'arbre. Le niveau d'infestation par les nématodes (nombre de nématodes libres dans le sol/g de racines) est en relation inverse avec la vigueur de l'arbre ($p = 0{,}01$). La croissance proportionnelle des racines fibreuses appartenant à un système radiculaire donné est également en relation inverse ($p = 0{,}05$) avec la vigueur de l'arbre. La proportion de jeunes racines dans la quantité totale de racines d'un échantillon est en moyenne de 44 % pour les arbres sains et de 72 % ($p = 0{,}05$) pour les arbres dépérissant lors des prélèvements effectués en janvier. Au cours de la présente étude les citrus adultes et vigoureux sont apparus moins sensibles au développement de *T. semipenetrans* qui n'infeste que les jeunes racines.

In several recent studies on the use of aldicarb for control of *Tylenchulus semipenetrans* Cobb in Florida citrus (Wheaton, Childers, Timmer, Duncan & Nikdel, 1985; yield response to aldicarb treatment was inversely related to response to aldicarb treatment was inversely related to overall grove yield performance. These data were consistent with the observation that the pathogenicity of *T. semipenetrans* to Florida citrus is enhanced by other forms of stress which reduce tree vigor such as suboptimal water management encountered by trees with restricted root zones caused by high water tables in many coastal groves (O'Bannon & Esser, 1985).

Variable patterns of fibrous root growth may account for some of these observations because *T. semipenetrans* infect and develop in the cortex of young primary root tissue (Cohn, 1964). If root initiation and growth is reduced in mature, nonperturbed trees, the nematode populations may be less abundant or less active on such root systems and cause less damage than on young growing trees or on trees that compensate for root damage with higher root growth rates. Citrus root initiation has been shown to be stimulated by infection by *T. semipenetrans* (Hamid, Van Gundy & Lovatt, 1985). Citrus roots may also be damaged by nonpathogenic agents such as waterlogging (Reitz & Long, 1955; Ford, 1965), and tree damage due to low temperature (Ford, 1963). Regrowth of roots following such events would provide a greater proportion of the overall root system suitable for infection and damage by *T. semipenetrans.* Understanding the influence of root growth on the suitability of the entire root system for infection by *T. semipenetrans* could influence nematode management in citrus groves.

The present paper reports fibrous root and *T. semipenetrans* population growth patterns during the period of fall root flush in a citrus grove on Florida's east coast. Differences in infestation rates between healthy and decline trees are analyzed with respect to different root growth patterns in the two groups of trees.

Materials and methods

The fibrous root densities and nematode population levels associated with individual " Valencia " orange trees on sour orange rootstock were estimated at monthly intervals. Seventy-eight trees in a grove on Florida's east coast were randomly selected and sampled in July 1985. Based on nematode population levels, some trees were replaced by new trees during the following sample period to obtain a wide range of infestation levels and the same trees were sampled each month thereafter until December 1985. Trees were thirty-eight-old, growing on single row beds of variable soil type, but predominantly loamy sand.

A single soil sample of 16 cores (30 cm × 2.5 cm diameter) was obtained from each tree each month. Cores were randomly obtained from within a circular area of 3 m radius measured from the trunk of each tree (Duncan, 1986). Samples were weighed, hand mixed, and juvenile and male *T. semipenetrans* in 50 cm^3 subsamples were extracted during 48 hr on Baermann funnels. The remaining soil was washed through a 2 mm mesh screen and fibrous roots 2.5 mm diameter were collected, weighed, and processed to recover female *T. semipenetrans* (Baines *et al.*, 1969).

All trees were subjectively rated in August for overall vigor using a scale of 1 (low vigor) to 4 (high vigor) based on tree size and canopy density. The monthly net root growth rates of trees with visual vigor ratings of 3.5 (high vigor, n = 26) were compared to growth rates of trees rated 2.5 (low vigor, n = 19) by t-tests.

Two groups of ten trees each were identified and labeled as healthy or decline based on fibrous root recovery. To reduce bias due to monthly sample error, trees in each group were chosen by standardizing the monthly fibrous root weights according to the mean monthly fibrous root recovery and summing the values for all months. On 8 January 1986, the ten trees with the highest or lowest adjusted root recoveries were sampled as described above. Fibrous roots from each tree were separated based on yellow (young) or brown (older) coloration and weighed separately.

Results

Both fibrous root and nematode densities increased during the period of the survey (Fig. 1). Fibrous roots grew in a pattern commonly characterized as the fall root flush (O'Bannon & Stokes, 1978; Bevington & Castle, 1985) and growth of soil populations of *T. semipenetrans* began later in the season in apparent response to the new

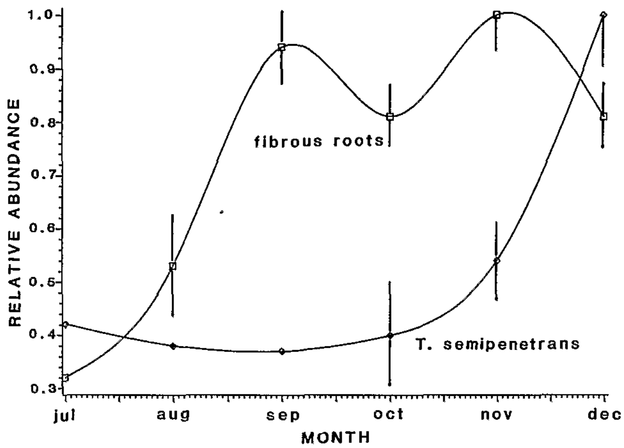

Fig. 1. Relative abundance of citrus fibrous roots (squares) and soil populations of *Tylenchulus semipenetrans* (diamonds) during the period of fall root flush.

food source. The quantity of fibrous roots in a sample was proportional (p = 0.01) to the visual rating of tree vigor (Fig. 2). August infestation rates (nematodes/g root) of *T. semipenetrans* were heaviest on trees with the lowest fibrous root densities (Fig. 3). Similar exponential decay trends were observed (p = 0.01) during each month of the survey. The magnitude of the regression slope of infestation level against the natural logarithm of sample root weight declined during the main period of root growth until September and then increased during the remainder of the survey period (Fig. 4).

The proportional fibrous root growth of individual trees was also inversely related to their initial fibrous root

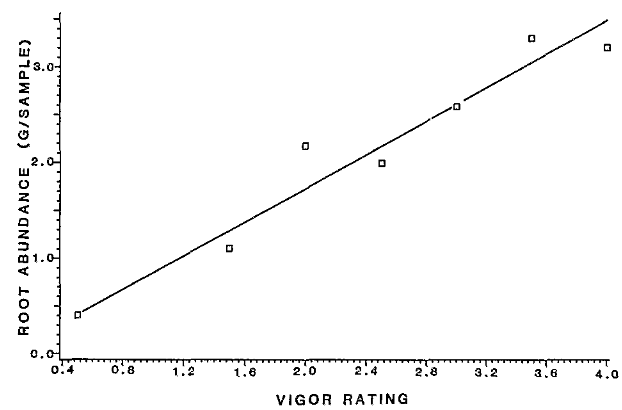

Fig. 2. The relationship in August between visual estimation (0-4 scale, 0.5 increments) of citrus tree vigor and mean fibrous root abundance in soil samples collected from a sample space of uniform area.

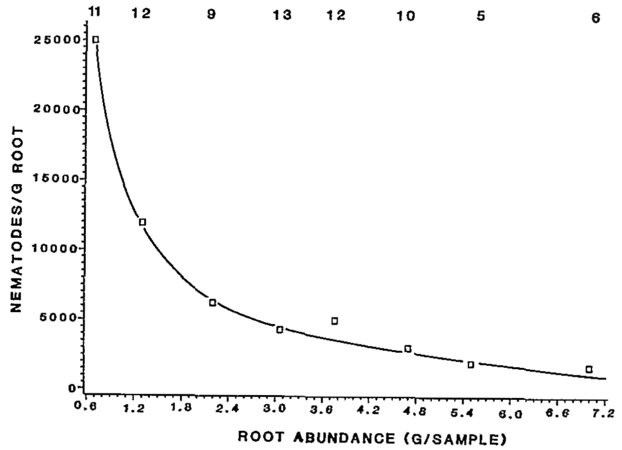

Fig. 3. The relationship between *Tylenchulus semipenetrans* infestation level/g feeder root and root abundance in soil samples collected in August from sample spaces of uniform area. Data represent mean infestation levels (Ferris, 1984) with n enumerated at top of figure.

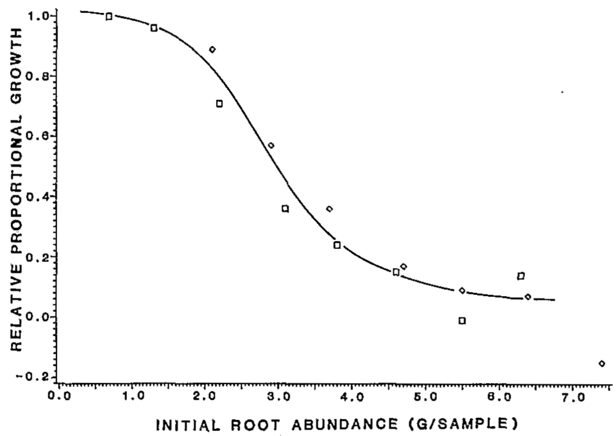

Fig. 5. Relative net feeder root growth rates during August and October as a function of root weight at the beginning of the measurement period.

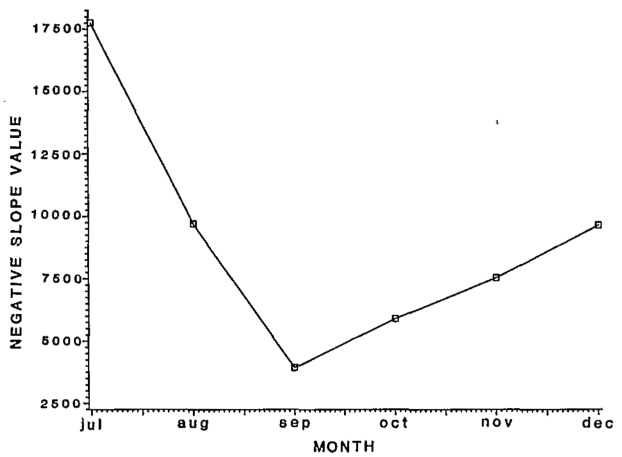

Fig. 4. Change during the fall root flush period of the magnitude of the slope of the linear regression of l_n nematode infestation level against l_n (root weight).

density. Root systems on decline trees added proportionately more to their fibrous root weight during the fall flush than did root systems of healthy trees. Mean fibrous root sample weights increased during the months of August and October and declined during September and December. The relative monthly growth rates of trees were consistent when they were blocked according to these periods of growth (Fig. 5). The net feeder root growth rates of low vigor trees were greater ($p = 0.05$) than high vigor trees during August (154 % *vs* 87 %) and October (48 % *vs* 17 %), and the rate of decline in net root weight during September was also greatest ($p = 0.05$) on low vigor trees (25 % *vs* 6 %).

Yellow roots averaged 72 % of the total sample root weights in the decline group of trees in January compared with 44 % ($p = 0.05$) in the sample from healthy trees.

Discussion

T. semipenetrans is a particularly well-adapted parasite of citrus, capable of strong population growth with only slight to moderate pathogenicity on mature host plants (Cohn, Minz & Monselise, 1965; Timmer & Davis, 1982). The diagnostic term slow decline applied to citrus disease symptoms caused by *T. semipenetrans* reflects the high degree of integration between the nematode and citrus, as do the relatively complex host-parasite etiology (Schneider & Baines, 1964; Van Gundy & Kirkpatrick, 1964; Cohn, 1965) and the narrow host range of the nematode. The most severe effects of infestation by *T. semipenetrans* on Florida citrus are generally noted under conditions of rapid growth, such as in greenhouse studies (Van Gundy & Tsao, 1963; Cohn, Feder & Mordechai, 1968), replant situations (O'Bannon & Tarjan, 1973), or under conditions that are suboptimal for root growth (O'Bannon & Esser, 1985). Groves on Florida's coastal region in which the normally deep citrus root systems are restricted within beds by high water tables often sustain root damage due to suboptimal soil moisture and are condidered to be areas in which citrus is susceptible to greater damage by *T. semipenetrans*. In contrast, *T. semipenetrans* is not considered to be as pathogenic on citrus planted in the deep sands of Florida's central « ridge » area. A similar situation is reported for *Pratylenchus brachyurus* another cortical parasite which is generally considered to be a citrus pathogen only on seedlings and young trees (O'Bannon, Tarjan & Bistline, 1973).

Differences in soil type are related to some of the above-mentioned effects because *T. semipenetrans* infection and reproduction rates are directly related to organic matter (O'Bannon, 1968) and clay content (Van Gundy, Martin & Tsao, 1964) of soils, both of which increase off of Florida's central ridge. The present survey supports the possibility that differential root growth is also an important determinant of *T. semipenetrans* infestation levels and consequently on the nematode's pathogenicity. Infestation levels (nematodes/g root) measured during this survey declined with increased tree vigor (Fig. 3). Because decline trees produced proportionally more roots during the fall flush (Fig. 5), this trend decreased each month until September and then began to reestablish itself as nematode reproduction increased in response to the availability of new fibrous roots (Fig. 4). These results imply that the proportion of young roots in a root system are an important consideration in *T. semipenetrans* management. Conditions that favor root growth such as normal seedling growth following replanting or growth in response to perturbations such as freeze damage or periodic flooding or drying of root zones may favor the buildup of *T. semipenetrans* populations. Nematode management during these periods may be particularly critical and optimal management may differ during periods of accelerated root growth from periods when growth is less pronounced.

The relationship between tree vigor and nematode infestation level measured in the present survey may represent a form of functional resistance to nematode population growth. While the suitability of individual types of tissues to population development by *T. semipenetrans* may not differ from tree to tree, individual trees may be differentially susceptible to infestation dur to the proportion of younger to older roots. This form of resistance is not simply age-related since mature trees may have different root growth rates in response to perturbation. It is most closely related to any condition which changes trees from their normal state when fully developed. Full development of a tree's growth potential in the sense that root growth becomes minimal may be influenced by spacing as well as soil nutrient and water status and the management of pests and pathogens. It is conceivable that tree spacing may influence nematode related crop losses if variable spacing changes root growth patterns.

The present results indicate the difficulty involved in measuring crop loss due to *T. semipenetrans* in citrus. The capacity for vigorous trees to support larger absolute populations (nematodes/volume soil) of *T. semipenetrans* than decline trees is logical and well-documented (Reynolds & O'Bannon, 1963; O'Bannon & Reynolds, 1967). Measuring nematode populations with respect to root density (Cohn, Minz & Monselise, 1965; Duncan, 1986), while estimating baseline tree vigor from soil samples of fibrous root density (Duncan, 1986), have been considered to help elucidate the pathogenicity of *T. semipenetrans* in field trials. However, due to differences in the proportion of old and young root tissue between individual root systems, comparing the effects of a given quantity of nematodes and roots recovered in soil samples of different trees is more complex than previously considered. Estimates of these proportional differences in root quality may be important parameters in models of the quantitative interactions between *T. semipenetrans* and citrus. Also, since root tissues of different age are differentially susceptible to parasitism by *T. semipenetrans*, it is important to better understand the relative contribution to tree vigor by roots of different development states.

In summary, infestation rates of *T. semipenetrans* on citrus were inversely related to tree vigor. This observation is consistent with recent results in which yield response to nematicide applications was inversely proportional to grove vigor. The inverse relationship between tree vigor and root-system growth rates measured in the present study may partially explain these observations and implies that nematode management practices may be most crucial at particular identifiable periods related to root development. Some of the most evident of these include tree growth following replanting in infested groves, following periods of root perturbation caused, for example, by water stress or freeze damage and prior to seasonal cycles of root growth. However, for the latter type of root growth, optimum nematode management in vigorous sections of grove may be different than in decline sections due to different rates of root growth and supports the suggestion of periodic rather than continuous nematode management (O'Bannon & Reynolds, 1967) in vigorous groves.

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