Verticillium Wilt Disease of Tomato: Influence of Inoculum Density and Root Extension Upon Disease Severity

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ABSTRACT

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Rate of infection of tomato by *Verticillium dahliae* increased with increases of inoculum density in four field experiments in which microsclerotia (MS) in naturally infected tomato plants was the inoculum. However, essentially all plants were infected by the end of the growing season regardless of inoculum density (range = 0.1–27 MS/g soil). Only slight external symptoms appeared in plants grown at inoculum densities of 0.1–9 MS/g in a friable clay loam soil in which root growth was unrestricted and plant growth otherwise was favored. Maximum loss under these conditions was about 40%, depending upon the experiment. In a sandy loam soil with a dense layer 15–60 cm below the surface however, the combination of wilt disease, restricted root growth, and poor water penetration was devastating to tomato. Maximum yield under these conditions was about 4.3×10^3 kg/ha compared with about 14×10^3 kg/ha under the more favorable growing conditions.

Additional key words: *V. albo-atrum*, soilborne pathogens, fungal disease, epidemiology.

Verticillium wilt of tomato (*Lycopersicon esculentum* Mill.) has been viewed as an unimportant disease by some workers and as extremely important by others, as discussed by Jones and Crill (6). The definitive tests of the latter, in which noninoculated and inoculated differentially tolerant cultivars were transplanted in the field, confirmed the yield reducing potential of *Verticillium dahliae* Kleb., the cause of this wilt disease. Yield reductions were 67% for cultivar Bonny Best, 38% for Walter, and 2 and 6% respectively, for Tropic and Florida MH-1. Recognition in 1971 of a strain of *V. dahliae* that induced severe disease of cultivars having the *Ve* gene for resistance (8) caused renewed interest in the disease in California (5). The new strain is called tomato strain-2 (5); it affects cultivars with the *Ve* gene like earlier prevalent populations affected older cultivars such as New Improved Pearson and Early Pak-7 (K. A. Kimble, *personal communication*). Jones and Crill (6) demonstrated the yield reducing potential of *V. dahliae* to inoculated tomato plants, but used only one inoculum density of a conidial/mycelial suspension in their tests.

To determine the rate of infection and disease severity for cotton as well as tomato in differentially infested blocks in the field, we used microsclerotia (MS) in naturally infected tomato plants as inoculum. Results for the cotton tests are published separately (2). We also studied root density in relation to infection and disease severity. Tests were made to determine whether plants with restricted root systems were more severely affected by wilt disease than those with unrestricted root systems. We became interested in mapping root systems following a report by Grimes, et al (4), which showed that root maps through depths of 150 cm accurately described water extraction by cotton and corn. For instance, plants with roots restricted by a compact subsurface layer, used little of the water in deeper layers and required more frequent irrigation than those with unrestricted root systems.

MATERIALS AND METHODS

Tests were made at two locations each in 1974 and 1975 but inoculum, except for small amounts of native inoculum, was the same at both locations (2). Soils were markedly different. Grimes et al (4) described the Hanford sandy loam soil at the Kearney Horticultural Field Station (KHFS) as "high strength" because it had a compacted layer at depths varying from 15–60 cm below the surface. Soil strength is a measure of bulk density and increases as moisture tension increases (9). It limits root extension when it offers an impedance greater than about 18 bars (4). Strength of the dense layer at KHFS ranges up to 30 bars. In contrast, West Side Field Station (WSFS) soil was homogeneously of low strength to a considerable depth and offered little impedance to root growth (4). We followed the procedure by Newman (7), as modified by Grimes, et al (4), to determine root length. Briefly, root segments are washed from duplicate 50-g soil samples dispersed with 1% sodium hexametaphosphate. They are decanted into a 15-cm Büchner-type funnel and the filter paper is removed and sandwiched between Plexiglas sheets. One sheet was etched with 10 mm squares. Root segments crossing one or more lines in 20 random squares were counted and those data formed the basis for calculating centimeters of roots per cubic centimeter of soil.

Tomato cultivar Early Pak-7 was used in all tests; it is intolerant of the *V. dahliae* populations prevalent in California soils, including the pathogenic type named Tomato strain-2 recently discovered by Hall and Kimble (5). Plots were planted in early April and mature fruit were hand harvested once in late August to late September. Sunburned fruit were counted separately in both 1974 and 1975.

Other more general experimental procedures are described in the preceding paper (2).

RESULTS AND DISCUSSION

Influence of soils on root development. Tomato plants grown in the high-strength soil at KHFS produced more roots in the surface 30 cm than those grown in the low-strength soil at WSFS. Root lengths were similar at the 30–60 cm depth at both locations, but at greater depths, root length was always greater in the low-strength soil (Fig. 1). Perhaps of more importance, root lengths were similar through 90 cm in the low-strength soil whereas root lengths diminished at each 30 cm increment of depth in the high-strength soil (Fig. 1).

Inoculum density and infection. Amounts of infection generally were low through mid July, regardless of inoculum density. Data for the 1975 WSFS test (Fig. 2) are typical of all four tests. We found that tomato, like cotton (2), had little infection (based upon isolation results) during the first 3 mo of the growing season. Thereafter, rates of infection varied with inoculum density, with differences between inoculum densities being greatest 1–1.5 mo before harvest. By harvest, however, essentially all plants were infected, regardless of inoculum density (Fig. 2). Tomato cultivar

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Early Pak-7 resembled the cotton cultivars Acala SJ-4 and Acala SJ-5 (2), that is, essentially all plants became infected at very low inoculum densities. However, the tomato cultivar was unlike cultivar Acala SJ-2 which required an inoculum density of four or more microsclerotia per gram of soil before essentially all plants became infected (1). Inoculum density had a variable quantitative effect due to fungistasis of MS in soil, as discussed in other reports (1,2), that is, the same amount of inoculum resulted in different amounts of infection, depending upon the year and location of tests.

Inoculum density and disease severity. *Symptomatology.* In both years, plants in the KHFS high-strength soil grew well and were dark green until early August when first fruit ripened. Rapid deterioration of vines followed, and most plants were dying by early September. Symptoms were similar at all inoculum densities.

Plants grown in the low-strength clay loam soil of WSFS were larger and thriftier in appearance than those grown in the high-strength soil of KHFS in both 1974 and 1975. Except for occasional yellowed leaflets, plants grown at inoculum densities of nine or fewer MS/g soil were free from external symptoms although essentially all plants were infected, as discussed earlier. At the highest inoculum densities (24 MS/g in 1974 and 17 MS/g in 1975), however, plants were yellow-green by 1 August. In addition to yellowing, there also was much killing of basal leaves.

Sunburn of fruit was especially common at KHFS, where there was essentially total collapse of vines. However, sunburn was not preferentially present at higher inoculum densities.

Yield. Fruit yields at WSFS were greater in 1974 than in 1975 but yield reductions caused by wilt disease also were greater in 1974 than in 1975. In 1974, yield losses for 2.6, 4.7, and 23.9 MS/g soil were, respectively, 27, 32, and 40% ($P = 0.05$), compared to the lowest inoculum density (1.9 MS/g soil) (Fig. 3A). On the other hand, in 1975, yields at 0.1 and 2.0 MS/g soil were similar ($P = 0.05$), with 8% and 25% reductions in yield, respectively, for 9.1 and 17.1 MS/g soil (Fig. 3B).

These observations both support and contradict the view of Chupp and Sherf (3) who reported that infected plants could be externally symptomless. Symptomless plants can, depending upon the growing season, exhibit reduced yield (Fig. 3A). Time of infection, as with other systemic diseases, probably is important in this regard. Moreover, the rate of development of infection was greater in 1974 than in 1975. In 1974, maximum infection about 20 July was 32% compared with 11% at the same time in 1975. Similarly, 70% or more of plants, regardless of inoculum density were infected by mid August in 1974. In 1975, however, only plots with the greatest inoculum density had more than 70% infected plants by mid-August (Fig. 2).

Data for KHFS (Fig. 3C, D) are more difficult to interpret than

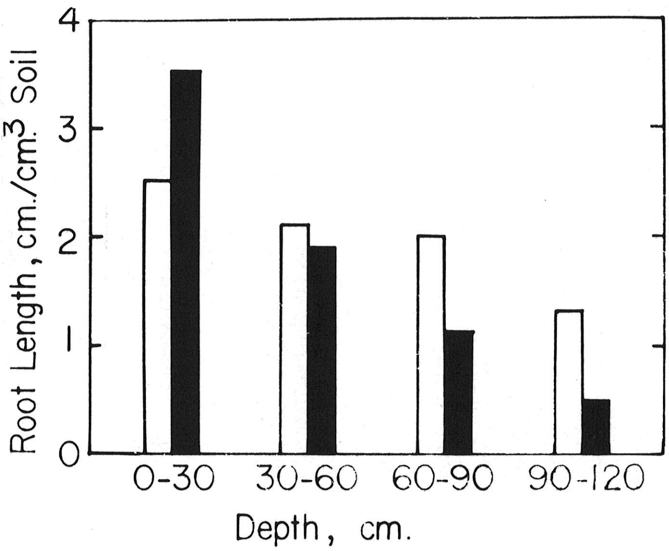

Fig. 1. Differential root development of tomato cultivar Early Pak-7 in a homogeneous friable clay loam soil (open bars) and in a sandy loam soil with a root-restricting dense layer 15–60 cm below the surface.

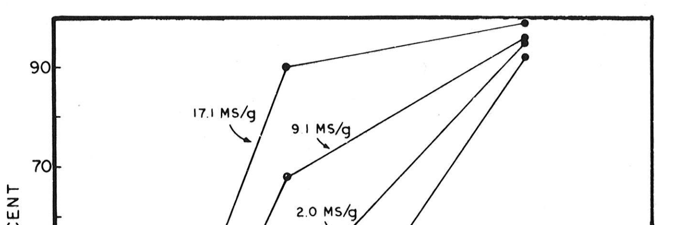

Fig. 2. Rates of infection of tomato by *Verticillium dahliae* at four inoculum densities in a deep friable clay loam soil at West Side Field Station, 1975.

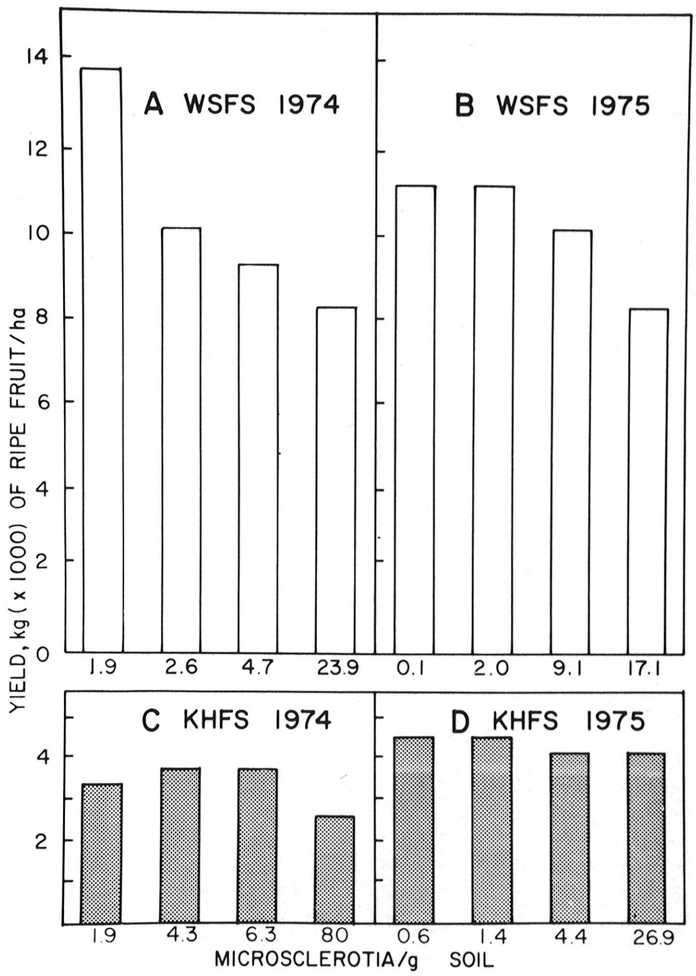

Fig. 3. Yields of tomato cultivar Early Pak-7 exposed to ranges of *Verticillium dahliae* inocula in California at the West Side Field Station (WSFS) (homogeneous, deep, friable clay loam) in **A)** 1974 and **B)** 1975 and at the Kearney Horticultural Field Station (KHFS) (sandy loam soil with a compacted layer 15–60 cm below the surface) in **C)** 1974 and **D)** 1975.

those for WSFS. Yields were poor, regardless of inoculum density at KHFS, and never exceeded 4.5×10^3 kg/ha. The poor performance of plants at KHFS was probably due to the cumulative effects of poor root distribution (Fig. 1), poor water penetration because of the subsurface dense layer, and wilt disease. Whether these parameters might be synergistic is not known since a disease-free treatment was absent. However, tomato appears to be quite tolerant of wilt disease (Fig. 3A, B) provided other factors such as root development (Fig. 1) are favorable for plant growth.

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