Hydraulic Conductivity of Stem Internodes Related to Resistance of American Elms to Ceratocystis ulmi

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ABSTRACT

Segments of healthy internodes 3 or 4 years old from 32- to 36-year-old American elms previously selected as resistant to *Ceratocystis ulmi*, had significantly less capacity to conduct water than comparable segments from susceptible trees. Compared with noninoculated branches, water conductance 11 days after inoculation with *C. ulmi* was reduced 27% and 66% in resistant and susceptible trees, respectively. Ramets 2- to 4-year-old, of clones from resistant and susceptible trees showed no consistent differences in water conductance before or after inoculation with *C. ulmi*. Xylem pressure potentials of healthy clonal stock and clone-parent trees were not related to resistance.

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American elms resistant to *Ceratocystis ulmi* (Buis.) C. Moreau are capable of tolerating systemic Dutch elm disease (7), and of localizing or limiting internal spread of branch infections (8). Resistance is associated with subnormal dimensions of xylem vessels (9), suggesting the possibility of differences in water relations of resistant and susceptible trees. Therefore, we studied the relative water conductivity of stem segments and xylem pressure potentials of shoots from resistant and susceptible trees, and from ramets propagated from them.

Three types of American elm material were used: (i) clone-parent trees previously identified (7) as resistant or susceptible to *C. ulmi*; (ii) 2-year-old potted ramets (individual plants within clones) propagated from the clone-parents by cuttings; and (iii) similarly propagated 4-year-old ramets, 1.0 to 1.5 m tall, in a nursery. The susceptible clone-parents were sprouts from stumps of trees top-killed by Dutch elm disease 6 to 7 years earlier. The resistant trees were 32 to 36 years old.

Inoculum of *C. ulmi* was prepared by combining equal numbers of bud cells, determined with a haemocytometer, from each of four isolates grown in malt extract shake culture for 4 to 7 days at 20 to 25 C and diluting with sterile water to the desired concentration. Trees were inoculated by delivering one drop of inoculum (average volume 7 μliters) and then two drops of sterile water via a blunt-tip 0.40-mm diameter (26-gauge) hypodermic needle into a hole 1.6×4 mm drilled through the bark into the xylem. Controls received three drops of sterile water. Mainstem inoculations were made on potted trees; branch inoculations were made on clone-parent and nursery trees. Branches were prepared for inoculation by removing twigs for 30 cm above and below the inoculation point one day before inoculation. This insured that the initial spread of propagules of *C. ulmi* would occur entirely within the main axis of the branch rather than partially into side shoots. Points of inoculation were at least 30 cm distal to branch junctions, and the inoculated internodes were 3 or 4 years old. Inoculations were performed on sunny afternoons. Potted trees were inoculated while the soil mixture was near field capacity.

Xylem pressure potential (ψ) of shoots was measured by the pressure-chamber technique (5) with a commercially available instrument (PMS Instruments, Corvallis, Ore.).

For measurements of water conductivity of stem segments, a reservoir of distilled water was placed in the same pressure chamber and water under 3.4 bars pressure was forced through 10.0 cm segments as previously described (8) until 10 ml were collected. Relative conductivity (RC) was calculated by Heine's formula (2) except that the viscosity term was deleted. Thus:

$$RC = \frac{V}{TALP}$$

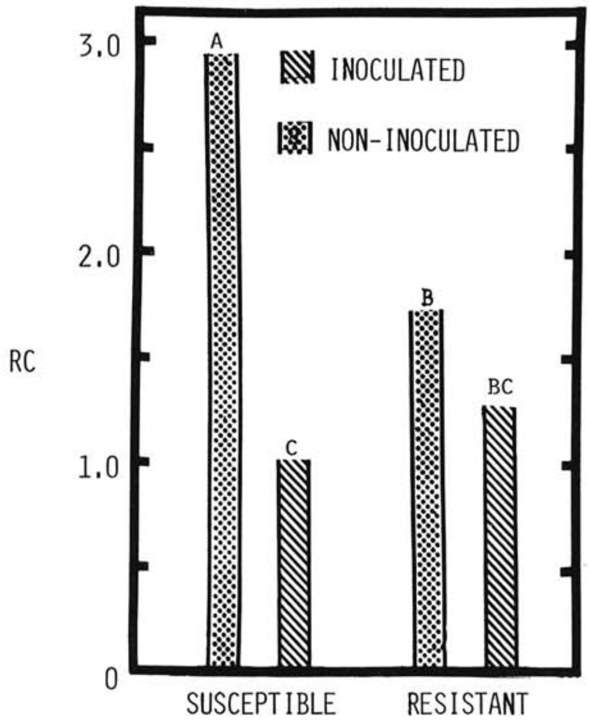

Fig. 1. Relative water conductivity (RC) of branch segments of American elms resistant and susceptible to *Ceratocystis ulmi* as influenced by inoculation with *C. ulmi*. RC = time (minutes) required to pass 10 ml of water at a pressure of 3.4 bars through a 10-cm length of internode having unit cross-sectional area. Bars topped by any common letter are not significantly different, $P = 0.05$.

where V is the volume (ml) of water collected, T is time for collection in minutes, A is the average cross-sectional area of the xylem in cm^2, L is length of the segment in centimeters, and P is pressure in bars.

RESULTS AND CONCLUSIONS.—Psi (ψ)-values of healthy shoots from five susceptible and five resistant clone-parent trees ranged from −9.5 to −21.2 bars during a clear August afternoon. No significant difference was detected between the resistant and susceptible groups. Variability in ψ (standard deviation = 3.0 bars) was associated with height of the shoot above ground, the time when the shoot was severed, and the degree of exposure to sun and wind. The ψ-values became more negative with increasing height and greater exposure.

An experiment was done in which three branches on each of 10 resistant and 10 susceptible clone-parent trees were each inoculated in early August with about 2×10^3 cells of *C. ulmi*; one control branch per tree received sterile water. ψ of each branch was determined between 0530 and 0845 hours, 6 and 11 days after inoculation, during which time no external symptoms had developed. Branches were then harvested for determination of RC of a segment 21-31 cm above the point of inoculation on each branch.

The data confirmed the lack of difference in ψ between resistant and susceptible nonsymptomatic trees, but showed that the resistant and susceptible groups differed in RC of healthy branches and in impairment of RC after inoculation. Mean ψ-values varied only from −3.6 to −4.6 bars without relation to inoculation or to resistance or susceptibility of the trees. However, control branches from susceptible trees had a significantly ($P = 0.05$) higher mean RC value (2.95) than controls from resistant trees (1.74). The mean RC values of inoculated branches of susceptible and resistant trees were 1.01 and 1.27, respectively. These values represented reductions of 66% and 27% from the comparable controls. The 66% reduction was significant at $P = 0.01$ (Fig. 1).

Nursery ramets were used in a similar experiment. One branch of each of three ramets from two resistant, and three susceptible, trees was inoculated with *C. ulmi* in early August; one branch of a fourth ramet of each clone received sterile water. In a third clone from a resistant tree, of which only two ramets were available, one branch of one tree was inoculated with *C. ulmi*, while one branch of the other tree received distilled water. Measurements of ψ and RC 11 days later revealed no significant differences between clones from resistant and susceptible parents. All ψ-values were uniformly low (−1.3 to −1.9 bars) and RC showed more variation within than among clones. Another experiment with potted ramets gave the same result.

In common with previous studies (6, 8), the results of this one emphasized that clonal differences in resistance of American elms to *C. ulmi* may be indistinct or absent in small ramets although clearly expressed in clone-parent trees.

The lack of relationship of ψ of healthy trees to resistance or susceptibility to *C. ulmi*, suggests that no characteristic differences in internal water balance exist between resistant and susceptible trees until after Dutch elm disease causes xylem dysfunction (decrease in RC) in shoots and twigs. Then water stress may become more acute and lead to more extensive wilting, or yellowing and abscission, of leaves in susceptible than in resistant trees.

RC is influenced by anatomy of the xylem. Pope (4), Elgersma (1), Mc Nabb et al. (3) and Sinclair et al. (9) have found that in comparison to susceptible trees, resistant trees have vessels of smaller mean diameter, fewer springwood vessels, larger proportions of relatively short vessels, and fewer contiguous vessels in transverse sections. One would thus expect less water conducting capacity in stem segments from resistant trees. Elgersma (1) reported such a relationship for resistant and susceptible clones of *U. hollandica*.

Because of the greater water conducting capacity of small branches of susceptible trees, passive spread of propagules of *U. ulmi* when first introduced into their sap stream might be more rapid and extensive than in resistant trees. This could contribute to the greater effect of Dutch elm disease on RC in susceptible trees. Conversely, the smaller capacity for water movement in resistant trees may retard passive spread of propagules, and thus play a contributory role in localization of infection. Localization, in any case, would preserve part of the water-conducting capacity of the xylem, as indicated by the nonsignificant decrease in RC of resistant trees after inoculation in this study.

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