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Length and diameter of xylem vessels as factors in resistance of elms to Ceratocystis ulmi

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Abstract

Conductivity of the vascular system of 2-year-old shoots as regards air and water was higher in susceptible than in resistant elms. The xylem vessels of resistant elms were relatively shorter and the percentage of short vessels was greater than in susceptible elms. The percentage of vessels with a large diameter was smaller in resistant elms than in susceptible ones. These results might explain the limited spreading of the spores in the new annual ring of resistant elms.

Data of resistance mechanisms of elms to *Ceratocystis ulmi* (Buisman) C. Moreau are scarce. Pope (1943) found some anatomical differences between the susceptible *Ulmus americana* L. and the resistant *U. pumila.* In the latter the vessels of the springwood were smaller than in the former. Frequently in *U. pumila* only one row of these vessels was found. In this elm species formation of summerwood took place earlier in the growing season than in *U. americana.* In the latter the amount of branching between different vessel bundles, both radially and tangentially appeared to be more frequent than in *U. pumila,* which might result in a more extensive spreading of the spores of *C. ulmi* after infection in *U. americana* than in *U. pumila.* In both species, however, the summerwood was characterized by a lack of interconnections between vessels, limiting the distribution of the spores.

More recently Elgersma (1967) reported that the resistance in *U. hollandica* cl. 390 was due to a limited spreading of the fungus in the vascular system. As rate of multiplication of spores in the vessels of susceptible and resistant elms appeared to be similar during the first 3 days after inoculation, anti- fungal substances did not seem to be a factor in resistance. It was suggested that gum and tylose formation might occlude the infected vessels faster in resistant elms than in susceptible ones. By this occlusion transport of spores is hampered. No difference in rate of blockage of vessels, however, could be traced between susceptible and resistant elms during the first 3 days after inoculation examining fixed plant material (Elgersma, 1969). So a faster blockade of vessels as resistance mechanism appears not to be evident.

Another possibility may be, as was supposed at the First International Symposium on Dutch elm disease in 1968 (Elgersma, in press), that differences in anatomical structure such as vessel length and diameter might be important in limiting the transport of the spores in resistant elms. In clones with relatively short vessels the fungus has to penetrate more mechanical barriers than in clones with relatively long vessels, thus giving the plants the opportunity to produce an effective barrier of gums and tyloses in front of the fungus, thus restricting the infection. Moreover the spores will earlier be caught by gums and tyloses in clones with vessels of relatively small diameter, than in clones with vessels of relatively large diameter. A factor which might as well play a part in transport of the spores of *C. ulmi*.

In this study this hypothesis was tested. From the susceptible elms, *U. hollandica* 'Belgica' and *U. americana* and from the resistant ones *U. hollandica* cl. 296, cl. 390, cl. 405 and cl. 496, ten 2-year-old shoots of a length of 20 cm and of about the same diameter were cut during the susceptible period. Plant material from cl. 405, cl. 496 and one set of cl. 'Belgica' were obtained from the nursery of the Forest Experiment Station "De Dorschkamp" at Wageningen. The other clones used were grown in the nursery of the Phytopathological Laboratory "Willie Commelin Scholten" at Baarn. Because of differences in origin data from clones grown at Wageningen could not be compared with those from the other clones.

Conductivity of the vascular system of the shoot pieces as regards air and water was determined. 250 ml of air at a pressure of 1080 g/cm^2 was pressed through the shoot pieces, and 2 ml of a safranin solution (50 ppm) was sucked through by means of a vacuum pump. The time needed for these treatments could be considered as a measure of conductivity. A safranin solution was used in order to trace the vessels through which water was sucked. Table 1 shows that conductivity as regards air as well as safranin solution was higher in susceptible than in resistant clones. (significant, Wilcoxon's two sample test; $\alpha = 0.01$). From the fact that only part of the total number of large vessels in cross sections showed coloured walls and that air could not be pressed through terminals walls (Greenidge, 1952) it was assumed that vessels coloured by the safranin solution were open throughout the shoot pieces. As the total number of open vessels and the size of their diameter might be of influence on conductivity all safranin-coloured vessels were counted in cross section. They were found in the new annual ring; hardly any were present in the older xylem. The coloured

Table 1. Average conductivity of 10 shoot pieces of susceptible (S) and resistant (R) clones measured in seconds needed for pressing through 250 ml of air at a pressure of 1080 g/cm^2 or sucking through 2 ml of safranin solution.

Clone	Air	Safranin solution
S *U. hollandica* 'Belgica'	71	37
S *U. americana*	82	36
R *U. hollandica* 390	193	88
R *U. hollandica* 296	222	82
S *U. hollandica* 'Belgica'*	108	58**
R *U. hollandica* 405*	242	104**
R *U. hollandica* 496*	179	93

* Obtained from the nursery "De Dorschkamp" at Wageningen.

** Significant, Wilcoxon's two sample test; $\alpha = 0.05$

Tabel 1. Gemiddelde geleidbaarheid van 10 scheuten van vatbare en resistente klonen gemeten in seconden nodig om 250 ml lucht met een druk van 1080 g/cm^2 door te persen of om 2 ml safranine oplossing door te zuigen.

Table 2. Average number of vessels large than 40 μm in diameter in 10 shoot pieces, 20 cm in length, cut from susceptible (S) and resistant (R) clones and through which 2 ml of safranin solution (50 ppm), was sucked. Large vessels: over 65 μm in diameter.

	Number of vessels			
	total	coloured	large coloured	large
U. hollandica 'Belgica'	S 372 (100)	118[a] (32)[a]	98[a] (26)[a]	227 (61)[a,b]
U. americana	S 309 (100)	89[a] (29)[a]	76[a] (25)[a]	177 (57)[a,d]
U. hollandica cl. 390	R 547 (100)	70[a] (13)[a]	53[a] (10)[a]	256 (47)[b,d]
U. hollandica cl. 296	R 597 (100)	60[a] (10)[a]	45[a] (8)[a]	192 (32)[a]
U. hollandica 'Belgica'*	S 460 (100)	94[a,c] (20)[a,b]	77[a] (17)[a]	229 (50)[a,c]
U. hollandica cl. 405*	R 483 (100)	46[a] (10)[a]	38[a] (8)[a]	144 (30)[a]
U. hollandica cl. 496*	R 459 (100)	70[c] (15)[b]	52[a] (11)[a]	183 (40)[c]

* Obtained from the nursery "De Dorschkamp" at Wageningen.
Bracketed figures indicate percentage of total number of vessels. To compare susceptible clones to resistant ones the indications a, b, c and d were used for the different levels of significance: $\alpha = 0.01, 0.02, 0.05$ and 0.10, respectively (Wilcoxon's two sample test).

Tabel 2. Gemiddelde aantal vaten groter dan 40 μm in diameter in 10 scheuten van 20 cm lengte, afkomstig van vatbare en resistente klonen en waardoor 2 ml safranine oplossing (50 ppm) was heen gezogen. Grote vaten: groter dan 65 μm in diameter.

vessels were divided into two groups; those from 40–65 μm in diameter and those larger than 65 μm, as vessels smaller than 40 μm in diameter did not show any trace of safranin. In all cases the total number of coloured vessels was greater in the susceptible clones than in the resistant ones (Table 2), which may explain the higher conductivity in the former. It appeared that nearly all coloured vessels were also vessels with a large diameter.

The ratio between the number of open vessels (coloured ones) and the total number of vessels found in susceptible and resistant clones is indicative for their relative vessel length. It appeared that the percentage of the total number of coloured vessels and also of the large coloured ones was higher in susceptible than in resistant clones. This indicates that the percentage of long vessels in susceptible clones is greater than in resistant ones. On the other hand the total amount of vessels in resistant clones was equal to the total number in susceptible clones or even exceeded it, but the open or long vessels were significantly smaller in number. So the relative length of the vessels is greater in susceptible clones than in resistant ones; a factor favouring a rapid transport of spores.

The ratio between large and small vessels might be important in disease development since large vessels will not be occluded as rapidly by gums and tyloses as small ones; thus providing a more extensive distribution of spores in the vascular system. In cross sections all xylem vessels larger than 40 μm were measured and divided into the two groups mentioned above (Table 2). The percentage of vessels with a large diameter was greater in susceptible clones than in resistant ones, which can also be considered as a factor promoting the transport of spores and therefore influencing the disease severity. Another important factor in resistance to *C. ulmi* might be the number of anastomoses providing tangential and radial transport as reported by Pope (1943).

Samenvatting

Lengte en diameter van de houtvaten als resistentiefactoren bij iepen tegen aantasting door Ceratocystis ulmi

Tweejarige scheuten van resistente iepen bleken lucht en water minder snel door te laten dan vergelijkbare scheuten van vatbare iepen. De vaten bij resistente iepen waren relatief kort en het percentage korte vaten was groter dan bij vatbare iepen. Het percentage grote vaten was kleiner bij resistente iepen dan bij vatbare. Dit zou een verklaring kunnen zijn voor de relatief geringe verspreiding van de sporen in de nieuwe jaarring van de resistente iepen.

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