# Influence of Specific Combining Ability and Sex of Gametes on Transmission of *Ceratocystis ulmi* Resistance in *Ulmus*

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## ABSTRACT

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When used as male or female parents, single selections of *Ulmus glabra, U. carpinifolia, U. pumila, U. rubra, U. parvifolia, U. japonica,* and a Netherland's selection, N248 (*U. wallichiana* × *U. carpinifolia*) varied in ability to transmit moderate resistance to Dutch elm disease and rapid growth rate to their progeny. Symptoms among progenies varied more 4 and 12 wk after inoculation than after 56. Significant interaction (specific combining ability) occurred between parents in giving slight to moderate resistance to offspring. As male parents, *U. carpinifolia* 61 transmitted significantly more resistance than did *U. glabra* 72, when *U. glabra* 19 served as a female parent. With *U. pumila* 8 as the female parent, however, *U. glabra* 72 was a significantly better pollen parent than *U. carpinifolia* 61. *Ulmus pumila* 8 gave much more resistance as a female parent than as a male parent when crossed with *U. glabra* 72. Clones of *U. pumila* and *U. parvifolia* were about equally effective as male parents in increasing resistance to Dutch elm disease in progenies from several female parents.

*Additional key words*: disease resistance, selection, tree breeding, variation.

The widespread destruction of elms by Dutch elm disease has encouraged selection and breeding programs for resistance in the Netherlands (2), Wisconsin (3,4,9), the District of Columbia (5,6), New York (8), and Ohio (1,11–13). Wide intraspecific and interspecific variation has been found in the resistance to the causal fungus, *Ceratocystis ulmi* (Buis.) C. Moreau. Generally, Asiatic elms are most resistant, elm species from America are least resistant, and European elm species are intermediate (10).

In earlier work, significant differences were found in height, stem diameter, leaf length and width, earliness of spring flushing, and germination among progenies resulting from hybridizing different male clones with a single female parent or from different females crossed with one male (11). The objective of this study was to determine the transmission of resistance and of growth rate by various clones of European, American, and Asiatic elm species. More specifically, information was sought on how the sex of parents and the interaction between parents might influence transmission of resistance to progenies.

## MATERIALS AND METHODS

Clones (single trees, ortets) used as parents in the hybridizations were: *Ulmus glabra* Huds., USDA Nos. 19 and 72; *U. carpinifolia* Gleditsch, USDA Nos. 61 and 71; *U. pumila* L., USDA Nos. 8 and 13; *U. rubra* Muhl., USDA No. 64; *U. parvifolia* Jacq., USDA No. 76; *U. japonica* (Rehd.) Sarg. USDA No. 1; and a Netherlands' selection, N248 (*U. wallichiana* Planch. × *U. carpinifolia*). All of these clones except *U. glabra* 19 and N248 had been inoculated at least once. All those inoculated showed less than 15% of the crown with dieback and wilting 6 wk and again 1 yr after inoculation, and they were judged to be resistant (12). Unfortunately, records on seedling sources of the USDA clones are not available; seed and nursery origins are unknown. According to Hans Heybroek (*personal communication*), leader of the elm breeding program in the Netherlands (2), clone N248 is resistant. Dr. L. R. Schreiber had selected *U. glabra* 19 for horticultural desirability, not for resistance to Dutch elm disease.

Controlled hybridizations were made in the spring of 1971 by methods described previously (11). Seedlings resulting from crosses were transplanted to a site (Morley silt loam) in a randomized block design, with at least three plots per hybrid combination. Each plot contained one to five trees. Heights were measured in September 1973. On 22 May 1974, all seedlings were inoculated through a wound in the trunk with a mixed spore suspension of aggressive (Colorado and North Dakota) and nonaggressive (Ohio, Massachusetts, and North Carolina) isolates of *C. ulmi* (7).

The percentage of crown showing dieback and wilting (percent symptoms) was estimated 4 wk after inoculation. Percentage of the central leader showing dieback was estimated 12 and 56 wk after inoculation.

## RESULTS

Selections differed widely in ability to transmit rapid growth and disease resistance as male parents (Table 1). Variability of symptoms among progenies generally was greater 4 and 12 wk after *C. ulmi* inoculation than after 56 wk.

Significant interaction occurred between parents in transmission of resistance. The amount of resistance given by the male parent often depended on which female parent was used and vice versa. For example, *U. carpinifolia* 61 was a better male parent for transmitting moderate resistance than was *U. glabra* 72 when *U. glabra* 19 was the female parent. When *U. pumila* 8 was the female parent, however, *U. glabra* 72 was a significantly better male parent than *U. carpinifolia* 61. Similarly, *U. glabra* 72 and *U. parvifolia* 76 as males were equal in transmission of resistance to *U. pumila* 8 progeny, but they differed widely in their effectiveness as pollen parents on *U. carpinifolia* 61.

The progenies from reciprocal crosses between *U. pumila* 8 and *U. glabra* 72 differed in the degree of symptom expression. Symptoms were less severe when *U. pumila* 8 was the female rather than the male parent.

With *U. glabra* 72 as a female parent, *U. carpinifolia* 61 and *U. pumila* 8 were significantly better in transmitting rapid growth rate than were *U. rubra* 64 and *U. japonica* 1 (Table 1). *U. pumila* 8 as a male gave more resistance to its progeny than did *U. carpinifolia* 61 and *U. japonica* 1 at 4 wk after inoculation. By 12 and 56 wk after inoculation, however, differences among progenies from different males were not significant. Only 17% of seedlings from *U. glabra* 72 × *U. pumila* 8 had 25% or less symptoms 56 wk after inoculation.

Offspring of *U. glabra* 19 (as female) also varied in height and symptoms depending on the male parent. When this clone was hybridized with *U. carpinifolia* 61 (as male), hybrid vigor in height

TABLE 1. Variation in resistance to Dutch elm disease and in average height among 3-yr-old Ulmus hybrids[y]

| Female parent | | Male parent | No. of trees | Av. height September 1973 (cm) | Av. symptoms (%) after inoculation[z] | | | Trees with no more than 25% symptoms (%) |
|---|---|---|---|---|---|---|---|---|
| | | | | | 4 wk | 12 wk | 56 wk | 56 wk |
| *U. glabra* 72 | × | *U. carpinifolia* 61 | 14 | 273 a | 54 b | 84 a | 95 a | 0 |
| | × | *U. pumila* 8 | 18 | 259 a | 38 c | 60 b | 80 a | 17 |
| | × | *U. rubra* 64 | 16 | 186 b | 40 bc | 79 ab | 92 a | 0 |
| | × | *U. japonica* 1 | 4 | 216 b | 89 a | 95 a | 93 a | 0 |
| *U. glabra* 19 | × | *U. carpinifolia* 61 | 19 | 327 a | 42 b | 48 b | 64 a | 12 |
| | × | *U. glabra* 72 | 16 | 243 b | 65 a | 95 a | 100 b | 0 |
| | × | *U. pumila* 8 | 4 | 143 c | 32 b | 30 b | 66 a | 0 |
| *U. carpinifolia* 61 | × | *U. parvifolia* 76 | 12 | 175 cd | 23 b | 29 b | 34 c | 50 |
| | × | *U. glabra* 19 | 11 | 239 ab | 34 a | 61 a | 58 abc | 18 |
| | × | *U. glabra* 72 | 10 | 265 a | 47 a | 66 a | 76 a | 10 |
| | × | *U. pumila* 8 | 18 | 135 d | 26 b | 22 b | 44 bc | 33 |
| | × | self | 5 | 207 bc | 49 a | 33 b | 69 ab | 17 |
| *U. carpinifolia* 71 | × | *U. carpinifolia* 61 | 3 | 124 a | 22 b | 78 a | 72 a | 33 |
| | × | *U. rubra* 64 | 11 | 220 b | 38 a | 59 a | 92 a | 0 |
| *U. pumila* 8 | × | *U. parvifolia* 76 | 16 | 221 a | 27 b | 17 a | 30 b | 72 |
| | × | *U. carpinifolia* 61 | 17 | 173 b | 26 b | 28 a | 62 a | 23 |
| | × | *U. glabra* 19 | 5 | 229 b | 35 b | 15 a | 50 ab | 33 |
| | × | *U. glabra* 72 | 8 | 228 a | 24 b | 15 a | 31 b | 62 |
| | × | N248 | 18 | 220 a | 32 b | 30 a | 34 ab | 67 |
| | × | *U. pumila* 13 | 4 | 182 b | 6 a | 11 a | 40 ab | 60 |
| *U. pumila* 13 | × | *U. pumila* 8 | 19 | 228 a | 39 a | 29 a | 36 a | 63 |
| | × | self | 15 | 182 b | 28 a | 25 a | 42 a | 53 |

[y]All trees were inoculated on 22 May 1974.
[z]Values followed by the same letter in each column for progeny of each female parent are not significantly different at the 5% level by Duncan's new multiple range test. Percentage of the crown showing dieback and wilting represents percent symptoms 4 wk after inoculation. Percentage of the central leader showing dieback represents symptoms 12 and 56 wk after inoculation.

growth (327 cm) resulted (Table 1). In contrast, *U. pumila* 8 as a male gave very poor growth (only 143 cm). Both *U. carpinifolia* 61 and *U. pumila* 8 were superior to *U. glabra* 72 in transmitting disease resistance.

As a female, *U. carpinifolia* 61 more effectively transmitted resistance than did *U. glabra* 72 and *U. glabra* 19 (Table 1). Height and disease symptoms differed significantly among the progenies of the male parents used to pollinate it. Both *U. glabra* clones transmitted the fastest growth potential and the least resistance. *U. parvifolia* 76 and *U. pumila* 8 as males functioned most effectively in increasing resistance, but symptoms on their progenies were more severe after 56 wk than after 12 wk. After 56 wk, only one-half of the *U. carpinifolia* 61 × *U. parvifolia* seedlings and only one-third of the *U. carpinifolia* 61 × *U. pumila* 8 seedlings averaged 25% or less expression of symptoms.

With *U. pumila* 8 as a female parent, *U. pumila* 13 was the best male parent after 4 wk. Progenies of the different male parents did not differ significantly after 12 wk (Table 1). Significant differences in symptoms appeared again after 56 wk, when progenies from *U. carpinifolia* 61 and from *U. glabra* 19 showed the most symptoms and lowest percentage of trees with 25% symptoms or less. Progeny from crosses with *U. parvifolia* 76, *U. glabra* 72, *U. pumila* 13, and N248 showed good resistance.

## DISCUSSION

The relatively high symptom expression of most progenies probably is an overestimate of their true natural susceptibility. Trees were inoculated in the main stem. This insured rapid movement of *C. ulmi*, but it was probably excessively harsh treatment compared with natural inoculation by beetles feeding in twig crotches.

Because interaction between parents influenced resistance of progenies, future breeding should concentrate on specific combining ability. The cross *U. glabra* 19 × *U. carpinifolia* 61 yielded relatively few seedlings with low symptom expression, but these few were rapid growers and symmetrical and desirable in form. These are being propagated and will be further tested for resistance in a seasonal susceptibility test (12), followed by outplanting and inoculation in different geographic areas.

For transmission of resistance, *U. pumila* 8 functioned more effectively as a female than as a male parent. Maternal inheritance of resistance may be present, but further crosses are needed to test this observation fully.

Santamour (6) suggested the use of *U. parvifolia* instead of *U. pumila* as a source of genes for Dutch elm disease resistance. We found that the clones of *U. pumila* and *U. parvifolia* were about equal in giving resistance to progeny.

*U. glabra* 19 is an attractive tree with superb form. It has never been inoculated for fear of losing it to Dutch elm disease. *U. glabra* 72 has been inoculated and has proved to be resistant. In this study, these *U. glabra* clones appeared about equal in transmitting susceptibility to Dutch elm disease.

Most of the parents of progenies in this study appear to be equally resistant phenotypes, but very few effectively transmitted good resistance to Dutch elm disease. As shown earlier with other clones (13) and again here, clonal resistance is not necessarily correlated with the ability to transmit that resistance to seedling progenies.

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