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Variation in Growth and Response to *Ophiostoma ulmi* among Advanced-Generation Progenies and Clones of Elms¹

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Abstract

Controlled pollinations between five disease-tolerant elm (*Ulmus* L.) clones (Number 970, 'Urban', and clones that were later named 'Homestead', 'Pioneer', and 'Prospector') yielded 686 seedlings. Various crosses produced from zero to over 90 seedlings. Only one of four female parents produced any viable selfed seedlings. At age four, all seedlings were inoculated with *Ophiostoma ulmi*, (Buism.) C. Nannf., the causal fungus for Dutch elm disease. A factorial analysis showed male parent, female parent, and male x female interaction influenced disease symptoms 4 and 8 weeks after inoculation. After a few years of further evaluation of the seedlings, 10 clones were selected for a combination of disease- and insect-tolerance and horticultural desirability. These clones were propagated and established along with four disease-tolerant cultivars and American elm seedlings in a replicated field plot. Three-year-old clonal plants inoculated with *O. ulmi* varied significantly in their disease symptoms 4 weeks, 1 year, and 2 years after inoculation. Even clones from the same full-sib family showed significant differences in disease tolerance. Results indicate that both specific and general combining ability are important in determining tolerance to Dutch elm disease.

Index words: *Ulmus*, diploid elms, disease tolerance, controlled crosses, hybridization.

Significance to the Nursery Industry

Elms (*Ulmus* L.) are known for their adaptability and pollution tolerance, and several cultivars with tolerance to Dutch elm disease have been released to the nursery trade. Results of this study demonstrated that growth rate and disease tolerance can be improved by making controlled crosses between superior elm cultivars or selections, followed by clonal selection from within each of the full-sib families created. Both specific and general combining ability were found to be important in breeding and selecting for Dutch elm disease tolerance. Several clones with combined disease and insect tolerance have been developed from this study and are under evaluation for potential release to the nursery industry.

Introduction

The loss of millions of American elms in the United States as a result of Dutch elm disease (DED) (caused by *Ophiostoma ulmi* (Buism.) C. Nannf.) has stimulated the initiation of several breeding programs for the development of disease-resistant elms (2, 8, 16). The U.S. National Arboretum, U.S. Department of Agriculture, Agricultural Research Service, has released several new cultivars, including 'Dynasty' (3), 'Frontier' (15), 'Homestead' (12), 'Ohio' (16), 'Pathfinder' (16), 'Patriot' (17), 'Pioneer' (13), 'Prospector' (14), and 'Urban' (6). All of these cultivars have good

levels of DED tolerance and are beginning to be used in the nursery, landscape, and arboricultural industries.

This paper presents results of a long-term study of attempts to combine superior traits of many of the above cultivars through an advanced-generation crossing program. The effort involved two major phases. The first, the breeding and selection phase, centered on making controlled pollinations between many of the Arboretum's best elm selections and cultivars, outplanting the resulting seedlings in a replicated field test, inoculating these trees with *O. ulmi*, and then making clonal selections. The purpose of the second, or intensive evaluation phase, was to identify clones with the highest level of disease tolerance. This phase involved propagating from 10 of the best clones in the field test and outplanting their propagules along with ramets from other cultivars in another replicated field experiment. This was followed by inoculation and subsequent determination of disease symptoms. The two phases of this research were conducted over a 14-year period which demonstrates the long-term nature of breeding and selecting elms for disease-tolerance. Many new disease- and insect-tolerant trees reported on here offer promise for eventual release to the nursery, landscape, and arboricultural industries.

Materials and Methods

Breeding and selection phase. Five elm clones were used as parents in the breeding program. One of these, 'Urban' ((*U. x hollandica* 'Vegeta' x *U. carpinifolia* Gleditsch) x *U. pumila* L.), had been named and released as a cultivar (7). The other four parental clones were numbered 470, 205, 314, and 970 at the time of crossing, but later 470, 205, and 314 were named and released as 'Homestead' (12) (*U. pumila* x [(*U. hollandica* 'Vegeta' x *U. carpinifolia*) x (*U. pumila* x *U. carpinifolia*)]); 'Pioneer' (13) (*U. glabra* Huds. x *U. carpinifolia*); and 'Prospector' (14) (*U. wilsoniana* Schneid.), respectively. Clone 970 ((*U. glabra* x (*U. wallichiana* Planch. x *U. carpinifolia*)) has shown good disease tolerance, but has not been released.

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Table 1. Variation among elm progenies in growth and response to *Ophiostoma ulmi*.

Parents			Three-year-old trees		Percent (%) disease symptoms on four- and five-year-old trees		
			Height	Caliper	Time after inoculation (weeks)		
			cm	mm	4	8	55
Female	Male	No. of trees [†]					
'Pioneer'	x 'Prospector'	2– 1	77	16	10	10	0
'Pioneer'	x 'Homestead'	93– 78	202a [‡]	48a	0a	2a	2b
'Pioneer'	x 970	104– 64	153b	33a	2a	5a	12a
'Pioneer'	x 'Urban'	2– 1	206	48	0	20	45
'Pioneer'	x Self	0	—	—	—	—	—
'Homestead'	x 'Pioneer'	95– 73	172a	41ab	0a	4a	3a
'Homestead'	x 'Prospector'	9– 7	152a	31b	0a	0a	1a
'Homestead'	x 970	71– 54	203a	43ab	1a	4a	9a
'Homestead'	x 'Urban'	14– 11	159a	38ab	1a	8a	2a
'Homestead'	x Self	6– 4	226a	54a	0a	0a	0
970	x 'Pioneer'	59– 41	140a	30a	1a	8a	14a
970	x 'Prospector'	5– 3	257	45	11	31	17
970	x 'Homestead'	23– 14	117a	26a	2a	2a	0b
970	x Self	0	—	—	—	—	—
'Urban'	x 'Pioneer'	41– 27	224ab	49a	1a	6ab	0a
'Urban'	x 'Prospector'	74– 70	253a	54a	3a	9a	6a
'Urban'	x 'Homestead'	94– 73	196b	52a	2a	2b	3a
'Urban'	x Self	0	—	—	—	—	—
Significance among all 15 progeny groups [§]			.004	.001	.041	.035	.061

[†]No. of trees is the maximum and minimum number of trees across the five variables for each progeny group; based on survival at the time data were collected.

[‡]Mean comparisons among males on the same female by LSD, 0.05 level. Values with less than 6 trees were excluded from mean comparisons.

[§]The 15 progeny groups analyzed by analysis of variance were those groups having at least 2 live trees at the time of inoculation.

Crosses between clones were made in many combinations (Table 1) with each tree serving frequently as both a female and male parent. Non-woven cloth bags were placed over unopened flower buds on the female trees in late March, 1980. Controlled pollinations were made from April 7 to April 11, 1980. Fruit were collected on May 19 and May 20, and immediately planted in flats in a mixture of peat:perlite:soil (2:2:1 by vol). Seedlings from the flats were transplanted to 8 × 8 × 28 cm decomposable cardboard containers and placed outside for further growth and eventual overwintering. In April, 1981, seedlings were transplanted to a field site of silt loam soil near Delaware, OH. A randomized block design with four blocks was followed; the number of trees planted per cross varied and depended on the success of each cross (Table 1). On May 21, 1984, a 1.6 mm (0.06 in) diam hole was drilled 7mm (0.28 in) deep with a battery-powered drill in two separate branches in the top third of each tree. A spore suspension (1.4×10^6 spores per ml) of a mixture of aggressive and nonaggressive (7) isolates of *O. ulmi* was introduced into each hole, filled to overflowing, and then covered with plastic tape. Height, caliper measured 15 cm (6 in) above ground level, and disease symptoms 4, 8, and 55 weeks after inoculation were measured when trees were 3, 4, or 5 years old.

Analyses of variance were computed by using the mixed model procedure of SAS (5). Because only 15 of the possible 25 progeny groups (female x male crosses) were available (Table 1), it was not possible to model the progeny groups as a complete factorial. Therefore, factorial analyses were carried out on a subset of crosses that were complete, specifically those six progeny groups resulting from crossing

'Homestead', 'Urban', and 970 (used as females) with 'Pioneer' and 'Prospector' (used as males).

Intensive evaluation phase. Ramets representing 10 hybrids produced from the breeding and selection phase were planted with American elm seedlings and ramets from four cultivars ('Prospector', 'Homestead', 'Frontier', and 'Pathfinder') into a field plot at Glenn Dale, MD, in 1989 and 1990. All 10 of the hybrid clones had shown symptom development of 5% or less after inoculation in the first phase of this study. They had also shown tolerance to feeding by the elm leaf beetle (*Xanthogaleruca luteola* (Muller)) (1). Trees were planted in a randomized-block, split-plot design with 7 blocks, and, depending on the number of trees available, four trees per clone or seedling group in each whole plot within a block. Half the trees in each whole plot were inoculated May 18, 1992. The other half were inoculated on May 27, 1992 (sub-plot treatment), following the procedure described in an earlier paper (18), by using a basal inoculation with two aggressive and two non-aggressive isolates of *O. ulmi* (18). The percentage of the crown showing wilting or death of the foliage was estimated 4 weeks after each inoculation date. The percentage of the crown's branches showing a lack of foliage, or dieback, was estimated 1 and 2 years after each inoculation date. Data analyses were carried out by using the mixed model procedure of SAS (4).

Results and Discussion

Breeding and selection phase. Success of the controlled crosses varied widely, with some crosses such as 'Pioneer' x

970 yielding as many as 104 seedlings and others (970 x 'Urban' and 'Urban' x 970) failing to produce offspring. 'Prospector' was tried as a female parent but produced no seedlings as selfs or as outcrosses; therefore, no data are shown for this parent. As a male parent, 'Prospector' yielded only two to nine plants when mated with three of the female parents, 'Pioneer', 'Homestead', and 970 (Table 1). Only when 'Prospector' was crossed with 'Urban' was it prolific. Of the four female parents, only 'Homestead' produced viable selfed seedlings, and then only in very small numbers (Table 1). The general lack of selfing in these parents confirms the pattern found earlier (9, 10, 11) with diploid species and hybrids.

Analyses of variance showed differences among the 15 progeny groups in height, caliper, and 4 week- and 8 week-disease symptoms (see progeny group significance at bottom of Table 1). Considering only those groups with at least six trees represented, the slowest-growing progenies were 970 x 'Pioneer' and 970 x 'Homestead', the latter progeny being only about half the size of the fastest-growing groups (LSD, $p < 0.05$), 'Urban' x 'Prospector', 'Urban' x 'Pioneer' and 'Homestead' selfed (Table 1). Male parents varied significantly in transmitting height-growth potential when crossed with 'Pioneer', and also with 'Urban' and varied in transmitting diameter growth potential when crossed with 'Homestead' (Table 1). A factorial analysis of three of the female and two of the male parents showed a significant female, but not male, effect for height and caliper (Table 2).

Considering the general pattern of disease-symptom development after inoculation, all groups can be considered disease tolerant, with no highly susceptible progenies found (Table 1). This overall pattern is not surprising, given that all the parents used in the crosses were disease tolerant. Some differences among progenies did occur, however. Disease response 4 and 8 weeks after inoculation indicated the 'Pioneer' x 'Urban' and 970 x 'Prospector' groups to be slightly more susceptible, but their difference in percentage symptoms may have resulted from small replication (Table 1). Because of frequent cases of small replication, mean comparisons are reported only for progeny groups with six or more offspring, as footnoted in Table 1.

Progenies from different male parents crossed with 'Urban' (female) varied in disease symptoms 8 weeks after inoculation from 2 to 9% (Table 1). A factorial analysis of three female ('Homestead', 'Urban', and 970) and two male ('Pioneer' and 'Prospector') parents showed male parent,

female parent, and male x female parent interaction affected disease symptoms during the year of inoculation (Table 2). This corroborates the importance found in earlier studies (10, 11) of both general and specific combining ability in determining tolerance to *O. ulmi*, even in the complex advanced generation crosses used in this study.

Crown dieback 55 weeks after inoculation was not different across all 15 progenies, but the LSD test indicated significant, albeit small, differences among progenies resulting from different males bred to the same female (Table 1). For example, the progeny group 'Pioneer' x 970 expressed more dieback (12%) than the 'Pioneer' x 'Homestead' group (2%) (Table 1). Similarly, seedlings from the 970 x 'Pioneer' cross showed more dieback (14%) than seedlings from the 970 x 'Homestead' hybridization (0%).

The disease response of four progeny groups ('Pioneer' x 'Homestead'; 'Pioneer' x 970; 'Homestead' x 970; and 'Homestead' x 'Urban') were compared to their exact reciprocals ('Homestead' x 'Pioneer'; 970 x 'Pioneer'; 970 x 'Homestead'; and 'Urban' x 'Homestead', respectively) using analysis of variance contrasts. We found no significant differences in symptom expression between any of the four reciprocal progenies at 4, 8, and 55 weeks after inoculation. Evidence for maternal inheritance of *O. ulmi* found in an earlier study (11) was, therefore, not corroborated.

Intensive evaluation phase. From the 692 seedlings (including the six selfs), 10 clones were selected for superior insect- and disease-tolerance and attractive, symmetrical form. Field and laboratory tests enabled us to choose these 10 elite clones for their tolerance to the elm leaf beetle (*Xanthogaleruca luteola*, with 'Prospector' providing a major source of insect-resistance genes (1). Many of the crosses produced clones with high levels of disease tolerance, but often neither parent showed adequate insect tolerance to produce a high level of that tolerance in the progeny. Each of the 10 trees was then propagated for the second phase, in which they were intensively screened for the highest levels of disease tolerance.

Analyses of variance of the clonal test showed highly significant differences among clones or seedling groups for height before inoculation and disease symptoms 4 weeks, 1 year, and 2 years after inoculation. Variation in height may be due to differences in inherent growth potential, but also may have been influenced by differences among clones in the time of planting and in initial heights at the time of planting. An analysis of variance showed that the first in-

Table 2. Factorial analyses of variance of elm progenies from advanced generational crosses.

Source of variation	df	Mean squares				
		Three-year-old seedlings		Disease symptoms		
				Time after inoculation (weeks)		
		Height	Caliper	4	8	55
Female parent ^a	2	60,742**	30**	313**	1685**	872**
Male parent	1	35,278	2	173**	1027*	42
Female x male parent	2	25,644	9	142**	984**	114

^aFemale parents were 'Homestead', 'Urban', and clone 970 (*U. glabra* x (*U. wallichiana* x *U. carpinifolia*)). Male parents were 'Pioneer' and 'Prospector'.

*, ** 0.05 and 0.01 probability levels, respectively. Mean squares without asterisks were not significant.

Table 3. Response of elm clones and seedlings to *Ophiostoma ulmi* inoculation.

Clonal or seedling group	No. of trees	Height (cm) March 1992	Foliar symptoms (%) 4 weeks after inoculation			Crown dieback (%) One year after inoculation			Crown dieback (%) Two years after inoculation		
			Inoculation date (1992)			Inoculation date (1992)			Inoculation date (1992)		
			May 18	May 27	Combined	May 18	May 27	Combined	May 18	May 27	Combined
Amer. seedlings	25	152h ^y	87a	81a	84a	89a	90a	89a	76a	74a	75a
15-87 (U x P) ^z	24	293g	61b	30b	45b	77a	37b	58b	66a	26b	46b
'Prospector'	28	293g	47bc	16bcdef	30bcd	6de	3e	4fg	0e	0c	0e
16-87 (U x P)	26	358fg	47bc	14bcdefg	29bcd	16cd	6de	10def	4cde	3c	4cde
14-87 (U x P)	28	458abc	43bc	30b	36bc	6de	2e	4fg	0e	0c	0e
6-87 (U x P)	28	432cde	41bc	30b	36bc	28bc	24bc	26c	17bc	8bc	12c
1-87 (H x P)	28	382def	40c	17bcde	28cde	9de	4e	6fg	1de	0c	1e
'Frontier'	28	444bcd	36c	25bc	31bc	15cd	5e	9ef	7cde	3c	5cde
18-87 (U x P)	27	392cdef	29cd	23bcd	26cde	11d	7de	9ef	4cde	2c	3de
5-87 (H x 970)	16	203h	30cd	7defgh	17def	39b	10cde	23cd	26b	7bc	15c
'Homestead'	19	530a	17de	3gh	9f	0e	0e	0g	9bcd	0c	2de
24-87 (U x P)	28	369ef	19de	6efgh	11f	12cd	2e	6fg	3de	1c	2de
1-85 (U x P)	28	504ab	17de	13cdefg	15ef	19bcd	20bcd	20cde	9bcd	7bc	8cd
17-87 (U x P) ^x	24	292g	11e	5fgh	8f	0e	0e	0g	0e	0c	0e
'Pathfinder'	9	113i	0f	0h	0g	0e	0e	0g	0e	0c	0e

^xU = 'Urban', P = 'Prospector', H = 'Homestead'.

^yMean separation within columns by LSD, .05 level.

^zClone 17-87 was named and released as 'Patriot' elm.

oculation evoked greater symptom development than the second inoculation, following a pattern found earlier with American elm clones (18). Although the American elm seedlings distinctively showed the greatest level of destructive symptoms in response to *O. ulmi*, variation in symptoms occurred among the diploid elm clones, even within full-sib progenies. For example, two clones from the cross 'Urban' x 'Prospector', numbers 15-87 and to a lesser extent, 6-87, appeared less disease-tolerant than many of their sister siblings, especially 17-87 (eventually named 'Patriot') and 24-87 (Table 3). Variation among full-sib seedlings in disease tolerance could be explained by the specific combining ability, which in the first phase of this study was found to be of equal importance to general combining ability. The expression of full-sib clonal variation in response to *O. ulmi* is therefore probably a result of specific combining, or non-additive, gene effects; dominance or epistasis are examples of such gene action (19).

The cultivars included in this study initially varied in response to inoculation (Table 3). 'Prospector' and 'Frontier' showed more 4-week symptoms than 'Homestead', 'Patriot', and 'Pathfinder', but differences in symptoms among the first four cultivars 1 year later were less pronounced; after 2 years, there were no differences. 'Prospector' and 'Frontier' in previous studies (14, 15, 16) have shown high levels of Dutch elm disease tolerance. Severe basal inoculation creates disease symptoms in highly disease-tolerant germplasm (16, 18). As a result, natural field tolerance is underestimated in this study. Therefore, the initial disease response of 'Frontier' and 'Prospector' to severe basal inoculation should not be of concern, but can be expected with almost any elm given the right environmental conditions.

This long-term study showed the effectiveness of making advanced-generation crosses in creating progenies which combine insect- and disease-tolerance with desirable horticultural attributes. We found that even with those clones from within the same cross, intensive screening was worth-

while for identifying disease-tolerant genotypes. Many of the 10 clones selected are presently under national evaluation, and one of these, 17-87, has been released as the 'Patriot' elm (17).

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Differential Resistance to Entomosporium Leafspot Disease and Hydrogen Cyanide Potential in Photinia¹

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Abstract

Photinia serrulata Lindl., *P. glabra* (Thunb. ex J.A. Murr.) Maxim., and two of their progeny, *P. x fraseri* Dress. 'Birmingham' and 'Kentucky' were screened for susceptibility to *Entomosporium* leafspot and for hydrogen cyanide potential using detached leaf assays. *Photinia serrulata* was least susceptible to the fungus, while *P. x fraseri* 'Birmingham' and *P. glabra* were most susceptible. Young leaves were much more susceptible than mature leaves in all taxa except *P. glabra*, which was found to be acyanogenic. Although distinct differences in hydrogen cyanide potential occurred among the clones, a direct correlation to disease susceptibility was not indicated.

Index words: *Entomosporium mespili*, *Photinia serrulata*, *P. serratifolia*, *P. x fraseri* 'Birmingham', *P. x fraseri* 'Kentucky', *P. glabra*, disease screening, detached leaf assay, cyanogenesis.

Significance to the Nursery Industry

Photinia taxa and specifically *P. x fraseri* 'Birmingham' are landscape staples in the southern United States, Japan, Australia and New Zealand. However, *Entomosporium* leafspot disease has significantly reduced the use of the plants. Nursery production of 'Birmingham' has decreased over 50% in the southeastern U.S. during the past six years. The results of this paper show that a high level of resistance occurs within *P. serrulata*. Interclonal variation in resistance was evident between *P. x fraseri* 'Birmingham' and 'Kentucky'. The opportunity exists to reconstruct the crosses between *P. serrulata* and *P. glabra* or a more resistant clone of *P. x fraseri*, select for vivid red foliage, screen for disease

resistance, and back-cross superior seedlings with *P. serrulata* to attain increased disease resistance. Perhaps a multiclonal series with similar ornamental traits and high degrees of leafspot resistance could be introduced. Results of the detached leaf bioassay reported herein correspond with the observed landscape disease evaluations suggesting that the leaf bioassay could be used to rapidly screen seedling populations.

Introduction

Entomosporium mespili (DC. ex Duby) Sacc. (teleomorph = *Diplocarpon maculatum* (Atk.) Jorstad) causes a leafspot disease of 14 genera in the subfamily Pomoideae of the Rosaceae (7). The disease was first observed on *Photinia* spp., both *P. serrulata* Lindl. and *P. glabra* (Thunb. ex J. A. Murr.) Maxim., in Louisiana in 1957 (15). The disease continues to affect *Photinia* taxa grown in nurseries and as landscape plants in the United States, Japan and New Zealand (7).

Resistance to some leafspot diseases are associated with cyanogenesis, in which cleaving of cyanide-containing glucosides in the host, via pathogen and/or host glucosidases, yield hydrogen cyanide (HCN). Infection rates in the copperspot disease of trefoil (*Lotus corniculatus* L.), caused by *Stemphyllium loti* Graham are reduced as leaf HCN levels increase (12). *Helminthosporium* leafspot and *Gloeocercospora* leafspot of sudangrass (*Sorghum sudanese* Stapf. 'Piper') and a sorghum hybrid (*Sorghum bicolor* (L.)

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