PROSPECTS FOR ELM BREEDING IN WISCONSIN [1]

by

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Over the last 40 years, the Dutch elm disease *(Ceratocystis ulmi* (Buisman) C. Moreau) has spread radially from initial infections in the east-central states to a present distribution corresponding with most of the natural range of American elm *(Ulmus americana* L.). Spread of the disease has prompted major concern for the preservation of elms as a dominant feature of urban environment. The challenge of Dutch elm disease has evoked concerted efforts to protect elm trees with systemic fungicides and growth regulators, to prevent infection through insect vectors, and to intensively study the pathogen and pathogenicity. While economic and aesthetic considerations fully justify major emphasis on preservation of existing trees, genetic approaches to maintaining elms as a useful element in landscaping have been largely overlooked. This oversight is all the more unfortunate when we note the success of the Dutch in developing disease resistant elms (Heybroek, 1966). Most of the Dutch selections unfortunately have not proven fully hardy in the climate of the north temperate region [3] (Pomerleau and Bard, 1968). Although elms are of economic significance primarily as ornamentals, perhaps the techniques and long-term outlook of forest tree breeders are needed to initiate and carry on genetic and breeding research with elms in the United States.

Unique opportunities for a program of elm breeding are provided in the elm collections established by Dr. Smalley at the University of Wisconsin. Since 1958, more than 400 seed collections from 12 species and several hybrid progenies have been grown and screened for resistance to artificial innoculation with *C. ulmi*. Much of the surviving material is flowering annually in an arboretum near Madison.

Since 1966, both arboretum material and local trees from city plantings and native populations have been used in greenhouse and field pollination. The objectives of the crossing experiments include clarification of interspecific crossing patterns, estimation of variation in self-compatibility, and determination of the extent to which desirable traits can be transferred among species and individuals. Concurrent with the genetic studies are continued screenings of established and newly obtained progenies, anatomical and biochemical studies of resistant and susceptible individuals, and selection for desirable ornamental characteristics among resistant individuals.

TRAITS

Table 1 presents a classification of traits of interest in some of our elm materials and suggests relative possibilities for selection. Initially, choice of traits for selection is obvious. High resistance to *C. ulmi* is essential. In contrast to the forest, where often a few trees can be lost to disease without significant consequences, urban plantings are unlikely to include elms unless freedom from disease is assured.

After genotypes resistant to. *C. ulmi* are available, many traits of primarily esthetic appeal will attract the attention of the elm breeder. These traits of secondary importance are so numerous that priorities need to be assigned, however arbitrarily, in order to increase the probability of improvement through selection while using progenies of manageable size. The high probability of successful early evaluation for most of the traits is of major importance in keeping progeny test acreage within practical limits.

The traits of secondary importance are mostly of obvious interest for ornamental trees. *Gnomonia ulmea* (Schw.) Thum. is a leaf spot disease causing unsightly lesions and, in severe cases, premature leaf fall. Folding of leaves parallel to the mid-rib is a characteristic common to slippery elm *(U. rubra* Muhl.) and probably generally undesirable. High crown density would seem to be universally desirable. We consider that the remaining traits listed in Table 1 are traits for which no one type is necessarily the only desirable form. A range of types for each trait would provide a wide array of variation for landscape purposes. For example, variation in growth rate and in lateral branching produces types ranging from low shrubs to-large trees. Combining variation in leaf shape and color with the shrub habit might produce an array of highly attractive shrubs. Bark characteristics and crown form would be of more importance in tree types.

With these numerous traits in mind, our current approach to breeding is early screening for resistance to C. *ulmi* followed by selection of many ornamentally desirable types to be vegetatively propagated for release on an experimental basis. As the selections reach flowering age a crossing scheme intended to combine desirable traits will be initiated. However, our goal is not the ideal tree, but rather a wide array of ornamentally desirable variations.

TWO GENE POOLS OF INTEREST

The genetic basis for achieving our breeding objectives has received little attention in the U.S., even though results of the elm breeding program in Holland suggest that we can make substantial genetic progress. The choice of gene pools within which to work is not obvious at this point although some characteristics of some species are well known. In the

Wisconsin program, the current choice of species reflects both the availability of materials and knowledge of species characteristics.

Our materials can be divided into two gene pools, between which crossing seems to be extremely difficult if not impossible. American elm constitutes one gene pool; the other includes Japanese elm *(U. japonica* (Rehd.) Sargent), Siberian elm *(U. pumila* L.) and slippery elm. To date, attempts to enlarge the gene pool of American elm by interspecific hybridization have produced only a few unauthenticated seedlings (Britwum, 1960; Collins, 1967; Johnson, 1939, 1946). Authenticated hybrids of at least three additional species with Japanese or Siberian elm suggest that the Japanese-Siberian-slippery elm gene pool could be substantially enlarged.[4]

American Elm

The genetically predominant feature of American elm is tetraploidy. All other species of the genus are wholly, or at least chiefly, diploid (Darlington and Wylie, 1955). One of the genetic consequences of possessing four sets of chromosomes is illustrated in Table 2. The progeny sizes necessary to insure the recovery of certain genotypes reach relatively unmanageable proportions as the number of genes involved increases, and even in the most simple genetic system progeny sizes are a limiting consideration unless evaluation can be accomplished at an early age.

The production and utilization of American elm haploids, *i. e.* plants with one-half the typical chromosome number, would simplify studies of inheritance and might allow interspecific hybridization between American elm and diploid species. Haploids have been produced in a wide variety of plant species (Kimber and Riley, 1963), but, as yet, attempts to produce haploids of American elm have been unsuccessful.[5] The production of tetraploids from diploid species has been successful (Dermen and May, 1966). Whether these induced tetraploids can be crossed with American elm is uncertain. Presuming that interspecific hybridization will be possible, the genetic consequences of tetraploidy are still a disadvantage if crossing beyond the Fi generation is needed to develop desirable types.

The consequences of *tetraploidy are not entirely negative. Tetraploids can contain much latent genetic variation. Genetic variation has been studied in few traits of American elm, although a wide range of variation has been demonstrated in self-compatibility among 35 trees[5] and in seedling leaf size and growth rate among selfed progenies.[6] Variation in resistance to *C. ulmi* also has been noted in mass selection studies[7,8] (Pomerleau and Bard, 1968; Smalley and Kais, 1966). A one-generation crossing program followed by vegetative propagation of disease resistant, ornamentally desirable types may be an approach through which American elm can be maintained as an ornamental.

Japanese-Siberian-slippery Elms

The three diploid species used in our crossing studies encompass a wide range of phenotypic variation and desirable features (Table 1). The extent to which most of these traits can be transferred between species is speculative at the moment, although we have authenticated[9] progenies from which information on gene transfer will soon be available. Our crosses to date are summarized in Table 3. Up to three maternal trees were used in each cross. Pollens were single-tree collections or pollen mixes representing at least three trees. The indicated species crosses have been reported before[4], as have back crosses of *U. rubra* x *pumila* hybrids (Collins, 1967). The success of the cross *U. rubra* x *(U. japonica* x *pumila (?))* suggests that those crosses missing from the table will be successful when our *U. japonica* trees reach reproductive maturity. In the absence of unexpected genetic complications, it may therefore be possible to shuffle traits among these species and hybrids without great difficulty.

Two sets of evidence support an enthusiastic point of view. First, putative natural hybrids of Siberian and slippery elm have already found use in the commercial nursery trade. The clone *U. x Fremont* is one attractive hybrid selection of this type. Back crosses, especially to slippery elm, have been made in an attempt to develop a somewhat more ascending crown while determining whether resistance to C. *OM* is maintained.

A second set of promising evidence is the segregation in wind-pollinated progenies of Japanese x Siberian elm hybrids. Seed for these progenies was sown in 1964 and 1965. Although male parentage is unknown, a mixture of hybrid pollen and Siberian elm pollen is the most probable source of the male gametes. For the 1964 collection, selections were made in the seedbed at age 2 years for rapid growth rate and for large leaf size. A selection intensity of about 10 to 20 percent was applied. The selected seedlings were then transplanted in a 5 x 5 foot spacing. Artificial inoculations were made 1 or 2 years after transplanting. The inoculum contained a mixture of 14 isolates from naturally diseased trees and was applied to one branch during the estimated period of maximum susceptibility (Smalley and Kais, 1966).

In Table 4 the summarized results of inoculation are encouraging. Substantial numbers of trees received inoculations without producing any disease symptoms. The percentage of apparently resistant trees in the Japanese x Siberian elm progenies was more than double the percentage in a wind-pollinated progeny from the resistant Dutch selection N260.

Of major significance is the observation that resistance to *C. ulmi* is not closely linked to the small leaf type of Siberian elm. For the 1964 progeny any test of correlation between leaf size and resistance is precluded by seedbed selection. For the 1965 progeny of *U. japonica* x *pumila* (?), correlation between leaf size class and percent resistance is -.82 (non-significant at 5 percent probability, 3 degrees of freedom). Yet several symptom-free trees were produced in each leaf-size class. From among the trees exhibiting no response to inoculation, several individuals were selected as having ornamentally desirable characteristics. These trees will be artificially inoculated again, vegetatively propagated, and released for experimental trials to commercial nurseries.

SUMMARY

The range of phenotypic variation in traits of ornamental value is large among the four elm species presently used in the Wisconsin elm crossing project. Current objectives of the project include studies of how desirable traits can be transferred among species and hybrids with particular emphasis on resistance to *C. ulmi.* Complexity of gene transfer is expected in American elm as a consequence of tetraploidy. Preliminary data suggest that gene transfer among the diploid Species (Japanese, Siberian, and slippery elm) may be fairly easily accomplished. The high degree to which disease resistance to *C. ulmi* is maintained in some progenies from resistant parents and the apparent lack of tight linkage between resistance to *C. ulmi* and leaf type suggest that a breeding approach emphasizing production of a wide range of ornamentally desirable types may be feasible.

Table 1. Traits of interest in ornamental breeding of elms, priorities for selection, and observed opportunities for selection rated as very good (+++), good (++), some (+), or probably little or none (-). Estimated opportunities for selection are based on observations of phenotypic variation except where family differences are indicated (F).

		Species			
	Traits	*U. americana*	*U. japonica*	*U. pumila*	*U. rubra*
Early evaluation (up to 10 years from seed)					
Priority I	Resistance to *C. ulmi*	+	++	+++	++
Priority II	Resistance to *Gnomonia ulmea*	+			+
	Leaf flatness				-
	Leaf size	++(F)		+	
	Growth rate	++(F)		++	
	Early bark roughness				
Priority III	Leaf shape	++(F)		+	
	Immature leaf color	-	+		
	Mature leaf color	+		+	
	Bark color				
	Bark texture				
	Lateral branching	+		+	
Field evaluation (up to 25 years from seed)					
Priority II	Crown density			+	
	Ascending form	+			+

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2. Associate Professors, Departments of Forestry and Plant Pathology, respectively, University of Wisconsin, Madison.

3. Unpublished data, Dr. E. B. Smalley, Department of Plant Pathology, Univ. Wis.

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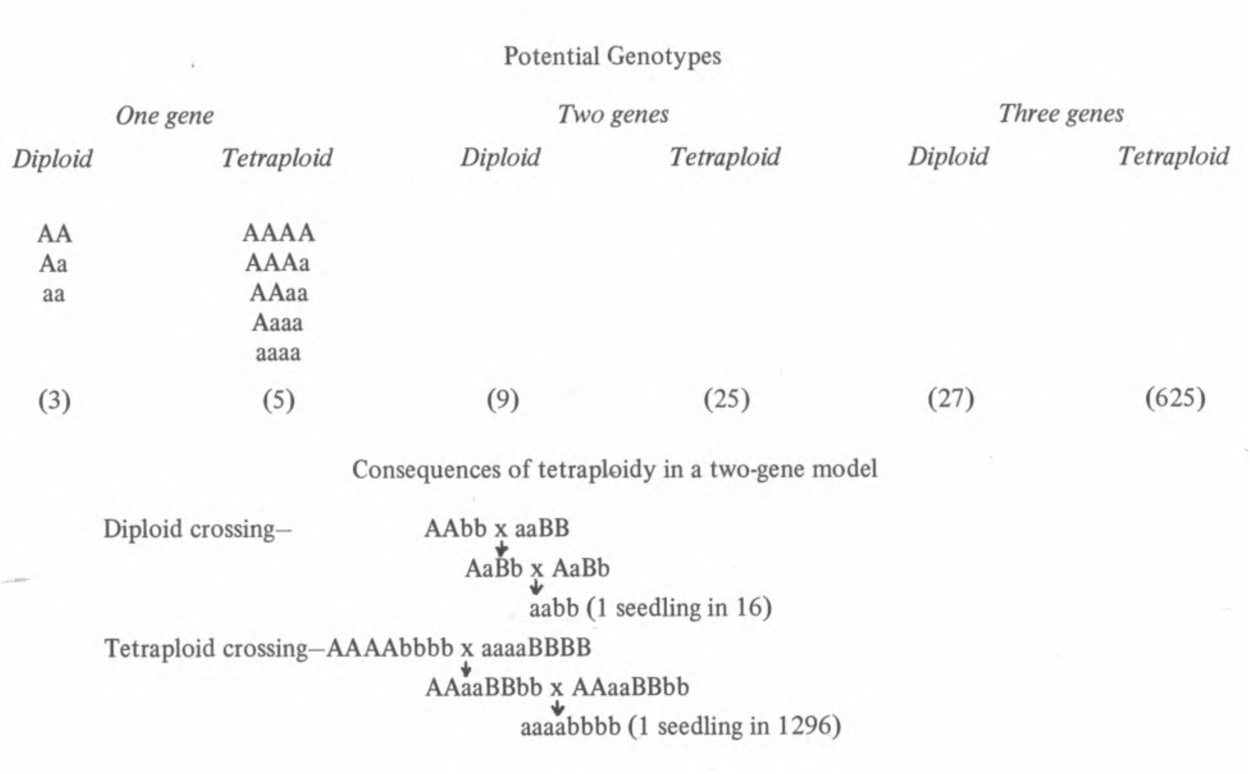
9. Hybridity was authenticated by morphological comparisons among progenies from hybrid and non-hybrid crosses.

Table 2. Potential genotypes in diploids and tetraploids.



Potential Genotypes

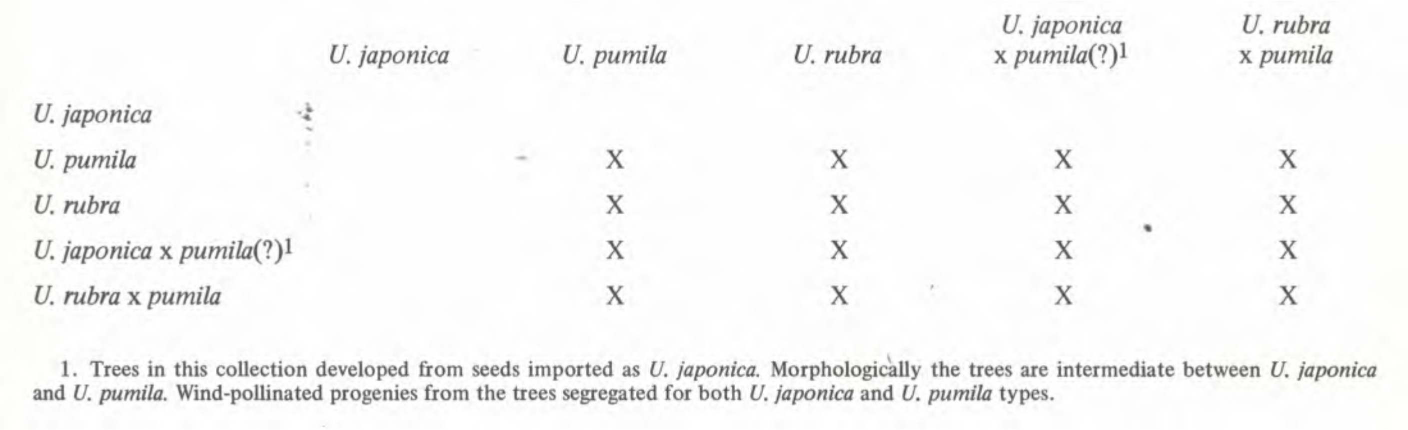
One gene		*Two genes*		*Three genes*	
Diploid	*Tetraploid*	*Diploid*	*Tetraploid*	*Diploid*	*Tetraploid*
AA Aa aa	AAAA AAAa AAaa Aaaa aaaa				
(3)	(5)	(9)	(25)	(27)	(625)

Consequences of tetraploidy in a two-gene model

Diploid crossing– AAbb x aaBB
↓
AaBb x AaBb
↓
aabb (1 seedling in 16)

Tetraploid crossing–AAAAbbbb x aaaaBBBB
↓
AAaaBBbb x AAaaBBbb
↓
aaaabbbb (1 seedling in 1296)

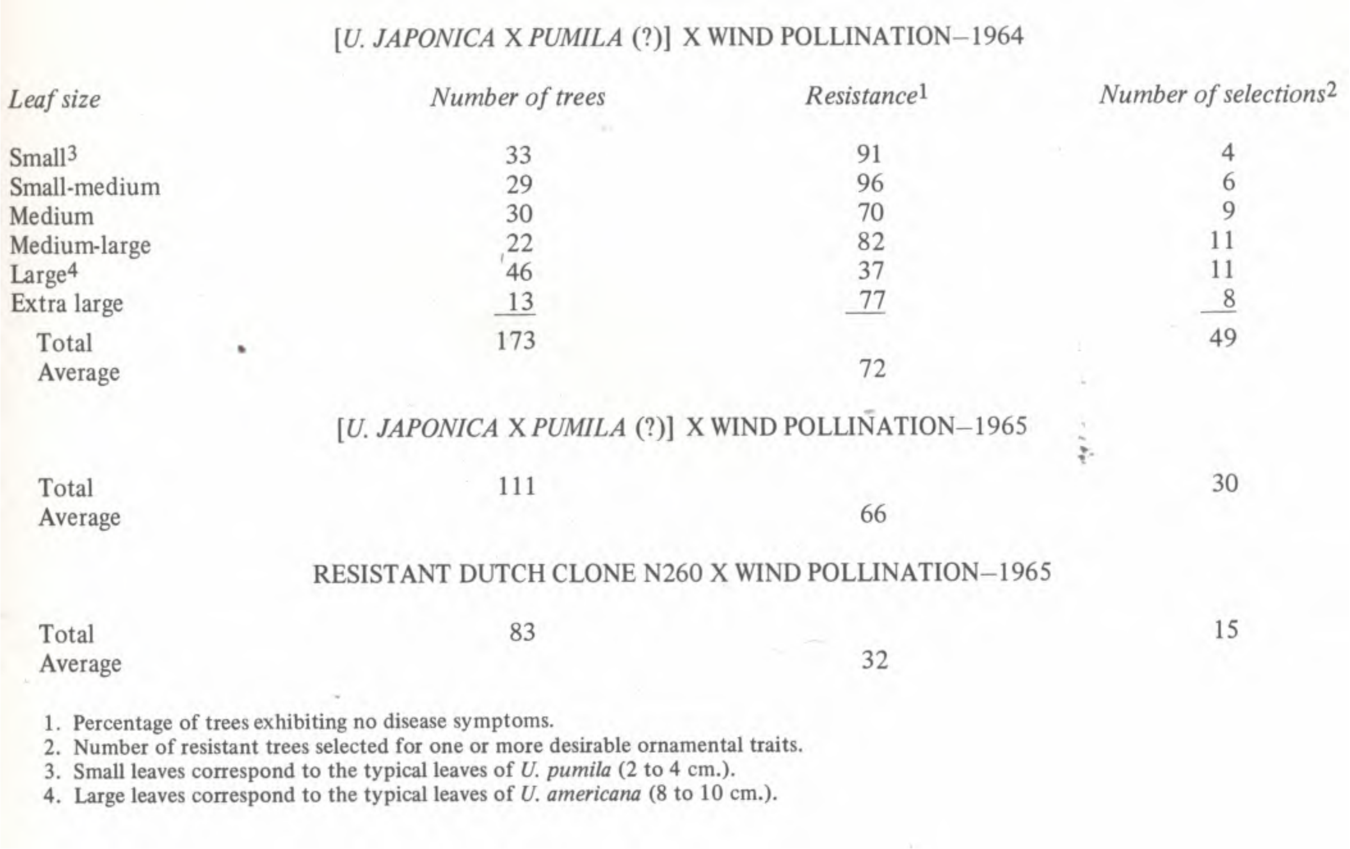
Table 3. Summary of authenticated elm families from field crosses. Crosses are represented by (X).



	U. japonica	*U. pumila*	*U. rubra*	*U. japonica* x *pumila*(?)[1]	*U. rubra* x *pumila*
U. japonica					
U. pumila		X	X	X	X
U. rubra		X	X	X	X
U. japonica x *pumila*(?)[1]		X	X	X	X
U. rubra x *pumila*		X	X	X	X

[1] Trees in this collection developed from seeds imported as *U. japonica.* Morphologically the trees are intermediate between *U. japonica* and *U. pumila.* Wind-pollinated progenies from the trees segregated for both *U. japonica* and *U. pumila* types.

Table 4. Summary of leaf types and disease resistance in three wind-pollinated progenies.



Leaf size	*Number of trees*	*Resistance*[1]	*Number of selections*[2]
[*U. JAPONICA* X *PUMILA* (?)] X WIND POLLINATION–1964			
Small[3]	33	91	4
Small-medium	29	96	6
Medium	30	70	9
Medium-large	22	82	11
Large[4]	46	37	11
Extra large	13	77	8
Total	173		49
Average		72	
[*U. JAPONICA* X *PUMILA* (?)] X WIND POLLINATION–1965			
Total	111		30
Average		66	
RESISTANT DUTCH CLONE N260 X WIND POLLINATION–1965			
Total	83		15
Average		32	

1. Percentage of trees exhibiting no disease symptoms.
2. Number of resistant trees selected for one or more desirable ornamental traits.
3. Small leaves correspond to the typical leaves of *U. pumila* (2 to 4 cm.).
4. Large leaves correspond to the typical leaves of *U. americana* (8 to 10 cm.).

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