Crossahility Patterns and Morphological Variation among Elm Species and Hybrids

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Introduction

The impact of Dutch elm disease has stimulated the development of elm-breeding programs in Europe and the United States. The Netherlands breeding program has led to the successful introduction of several disease-resistant clones (Heybroek, 1957). Some of these clones have been tested in the U.S. Unfortunately, many cannot tolerate the severe dry or cold climates of the Great Plains or northern states and therefore are of somewhat limited use in the U.S.

The elm-breeding program of the Agricultural Research Service, U.S. Department of Agriculture, is geared to supply the unique needs for improved elms in this country. To the present day, breeding and selecting has involved use of the wide variation in disease resistance, form, and growth rate of the diploid species (Whitten and Swingle, 1948; Arisumi and Higins, 1961; Santamour, 1972).

General hybridization patterns among the diploid species of Ulmus have been reported by Johnson (1939), Smith and Nichols (1941), Britwum (1960), Collins (1967), Heybroek (1968), Long (1971), Lester and Smalley (1969, 1972), and Santamour (1972). Many potential crosses, however, have never been attempted. Also, many of the hybrids reported in the literature were never authenticated by certification of hybridity, and we lack data on variation in morphological traits among Ulmus hybrids.

This paper reports on breeding studies of Ulmus during 1970, 1971, 1972, and 1973. The main objectives were (1) to determine crossability potential among species and hybrids; (2) to hybridize genotypes that have shown superiority in one or more valuable characteristics, such as disease resistance, growth rate, and form; and (3) to evaluate all progenies resulting from these crosses in verification of hybridity. Many of the parents used in the crosses were clones developed by the elm-breeding program in the Netherlands (Heybroek, 1957). By using these clones as parents, we capitalized on Netherlands breeding and selection advances through the F_1 generation.

Materials and Methods

Disease-resistant parent trees of species or hybrids listed in Table 1 were used. Two or 3 clones from each species were used as parents. Several of each of the following Netherlands clones were also used in the crosses: N248 = U. wallichiana Planch. X carpinifolia; N260 = U. pumila X (X hollandica Mill.); N282, N148, and N339 = U. X *hollandica* X carpinifolia; and N274 X N215 = (U. X *hollandica* X carpinifolia) X (U. pumila X carpinifolia). The origin of one other Netherlands clone, N262, is unknown (Heybroek, Personal communication).

Controlled pollinations were made in the spring of 1970, 1971, and 1972 and in the autumn of 1970, 1972, and 1973. About a month before normal anthesis, mature branches were brought inside and placed in water in separate greenhouse sections. Pollen was collected on glass, and then sieved and stored in a refrigerated desiccator until used. Because all female parents used were strongly protogynous, crosses were made without emasculation on trees growing outdoors. Nonwoven bags were placed over unopened flower buds. Controlled pollinations were carried out with artists' brushes between April 6 and 14 in 1970, 1971, and 1972 and between August 15 and September 9 in 1970, 1971, and 1973. In the selfing trials, artists' brushes were used in the same manner as with the controlled crosses. No seed was set when we tried to produce seed on cut branches of Siberian and American elms in the greenhouse, a method used by Wright (1949).

Most fruits were collected 5 to 6 weeks after pollination and planted in greenhouse flats in a mixture of peat : perlite : soil (2 : 2 : 1). Fruit from U. parvifolia was stratified for 45 days before sowing. When the number of sound seed was greater than 6, we planted the seed in at least 2, and in some cases 3, different flats. Germination rates on hybrids were noted at least every 3rd day. Seedlings from spring pollinations were transplanted directly from flats to a field site in a randomized complete-block design, with at least five replicates per hybrid combination, each plot containing from 1 to 5 trees. Seedlings originating from fall pollinations of U. parvifolia were transplanted from flats to the field site in May of the next year. Height and diameter were measured on all seedlings after 3 years of growth. On March 30, 1973, percentage of spring flushing was estimated on all progenies. During the third growing season, length and width were measured on three leaves randomly chosen from each seedling planted in the progeny test.

Results and Discussion

Crossability Patterns

Major hybridizations and their successes are summarized in Table 1. Of 31 strictly interspecific crosses attempted, 21 succeeded in producing verified hybrid seedlings. Most of the successful crosses produced a low percentage of hybrid seedlings. The number of seedlings produced for every 100 flowers pollinated ranged from 0.1 to 26.9. The most productive cross was U. carpinifolia (♀) X pumila (♂). No compatibility barriers appeared between the sections Madocarpus and Microptelea. Crosses of species from different series of Madocarpus generally succeeded. The following represent verified, interspecific progenies never before reported (♀ parent listed first):

U. carpinifolia X parvifolia
U. carpinifolia X *rubra*
U. glabra X rubra
U. pumila X parvifolia
U. japonica X parvifolia
U. rubra X glabra
U. rubra X carpinifolia
U. parvifolia X wilsoniana
U. parvifolia X glabra

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Table 1. — Results of interspecific crosses among *Ulmus* species and hybrids.

Female Parent		Male Parent[1]													
Section	Species	lae	ru	gl	ca	ja	wi	pu	pa	rxp	N248	N260	N148	N274 x 215	Self
Blepharocarpus, Dum.	*U. laevis*	396[2]	336	216		324			252						552
		3.5[3]	0	0		0			0						0
Ulmus (Madocarpus, Dum.)	*U. rubra*	728		700	812	924			504	364					500
		0		0.7	1.0	1.1			0	0					0.10
Ulmus (Madocarpus, Dum.)	*U. glabra*	280	390	760	910	600		750	550		250	320	500		1970
		0	6.9	3.4	5.4	1.2		6.8	0.9		0.8	0	1.6		0.10
Ulmus (Madocarpus, Dum.)	*U. carpinifolia*		650	870	2650			290	490		250				1260
			1.8	3.9	2.8			26.9	3.7		0				0
Ulmus (Madocarpus, Dum.)	*U. japonica*	368	848	432		2160			2272						4224
		0	0.1	0		0.5			0.3						.05
Ulmus (Madocarpus, Dum.)	*U. wilsoniana*						1652		3010			210	448	462	5124
							0.5		0			0	0	0	0
Ulmus (Madocarpus, Dum.)	*U. pumila*			4746	840			1120	1260			630	2282	490	2520
				0.9	10.1			3.5	4.8			1.7	7.5	20.4	0.60
Microptelea, Spach	*U. parvifolia*			8400	2640		840	3960	6300		5220				8724
				0.1	5.8		1.0	0.5	3.7		0.1				0.01
	U. rubra × *pumila*										372	600	1392	528	2160
											12.1	2.5	5.6	11.5	0
	N248			1476	1992		540	1116	456	696					2304
				0.3	6.0		0	2.9	0.7	3.6					0.13

[1] la = *U. laevis*, ru = *U. rubra;* gl = *U. glabra;* ca = *U. carpinifolia;* ja = *U. japonica;* wi = *U. wilsoniana;* pu = *U. pumila;* pa = *U. parvifolia;* r × p = *U. rubra* × *pumila;* N248 = *U. wallichiana* × *carpinifolia;* N260 = *U. pumila* × *hollandica;* N148 = *U. hollandica* × *carpinifolia;* (N274 × 215) = *(U. hollandica 'Vegeta'* × *carpinifolia)* × *(U. pumila* × *carpinifolia).*

[2] 396 = No. flowers pollinated.

[3] 3.5 = No. seedlings/100 flowers pollinated.

The success of many of the crosses depended on which of the two species was used as the male and which as the female. For example, the crosses *U. glabra* × *japonica* and *U. wilsoniana* × *parvifolia* yielded verified hybrids, but the reciprocals of these crosses failed completely. Although we found that *U. parvifolia* failed as a male parent with *U. rubra,* Santamour (1972) successfully completed the reciprocal cross. The number of attempts at our laboratory probably are too small to verify reciprocal differences in seed set.

U. laevis failed when used as either a female or male parent. Along with *U. americana, U. laevis* is a member of section Blepharocarpus. Heybroek (1968) reported difficulty in crossing *U. laevis* with other diploid species and attributed the incompatibility to genetic differences between section Blepharocarpus and other sections. Santamour (1972) successfully crossed *U. parvifolia* with *U. laevis,* but he used *U. parvifolia* as the female parent.

Crosses that involved a hybrid as a male or female parent or both showed no explicable pattern *(Table 1).* Twelve of the 18 attempts at controlled pollination in which a hybrid served as a female parent produced verified hybrid seedlings. The use of these hybrids as male parents yielded about the same percentage of verified progeny, with 11 successes out of 18 attempts. Among all hybrids used as females, *U. rubra* × *pumila* showed the greatest degree of success. In contrast, the Netherlands hybrid N274 × 215 *(U.* × *hollandica* × *carpinifolia)* × *(U. pumila* × *carpinifolia),* produced no progeny when the following species were used as male parents: *U. rubra* (pollinated 880 female flowers); *U. wilsoniana* (112 flowers); and *U. pumila* (450 flowers). The complexity of N274 × 215 probably contributed to its failure to hybridize easily with other genotypes. The clone N282 *(U. hollandica* × *carpinifolia)* also generally was unsuccessful as a female parent. Pollination of this clone was attempted by *U. rubra, U. glabra, U. wilsoniana, U. pumila,* and *U. parvifolia. U. rubra* and *U. pumila* as males yielded no sedelings. Percentage hybrid seedlings produced of the 3 other species ranged from 1 to 5, out of an average of 683 female flowers per species.

The Netherlands hybrids were more effective when used to pollinate *U. pumila* and *U. rubra* × *pumila* than when used on *U. wilsoniana. U. wilsoniana* appeared to be difficult to cross with the other species and hybrids; of eight attempts, only two succeeded. Smith and Nichols (1941) reported success in the cross *U. wilsoniana* × *japonica,* but did not try to verify hybridity.

Among most species and hybrids, a high degree of self-incompatibility occurred, with only 0 to 3 seedlings produced *(Table 1). U. pumila* showed the greatest degree of self-compatibility, with a yield of 16 seedlings from pollination of 180 flower buds, but its cross-fertility was much higher. Although self-incompatibiilty is common in *Ulmus* (Johnson, 1946; Heybroek, 1957; Britwum, 1960; Collins, 1967), considerable variation in this respect among individual trees within a species has been reported by Went (1954) and Lester (1971).

Table 2 presents success and failure of all crosses attempted here at this laboratory, as well as crosses reported in the literature, which has been summarized especially well by Collins (1967), Heybroek (1968), and Long (1971). Unfortunately, most crosses in the literature have not been authenticated. As shown in the table, not all potential crosses have been attempted. Combining my data with those of others indicates that there are probably no major barriers to crossing among diploid species, except for perhaps *U. laevis.*

Table 2 shows that *U. americana* reportedly has been successfully control-crossed with several diploid species. However, in none of the reports was data given to verify the authenticity of the hybrids produced, either cytologically or morphologically.

Morphological Characteristics

Analyses of variance indicated significantly different effects on height, diameter, leaf length, and leaf width among

Tabe 2. — Summary of interspecific *Ulmus* hybridizations, including those conducted by USDA-ARS, Delaware, Ohio, and those reported in the literature.

U. americana	am[1])																	
U. laevis	X[2])	la																
U. thomasii	X	X	th															
U. alata				al														
U. rubra	X	O	X		ru													
U. glabra		X			X	gl												
U. laciniata						X	lac											
U. bergmaniana	X	X				X		be										
U. wallichiana						X	X		wa									
U. carpinifolia		X			X	X	X		X	ca								
U. japonica	X	O				X			X	X	ja							
U. wilsoniana						X				X	X	wi						
U. procera										X			pr					
U. pumila	X	X	X	X	X	X			X	X	X	X	X	pu				
U. parvifolia		X	X		X	X	X		X	X	X	X		X	pa			
U. crassifolia															X	cr		
U. lanceaefolia																X	lan	
U. serotina					X				O					X				ser
U. macrocarpa																		X

[1]) am = *U. americana;* letters listed diagonally are abbreviations for same species listed vertically.

[2]) An X represents a successful cross either completed at Delaware, Ohio, or reported in the literature. A O represents an attempt but failure to obtain seedlings. COLLINS (1967) and LONG (1971) have summarized most of the crosses reported in the literature.

Table 3. — Variation in 3-yr-old *Ulmus* hybrids from 1970 and 1971 controlled pollinations[1]).

Female Parent	Male Parent[2])	Trees. (no)	Height (av) (cm)	Diam (av) (cm)	Leaf Length (av) (mm)	Leaf Width (av) (mm)	Spring Flushing[3]) (av) (%)
1970 Crosses:							
U. pumila	× N262	42	133^{c}	4.2^{b}	34^{bc}	17^{c}	56
U. pumila	× (N274 × 215)	53	231^{a}	6.5^{a}	46^{a}	24^{bc}	66
U. pumila	× N248	16	181^{b}	4.5^{b}	51^{a}	40^{a}	60
U. pumila	× N148	26	160^{b}	4.2^{b}	43^{ab}	25^{b}	58
U. pumila	× N260	68	136^{c}	4.4^{b}	33^{c}	18^{c}	50
U. rubra × *pumila*	× N262	12	142^{b}	3.1^{bc}	43^{bc}	29^{ab}	10
U. rubra × *pumila*	× N282	18	136^{b}	2.7^{c}	38^{c}	26^{b}	4
U. rubra × *pumila*	× (N274 × 215)	11	184^{a}	3.8^{a}	55^{a}	36^{a}	34
U. rubra × *pumila*	× N339	29	115^{c}	2.7^{c}	36^{c}	22^{b}	4
U. rubra × *pumila*	× N248	17	138^{b}	3.0^{bc}	55^{a}	30^{a}	10
U. rubra × *pumila*	× N260	17	101^{c}	3.3^{b}	50^{ab}	28^{b}	12
1971 Crosses:							
U. glabra 72	× *U. carpinifolia* 61	14	273^{a}	3.5^{a}	78^{a}	65^{a}	0
U. glabra 72	× *U. pumila* 8	18	259^{a}	4.6^{a}	64^{b}	38^{b}	52
U. glabra 72	× *U. rubra* 64	18	186^{b}	3.2^{a}	70^{ab}	46^{b}	8
U. glabra 19	× *U. carpinifolia* 61	19	327^{a}	5.2^{a}	71^{b}	50^{b}	48
U. glabra 19	× *U. glabra* 72	16	243^{b}	3.6^{b}	108^{a}	79^{a}	20
U. glabra 19	× *U. pumila* 8	10	143^{c}	2.7^{c}	48^{c}	30^{c}	10
U. carpinifolia 61	× *U. parvifolia* 76	12	175^{cd}	2.9^{c}	35^{b}	23^{b}	20
U. carpinifolia 61	× *U. glabra* 19	11	239^{ab}	3.5^{bc}	77^{a}	66^{a}	0
U. carpinifolia 61	× *U. glabra* 72	10	265^{a}	3.7^{ab}	74^{a}	60^{a}	4
U. carpinifolia 61	× *U. pumila* 8	18	135^{d}	3.1^{bc}	41^{b}	24^{b}	34
U. carpinifolia 61	× Self	6	207^{bc}	3.7^{ab}	38^{b}	25^{b}	20
U. carpinifolia 71	× *U. carpinifolia* 61	10	124^{d}	2.7^{a}	36^{a}	24^{a}	6
U. carpinifolia 71	× *U. rubra*	11	220^{b}	3.3^{a}	48^{a}	31^{a}	4
U. pumila 8	× *U. parvifolia* 76	18	221^{a}	4.5^{abc}	42^{bc}	21^{a}	70
U. pumila 8	× *U. carpinifolia* 61	19	173^{b}	3.7^{c}	40^{c}	24^{a}	26
U. pumila 8	× *U. glabra* 19	10	229^{a}	5.1^{a}	49^{ab}	24^{a}	46
U. pumila 8	× *U. glabra* 72	10	228^{a}	4.8^{ab}	53^{a}	27^{a}	82
U. pumila 8	× N248	18	220^{a}	4.5^{abc}	48^{ab}	22^{a}	84
U. pumila 8	× *U. pumila* 13	10	182^{b}	3.8^{bc}	41^{c}	21^{a}	80
U. pumila 13	× *U. pumila* 8	20	228^{a}	5.1^{a}	38^{a}	18^{a}	64
U. pumila 13	× Self	18	182^{b}	4.0^{b}	31^{b}	15	58

[1]) Values followed by the same letter in each column for progeny of each female parent do not differ significantly at the 95% level by DUNCAN's multiple-range test.

[2]) See text for parentage of male hybrids from the Netherlands.

[3]) Spring flushing was estimated on individual trees from 0% = no bud opening or enlargment, to 100% = individual leaves completely emerged from bud; observed 3/30/73.

several male parents used in 1970 to pollinate *U. pumila* and *U. rubra* × *pumila (Table 3).* The progeny of the male parent (N274 × 215) grew remarkably faster in height and diameter than progenies of N260, N262, and N339. The question can be asked: Are the differences in height among male progenies true indications of hybridity, or are the differences a manifestation of small differences at time of outplanting that persisted for 3 years? Average height data for several 1970 crosses are presented below:

Combination	Total average height (cm)		
	10/70	10/71	10/72
U. pumila × N262	26	69	133
U. pumila × N260	32	70	136
U. pumila × (N274 × 215)	28	97	231
(U. rubra × *pumila)* × N262	25	63	142
(U. rubra × *pumila)* × (N274 × 215)	28	88	184

It is evident from the above data that no true differences existed among progenies from the same female at one year of age. We can conclude, therefore, that the average height of the N274 × 215 progeny at 3 years of age is a true indicator of hybridity. We can also conclude that the faster growth potential transmitted by N274 × 215 was expressed in the second and third years of growth, and not during the first year. Greater differences in diameter growth and leaf width were shown by the progeny of *U. pumila* (♀) than by those of *U. rubra* × *pumila* (♀); male × female interaction was highly significant.

Significant differences among progenies from different male parents appeared for average leaf length, leaf width, and earliness of spring flushing *(Table 3).* Both (N274 × 215) and N248 progenies showed the longest leaves, whereas progenies of N262, N282, and N339 were characterized by significantly shorter leaves. The progeny from *U. pumila* × N248 showed significantly greater leaf widths than the corresponding progeny from N148 and (N274 × 215); leaf widths were more than double those of seedlings from N260 and N262. From these results, leaf size and shape, height, and diameter growth evidently can be considerably manipulated merely by selection of the proper male parent. According to Heybroek (1966), growth rate and leaf size have been important selection parameters in the Netherlands.

Not much variation in spring flushing was expressed among several males used to pollinate a single female, except that (N274 × 215) seedlings showed the earliest average flushing. Larger differences were expressed among different females crossed with the same male. All of the progenies from *U. pumila* flushed earlier than those from *U. rubra* × *pumila.*

Results of hybridizations made in 1971 between individual trees are presented in *Table 3.* Significant differences among male progenies from one female appeared for at least one, and most often several, of the following traits: height, diameter, leaf length, leaf width, and earliness of spring flushing. Among all progenies, those of *U. glabra* 19 × *carpinifolia* 61 (327 cm) and *U. glabra* 72 × *carpinifolia* 61 (273 cm) were tallest. The shortest progenies were from *U. carpinifolia* 71 × *carpinifolia* 61 (124 cm) and *U. carpinifolia* 61 × *pumila* 8 (135 cm). Differences in height growth among progenies from different males were greatest when *U. carpinifolia* 61 and *U. glabra* 19 served as the female parents *(Table 3). U. carpinifolia* 61 × *pumila* 8 seedlings were significantly smaller than all other progenies from *U. carpinifolia* 61 (♀), including the self. Also, the progeny from *U. pumila 8* × *carpinifolia* 61, the reciprocal of the above combination, was significantly smaller than *U. pumila* 8 selfed and *U. pumila* 8 × *glabra.* Therefore, interaction is evidently significant between *U. carpinifolia* 61 and *U. pumila* 8. Interaction between many parents was corroborated by statistical analyses of data not only of total height, but also of the other traits shown in *Table 3.*

When both *U. glabra* selections (61 and 72) served as either female or male parents, leaf length and leaf width values were larger than for those progenies of other selections. The difference in leaf size between corresponding male progenies from *U. glabra* 72 and *U. pumila* 8 was huge when *U. glabra* and *carpinifolia* 61 served as females *(Table 3). U. glabra* 19 as a male transmitted to its progeny longer leaf length than *U. parvifolia* 76 did as a male, when both were crossed to *U. carpinifolia* 61, but not when *U. pumila* 8 served as a female parent. When *U. glabra* 72 and *U. carpinifolia* 61 were used as males crossed with *U. pumila* 8 progenies did not show the leaf length differences that were shown by progenies of the same males crossed with *U. glabra* 19 and *U. carpinifolia* 61 females. The leaf length of *U. pumila* 13 selfed progeny was significantly less than that of *U. pumila* 13 × *pumila* 8.

Ultimate shape of the leaf was changed by choice of appropriate parents. For example, the *U. pumila* 8 × N248 progeny showed an extremely low ratio of leaf width to leaf length *(Table 3).* The progeny from the cross *U. glabra* 72 × *carpinifolia* 61, in contrast showed a corresponding high ratio. Average leaf width of offspring from *U. carpinifolia* 61 varied tremendously by male parent used. The average progeny from *U. glabra* (used as a male) showed double the leaf length and width of male progenies from *U. parvifolia* or *U. pumila (Table 3).* Interaction among combinations for leaf width appeared. The effects of *U. carpinifolia* 61 and *U. pumila* 8 as male parents were not consistent, for example, on *U. glabra* 72 (♀) and *U. carpinifolia* (♀).

Progenies from different males but from the same female parent varied in percentage of spring flushing by March 30, 1973 *(Table 3).* Generally, *U. rubra* and *U. glabra* as males retarded flushing in both of their progenies, compared to those of other male parents and the same female parents. Seedlings of *U. glabra* 72 × *carpinifolia* 61 and its reciprocal cross showed extremely slow flushing. *U. pumila* 8 was the most effective female parent in transmitting early flushing potential. *U. carpinifolia* 61 was more effective as a female than as a male parent in transmitting a tendency for early flushing.

Interaction appeared in many crosses. Striking differences were found in the cross *U. glabra* 19 × *carpinifolia* 61 and its reciprocal *(Table 3).* When *U. glabra* was used as a female parent in this cross, 100% of the trees showed early flushing, and average height was 327 cm. None of the *U. carpinifolia* 61 × *glabra* 19 progeny showed early flushing, and the average seedling height was only 239 cm. The degree of hybrid vigor between two species appeared to depend on which species served as a female and which as a male.

Several of the observations in this paper were related to differences between reciprocal progenies. Reciprocal differences result only when the two sexes make unequal contributions to the offspring. The presence of extrachromosomal inheritance (Jinks, 1964) could explain such phenomena. Possibly, for example, reciprocal differences in height growth are caused by maternal transmission of plastids that directly or indirectly control photosynthesis and growth. More detailed cytological studies must be done before we can prove extrachromosomal inheritance as the cause for differences in the reciprocal hybrids. Such factors as seed weight or size, and small numbers of trees (sampling variation) might also explain reciprocal differences.

Among progenies of males, variation in germination rates were considerable when *U. glabra* was used as a female parent:

Female parent	Seedlings 6/16/71 (final no.)	Germination by 6/3/71 (%)	Germination by 6/8/71 (%)
U. glabra 72 × *U. carpinifolia* 61	30	47	100
U. glabra 72 × *U. pumila* 8	46	74	100
U. glabra 72 × *U. rubra* 64	27	0	100
U. glabra 72 × *U. japonica* 1	7	0	100
U. glabra 19 × *U. carpinifolia* 61	27	41	67
U. glabra 19 × *U. glabra* 72	17	0	0

As shown above on *U. glabra* and also most other female parents, both *U. carpinifolia* 61 and *U. pumila* 8 enhanced the germination rate when they were used as male parents. These same two clones as females also transmitted a rapid germination rapid among progenies. *U. rubra* as a female transmitted the lowest average germination rate to its progenies.

From data presented in *Tables 2 and 3*, evidently great genetic progress can be made by selecting for general, as well as for specific, combining ability among parents that represent various species or hybrids. Depending on the traits desired, hybridization of specific clones yields progeny of desired parameters. Most of the parents used in these studies have shown high disease resistance; we can hope only that this resistance will be transmitted to the progenies discussed in this paper.

Summary

In compatibility tests between species of *Ulmus*, 31 attempts resulted in 21 verified, hybrid progenies. Generally, crossability barriers were weak or not present between various combinations of *U. glabra, U. carpinifolia, U. japonica, U. pumila, U. wilsoniana, U. parvifolia, and U. rubra.* An incompatibility barrier existed between *U. laevis* and the other *Ulmus* species used in breeding trials. Several new interspecific hybrids are reported. Success of many combinations depended on male-female interaction. Crosses involving the use of hybrids as parents were almost as successful as attempts between single species. Most species and hybrids had a high degree of self-incompatibility, with fewer than four seedlings produced in all attempted selves. *U. pumila* showed the highest degree of self-fertility.

Three-year-old hybrid progenies significantly differed in height, diameter, leaf length, leaf width, earliness of spring flushing, and germination rate. Significant variation was shown among progenies resulting from crossing different males with a single female parent or from hybridizing different females with one male. The magnitude of differences in various parameters among male progenies depended on the female parent; interaction between parents was common. *U. glabra* × *carpinifolia* progenies were tallest, and *U. carpinifolia* × *pumila* seedlings the shortest, of all interspecific combinations. Among the Netherlands hybrids used as parents, *(U. × hollandica × carpinifolia)* × *(U. pumila × carpinifolia)* transmitted to its progeny greatest potential for height and diameter size. The progeny from *U. wallichiana* × *carpinifolia,* when used as a pollen parent on *U. pumila,* displayed the lowest ratio of leaf width to length. The progeny from *U. rubra* and *U. glabra* generally showed late flushing. When used as male parents, *U. carpinifolia* and *U. pumila* enhanced germination rate.

Differences between reciprocal progenies were evident for height and diameter growth and time of flushing. The presence of extrachromosomal inheritance would explain differences between these progenies. However, other factors might also result in reciprocal differences.

Key words: compatibility tests, species of *Ulmus*, genetic gain, morphological variation.

Zusammenfassung

Von insgesamt 31 Kreuzungsversuchen mit jeweils verschiedenen Arten der Gattung *Ulmus* gelangen 21, d. h. aus letzteren Kombinationen gingen Hybrid-Nachkommenschaften hervor. Dabei zeigten sich nur in geringem Umfang Kreuzungsbarrieren. Solche waren überhaupt nicht festzustellen bei Kreuzungen mit *Ulmus glabra, U. angustifolia, U. japonica, U. pumila, U. wilsoniana, U. parviflora* und *U. rubra.* Dagegen konnte *U. laevis* nicht mit den übrigen, in den Versuchen benutzten Ulmus-Arten gekreuzt werden. Es wird über einige neue Art-Hybriden berichtet.

Viele der Kreuzungen gelangen nur in einer Richtung, d. h. z. B. *Ulmus glabra* ♀ × *U. japonica* ♂ usw., wobei die jeweils reziproken Kreuzungen ohne Erfolg blieben. Kreuzungskombinationen von Art-Hybriden gelangen ebenso wie solche von reinen Arten. Selbstungen gelangen nur vereinzelt und mit außerordentlich geringem Erfolg.

An den drei Jahre alten Hybrid-Nachkommenschaften konnten signifikante Unterschiede in Höhe und Durchmesser, Blattlänge und Blattbreite, Austrieb im Frühjahr und Keimungsrate festgestellt werden. Signifikant unterschieden sich auch Nachkommenschaften desselben Mutterbaumes nach Bestäubung mit verschiedenen Vaterbäumen oder aus der Kreuzung verschiedener Mutterbäume mit demselben Vaterbaum.

Die Nachkommenschaften von *Ulmus glabra* × *U. angustifolia* waren von allen Arten-Kombinationen am größten und diejenigen von *Ulmus carpinifolia* × *U. pumila* am kleinsten. Das größte Potential für Höhen- und Durchmesserleistung konnte durch die als Kreuzungseltern benutzten niederländischen Hybriden *(U. × hollandica × carpinifolia)* × *U. pumila* × *carpinifolia)* vermittelt werden.

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The Chromosome study of Giant Sequoia, Sequoiadendron giganteum[1][2]

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Awesome in size and height at maturity, the giant sequoia tree grows to be the most massive living organism in the world. *Sequoiadendron* is a monotypic genus belonging to the coniferous family of *Taxodiaceae* and related to another forest giant, the coastal redwood, *Sequoia sempervirens*.

Since the discovery of giant sequoia, botanical classification has been a problem. The tree has had no fewer than eight scientific names and is still called by an assortment of common namens. In recent years botanists have classified giant sequoia as *Sequoia gigantea* (Lindl.) Decne. (putting giant sequoia in the same genus as *Sequoia sempervirens* (D. Don) Endl. or *Sequoiadendron giganteum* (Lindl.) Buchholz (cf. Harlow & Harper, 1969). Presently, the latter name is accepted as correct, evidence being based primarily upon morphological, internal gametophytic, and embryological differences between giant sequoia and coastal redwood (Buchholz, 1939 a, b).

The haploid chromosome number, n = 11, was first observed by Buchholz (1939 a). Jensen and Levan (1941) recorded the diploid chromosome number (2n = 22) and described the centromere position in ten chromosome pairs as median or submedian and subterminal in the remaining pair. In an induced tetraploid plant they occasionally observed a small satellite to be proximally attached to a subterminal chromosome. Detailed karyotype analysis has not been conducted.

In this paper the results of cytological studies in *Sequoiadendron* will be briefly reported with special reference to the finding of an extraordinary chromosome pair in the somatic cells.

Materials and Methods

Root tips of two seedlings were used in the study. The somatic cells in the meristematic region were isolated and analyzed. Many of these cells were at metaphase and counts of the complete chromosome number were frequent.

The root tips were pre-treated with eight oxyquinoline for 36 hours at 4° C and fixed with 3 : 1 mixture of 95% ethanol and glacial acetic acid.

Staining Methods

Method I

Feulgen staining after hydrolyzing the materials for 10 minutes in 1 N HCl at 60° C.

Method II

Stained with acetocarmine after hydrolyzing the materials for 15 minutes in 1 N HCl at 60° C (Saylor, 1961).

The slides were prepared by using the squash technique and then made permanent by applying several drops of 10 : 1 mixture of 45% acetic acid and glycerol to the edge of the cover slip (Tsuchiya, 1971).

The nomenclature system of Levan *et al.* (1964) was used in the designation of the chromosomes, except for the SAT-chromosomes in which the length of the satellite has not been included in the arm length.

Results and Discussion

The somatic chromosome number is 2n = 22 *(Fig. 1—3)*, which confirms the results of previous work by Buchholz (1939) and Jensen and Levan (1941).

Jensen and Levan (1941) mentioned that 10 pairs were median and submedian, and one pair was subterminal without giving actual data.

Chromosome length was measured in the best cell in this study with results shown in *Table 1.* The two longest pairs are most likely metacentric chromosomes or M-type, eight pairs are near median or m-type, and the remaining pair,

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[2] This work was conducted as a part of the undergraduate training in the course "Special Study in Genetics" (Ag 495C) in the Department of Agronomy, Colorado State University.

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