1971

The Siberian Elm: Slippery Elm Hybrid

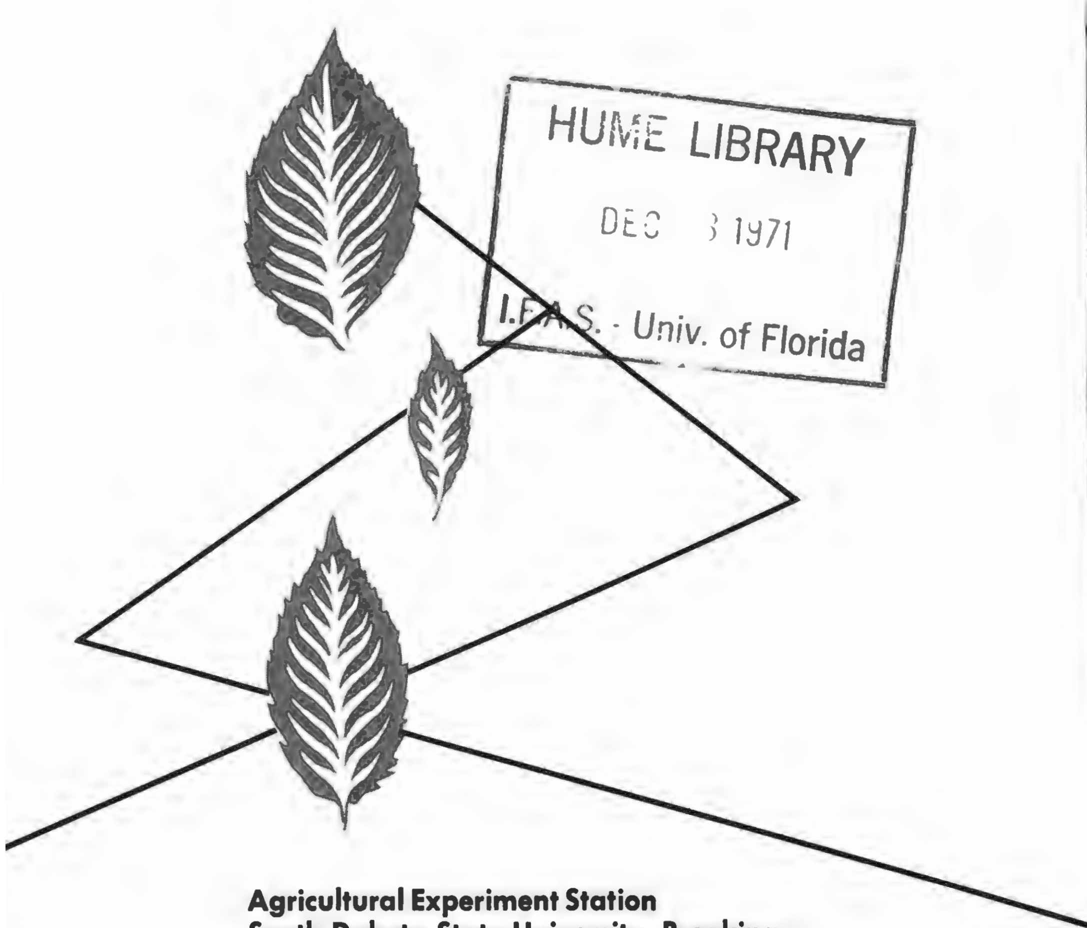
Paul E. Collins

Recommended Citation

Collins, Paul E., "The Siberian Elm: Slippery Elm Hybrid" (1971). *Agricultural Experiment Station Technical Bulletins*. 47.
http://openprairie.sdstate.edu/agexperimentsta_tb/47

Technical Bulletin 39
November 1971

The
Siberian Elm
Slippery Elm
Hybrid



Agricultural Experiment Station
South Dakota State University, Brookings

Abstract

Controlled crosses between several species of elm were initiated in 1953. Progeny of the early crosses between Siberian elm (*Ulmus pumila* L.) and slippery elm (*U. rubra* Muhl.) and of backcrosses were compared with parent trees in several leaf, fruit, flower and vegetative bud characteristics. Progeny of a cross between two F_1 hybrid elm trees (Slippery x Siberian elm) were also compared by the same morphological characteristics with the parent species. The hybrids tended to have intermediate characteristics between the parents in most cases. Height growth of 1964 crosses has been measured annually. In 1970, the F_1 hybrids averaged 3 to 4 feet taller than progeny of the Siberian elm parent. Growth cessation of the various hybrids at the end of the growing season did not differ from progeny of either parent species. Fruit collected from slippery elm trees growing near Siberian elm trees tended to have a high percentage of hybrid embryos. Fruit from slippery elm trees containing hybrid embryos germinated promptly while those having slippery elm embryos required cool stratification before germination took place.

The Siberian Elm Slippery Elm Hybrid

By **Paul E. Collins,** associate professor
Horticulture-Forestry Department

The information reported is based on a dissertation submitted to the Graduate School and School of Forestry, University of Minnesota in partial fulfillment of the requirement for the Ph.D. degree.

**Agricultural Experiment Station
South Dakota State University,
Brookings**

Contents

The Siberian Elm
Slippery Elm Hybrid

By **Paul E. Collins,** associate professor
Horticulture-Forestry Department

The Northern Great Plains Region of the United States is a natural grassland area. Native tree growth is limited to stream courses, lake shores, hillside breaks and mountainous areas where soil-moisture relationships are favorable for trees. For most of the area paucity of precipitation, heavy soils and low air humidity favors grasses over trees. Average annual rainfall over much of the area is 20 inches or less. Summer temperatures over 100° F. are not uncommon, and winter temperatures often drop to -20° F. or lower in January and February.

The first settlers who established homes in the region sought to improve the harsh environment by planting trees for shade, wind protection and aesthetic purposes. At first, wildings were dug from native stands and transplanted to home sites. Later trees were purchased from commercial sources. By trial and error and by organized tree planting trials at experiment stations, knowledge has been accumulated on adapted species and on cultural practices for successful establishment. Since the choice of native species is relatively limited, plant introductions from other areas of the United States and from other continents have become an important part of plains windbreak plantings. Some of the better introductions have come from Russia, Siberia and Northern China where the trees have developed under environmental conditions similar to the Great Plains. Among those now commonly used are Russian-olive (*Elaeagnus angustifolia* L.), Siberian peashrub (*Caragana arborescens* Lam.), Tatarian honeysuckle (*Lonicera tatarica* L.), common lilac (*Syringa vulgaris* L.), and Siberian elm (*Ulmus pumila* L.).

Although the introductions increase the number of species available for tree planting, tree improvement continues. Many tree species are beset by problems that limit their usefulness. The sub-humid to semi-arid climate of the plains destines trees to grow under conditions of moisture stress during most of the growing season except where ground water is near the surface. Consequently, many insect and disease problems which normally would be of secondary importance act as primary destructive agents to further weaken or kill the trees. Modern herbicides pose a serious threat to the native boxelder (*Acer negundo* L.) and other species. Dutch elm disease (*Ceratocystis ulmi* |Buism.| C. Moreau threatens to restrict or eliminate the use of American elm (*Ulmus americana* L.). Thus, there is a constant need to seek out better species, strains, and superior trees through introduction, seed source evaluation and selection. Tree hybridization, both inter- and intra-specific, offers an opportunity to up-grade the trees available for tree plantings.

One introduction, Siberian elm, found wide acceptance in the Northern Plains; fast growth, transplanting ease, drought resistance and an acceptable mature height combine to give it this standing. Fast growth is especially useful in farmstead windbreak planting where it provides protection from wind and snow just a few years after planting. By the time the Siberian elm rows begin to die out, slower growing, but longer-lived trees, are tall enough to provide the protection needed.

Many plantings of Siberian elm were planted in close proximity to the native slippery elm (*Ulmus rubra* Muhl.). Natural hybridization occurred between the two elms, and clones of the F_1 have been exploited by the nursery trade (Anon., 1950).

This study was initiated to further explore the hybridization patterns between these two species and to document useful growth data on the hybrids. Since an improved Siberian elm seed source had been identified, hybrids having the improved source as one of its parents should demonstrate reliable winter hardiness and drought resistance.

Parent Species

Slippery elm is a native species to all states east of the Great Plains including favorable sites in Eastern South Dakota (Harlow and Harrar, 1968). Siberian elm is an Asiatic elm of Eastern Siberia, North China and Turkestan (Rehder, 1940).

Siberian elm was first introduced into this country in 1905 (Wyman, 1951). Test plantings at various experiment stations showed satisfactory performance and soon farm and town plantings were made in the prairie areas of the United States. The number of trees planted reached large-scale proportions by the early 1930s. Wholesale importation of seed was necessary to produce enough planting stock. According to Webb (1948) most of the seed came from parent trees growing near Nanking, China, the same latitude as Ft. Worth, Texas. This seed source proved to be unsuitable when the 1940 Armistice Day freeze seriously damaged or killed a high percentage of Siberian elm trees in the Nothern and Central Great Plains (Engstrom and Matthews, 1942).

Some identifiable seed sources of Siberian elm were not injured by the sudden freeze. Seedlings from these sources were planted in a trial at the South Dakota State Agricultural Experiment Station. One of the sources, the Harbin seed, exhibited a relatively early cessation of growth, early enough to avoid injury from fall frosts (Maxon, 1951).

The Harbin source came from seed collected in the vicinity of Harbin, Manchuria, where the climate is characteristically continental north temperate. Winters are long and cold, summers are short and warm. The latitude of Harbin closely parallels the North Dakota-South Dakota border.

In 1952, the Harbin source was named Chinkota elm and released under state certification standards by the Experiment Station. Chinkota elm seedlings were planted in rows adjacent to a common commercial source in an experimental windbreak at Brookings in 1952. An early October freeze that same fall, injured or killed 80% of the commercial trees, while 90% of the Chinkota elms were alive to the tips or only slightly injured the following spring (Collins, 1955). Selected trees of the original foundation stock of Chinkota elm were used as parents in this study.

The slippery elm parent used in most crosses is a campus tree about 50 years old. Other slippery elm trees were used as parents in some phases of the hybridization study.

Slippery elm and Siberian elm are distinctly different in a number of morphological characteristics. Slippery elm is relatively large-leaved with few branched stout twigs and large buds. The upper leaf surface and young twigs are scabrous, and the elongate flower and vegetative buds are densely pubescent. In contrast, Siberian elm is small-leaved and develops a profusion of slender twigs with small buds. The upper leaf surface is smooth, and the young twigs are finely pubescent to glabrous. The spherical flower bud and vegetative bud are only sparsely pubescent. The samara fruit of slippery elm is densely pubescent over the seed cavity; the Siberian elm samara is glabrous.

Hybridization Studies

Previous work

The first report of artificially produced hybrids of forest trees was in Germany in 1845, when two species each of pine, oak, elm and alder were crossed (Larsen, 1956). Early tree hybridization in the United States has been reported by Schreiner (1937) in oaks, chestnuts and poplars.

Much of the early breeding work was initiated in response to diseases that threatened important tree species. Among the most important diseases for which disease-resistant trees have been sought are chestnut blight (*Endothia parasitica* [Murr.] A.S.A.), white pine blister rust (*Cornartium ribicola* Fisher) and Dutch elm disease. Richens (1945), Graves (1948), Clapper (1952), and Gerhold *et al.* (1966) have described these early tree breeding programs.

The identification of Dutch elm disease in The Netherlands in 1919 (Beattie, 1937), gave impetus to an elm breeding program in that country. Went (1938) summarized the early program of testing elm species and varieties collected from many parts of the world. More recent hybridization and selection work has been reported by Went (1954) and Heybroek (1962); Gerhold *et al.*, (1966). Accounts of the impact of Dutch elm disease and the programs initiated to solve the problem have been reported from other countries including England (Melville, 1944;

Peace, 1960; Anderson, 1961), Sweden (Ehrenberg, 1954), Italy (Goidanich, 1938) and Canada (Johnson, 1939; Anon., 1954). In the United States, progress in elm tree breeding has been reported by Smucker (1944), Graves (1948), Swingle *et al.* (1949), Clapper and Miller (1949), Clapper (1952), and Gerhold *et al.* (1966).

Studies have shown that resistance to Dutch elm disease exists in Asiatic elms. European elms are generally susceptible, but some species and varieties have shown varying degrees of resistance. American elms have proven to be the most susceptible. However, Smalley and Kais (Gerhold *et al.,* 1966) and other workers have found that a few sources of American elm have some resistance to severe crown damage and a few have even recovered from the infection. They also noted that some slippery elm seedlings show resistance to inoculations in somewhat the same manner as *Ulmus* x *hollandica vegeta* (Loud.) Rehd., a variety of Dutch elm.

Several selections of smoothleaf elm (*Ulmus carpinifolia* Gleditsch.), resistant to Dutch elm disease, have been released in Holland (Heybroek, 1962). More recently the cultivar *Ulmus* x *hollandica* 'Groeneveld' was released to growers in Holland. This resistant clone was the result of a cross between *Ulmus glabra* Huds. (Scotch elm) and *U. carpinifolia* (Heybroek, 1963). General hybridization patterns within the genus *Ulmus* were reported by Britwum (1961).

Controlled crosses between most elm species have not been difficult; however, attempts to cross American elm with other elm species has usually resulted in failure. All attempts to cross American elm with Siberian elm or slippery elm at the South Dakota Agricultural Experiment Station have failed. Probably a major barrier to successful interspecific crosses with American elm is the chromosome number. The basic number in elms is x=14 and most elm species are diploid (2n=28). However, American elm is a tetraploid (4n=56) (Sax 1933; Darlington and Wylie, 1956). Dermen and May (1966) and others have isolated apparent tetraploid Siberian elm seedlings after colchicine treatment and plan to use these trees in an attempt to obtain Siberian-American elm hybrids.

Controlled Crosses in Elm

The first controlled crosses between Siberian elm and slippery elm were made in 1953 and 1954 as shown in Table 1. Crosses also included American elm trees and two F_1 hybrid trees (Siberian x slippery elm). Pollinations were made by introducing pollen-bearing flowers into parchment bagged flowers on the parent trees, and then the branch with the bagged flowers was shaken. A small population of F_1 hybrids was obtained where slippery elm was the seed parent. The reciprocal cross gave only one plant. Backcross progeny were obtained from both of the parent species, though the number was quite small in the slippery elm backcross. The F_1 hybrid elm tree produced a good population of F_2 when crossed with another F_1 hybrid.

When F_2 populations are referred to in this report, it means the progeny of a cross between two different F_1 hybrid trees. The self-in-

Table 1. Inter-and Intra-Specific Ulmus Crosses and Selfings Made in 1953 and 1954

Female Parent	Pollen Parent														
	Siberian[1] Elm			Slippery Elm			American Elm			Hybrid[2] Elm			Selfs		
	B	F	S	B	F	S	B	F	S	B	F	S	B	F	S
Siberian Elm[1]	----	------	------	13	8	1	5	0	0	3	91	51	12	5	1
Slippery Elm	14	204	106	5	52	1	6	3	0	3	59	10	13	15	0
American Elm	4	0	0	4	0	0	10	177	21	----	------	----	2	1	0
Hybrid Elm[2]	5	255	155	3	37	8	----	------	----	10	184	96	4	1	0

B—number of bags; F—number of apparently filled seeds; S—actual number of seedlings obtained.

[1] "Chinkota" seed source.

[2] Slippery x Siberian elm (parent trees unknown).

compatible nature of F_1 trees used in this study precluded production of typical F_2.

Progenies from controlled crosses were transplanted in adjacent rows in 1954 and 1955 since the populations in all crosses were insufficient for a replicated trial. The trees provided a source of leaves, flowers, fruits and twigs for morphological measurements and gave some indication of growth rate and form.

Selfing Trials

Johnson (1946), Johnson and Heimburger (1946) and Went (1955) have reported a high incidence of self-sterility in elms. However, Went (1954) noted that individual trees varied in this respect. He found that a few hybrid elm trees were highly self-fertile.

Since attempts to obtain viable seed by selfing were not successful in these trials, several trees of four elm species were tested for self-compatability in 1959. Flower-bud bearing twigs on these trees were bagged prior to flowering and left until the fruit had matured. The results of the selfing trials are presented in Tables 2, 3, 4, and 5. Practically all trees tested showed high self-incompatability. Only two trees of slippery elm produced 20% or more apparently filled fruits out of the total crop. The F_1 hybrid trees (slippery x Siberian elm) produced no filled fruits.

Table 2. Selfing Frequency of Individual Trees in Slippery Elm

Tree No.	No. of Bags	No. of flower Clusters	No. of Fruit	No. of filled Seeds	Per cent filled Seeds
1	2	10	70	2	3
2	2	17	149	5	3
3	2	19	175	1	.6
4	2	26	270	3	1
5	2	19	142	77	54
6	2	14	129	7	5
7	2	9	10	2	20
8	2	28	157	0	0
9	2	23	162	1	6
10	2	30	230	0	0
11	2	21	65	1	2
12	1	7	105	0	0

Self-incompatible trees for controlled crosses are advantageous because the perfect flower of elm is very small, and emasculation requires magnification and painstaking care to remove all stamens without injury to the pistil. Some individual elm trees show marked protogyny, permitting artificial pol-

Table 3. Selfing Frequency of Individual Trees in Siberian Elm

Tree No.	No. of Bags	No. of flower Clusters	No. of Fruit	No. of filled Seeds	Per cent filled Seeds
1	1	21	300	1	3
2	3	106	590	0	0
3	2	58	530	0	0
4	2	90	950	22	2
5	2	57	580	4	.7
6	2	61	760	0	0
7	3	73	950	15	2
8	3	101	1000	4	.4
9	2	73	640	5	.8
10	2	69	800	0	0
11	3	89	800	0	0
12	3	49	725	3	.4
13	2	57	475	0	0

Table 4. Selfing Frequency of Individual Trees in American Elm

Tree No.	No. of Bags	No. of flower Clusters	No. of Fruit	No. of filled Seeds	Per cent filled Seeds
1	2	11	245	5	2
2	2	7	110	0	0
3	2	17	260	0	0
4	2	8	135	0	0
5	2	10	175	1	.6

Table 5. Selfing Frequency of Individual Trees in Slippery Elm x Siberian Elm

Tree No.	No. of Bags	No. of flower Clusters	No. of Fruit	No. of filled Seeds	Per cent filled Seeds
1	2	44	725	0	0
2	2	58	825	0	0
3	2	23	225	0	0
4	2	53	650	0	0
5	2	44	575	0	0
6	2	53	800	0	0
7	2	42	500	0	0
8	2	22	148	0	0
9	2	32	300	0	0
10	2	38	116	0	0

lination before anthers dehisce. This is a most useful feature in those trees not having a high degree of self-sterility. Figures 1, 2, 3, and 4 illustrate such flowers.

Siberian-Slippery Elm Hybrids

An effort was made in 1964, to produce F_1, F_2 and backcross populations to compare with seedlings of the parent species. Most of the crosses were made on trees, but additional pollinations were made on cut branches and bottle-grafted trees in the greenhouse. Unfortunately, high temperatures in the greenhouse caused most of the developing fruits to drop prematurely. Figure 5 shows a bottle-grafted tree on which a fruit cluster is nearing maturity. Figure 6 shows a 9-year-old bottle-graft of slippery elm with its prominent flower buds.

The field trees were bagged with parchment bags the first week of April. A severe windstorm on April 13, destroyed over half of the bags. The branches were re-bagged immediately after the storm, but some Chinkota elm flower buds were damaged and some pollen contamination may have occurred.

The trees were pollinated over a four-day period by forcing pollen into the bags with a syringe. By May 22, the fruit had ripened and was collected. The filled fruits were separated from empty fruits and counted. They were then stored in air tight containers under refrigeration. Results of the fruit yield are presented in Table 6. All crosses yielded ample quantities of fruit

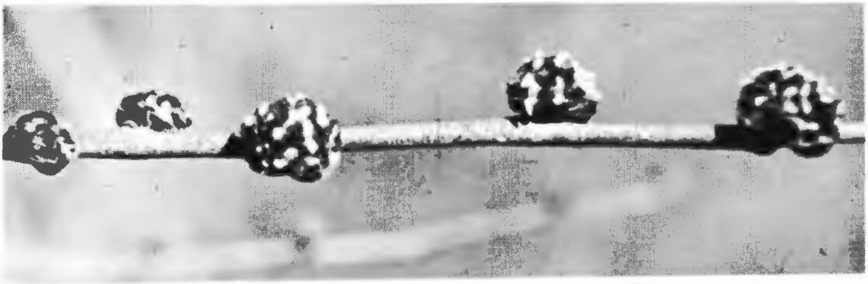


Figure 1. Protogynous (maturing of pistils before stamens shed pollen) Flowers of Siberian Elm.

except those between F_1 hybrid trees. This cross was repeated in 1965, with the same result. The F_1 trees used in these pollinations were from 1953-54 crosses, which were now old enough to bear fruit.

Growth

Exceptional growth and vigor have been reported in progenies of interspecific crosses in several tree genera. For instance, Stockwell and Righter (1947) suggested that pine hybrids would increase volume two to three times over natural stands. Comparable data in elm are somewhat fragmentary. Aljbenskii (1951; 1956) reported that hybrids of Siberian elm and European white elm (*Ulmus laevis* Pall.) grew taller and had larger diameters than the parent species. These hybrids also showed good drought and soil salinity resistance. Hartley (1927) reported that the Huntingdon elm (*U. glabra* x *U. montana*) grew twice as fast in height as other elms in the same plantation. Rockwell (1945) stated that in South Dakota hybrid elms (*U. pumila* x *U. rubra*) grew as fast in height as Siberian elm. By 1966, the F_1 hybrids

Figure 2. Protogynous Flowers of Slippery Elm.

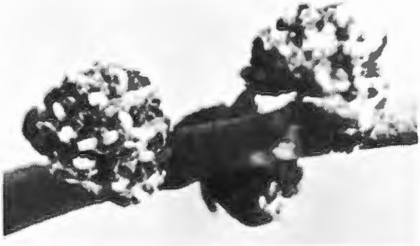


Figure 3. Protogynous Flowers of Slippery Elm x Siberian Elm.

Figure 4. Protogynous Flowers of American Elm.

of Siberian and slippery elm which were produced in 1954, averaged 35 feet in height—the tallest tree was 40 feet. In the same planting Chinkota elm averaged 33 feet.

The 1964 seed was sown in greenhouse flats on July 2. Prior to sowing all seeds were soaked in water, and the slippery elm seeds were stratified for 23 days at 41° F. The germinating seedlings were transplanted into peat pots after 12 days and kept in the greenhouse for about two weeks. They were then placed outside to harden for a few days.

On August 3, the seedlings were planted into the field site in a randomized complete block design in four tree plots and 10 replications. The seedlings were planted one foot apart in rows three feet apart.

Figure 5. Bottle-Graft of Scotch Elm on a Siberian Elm Seedling Showing Samaras on the Scotch Elm Nearing Maturity.

Figure 6. A Nine-Year-Old Bottle-Graft of Slippery Elm on a Siberian Elm Seedling Root. (Prominent buds on the slippery elm top are flower buds.)

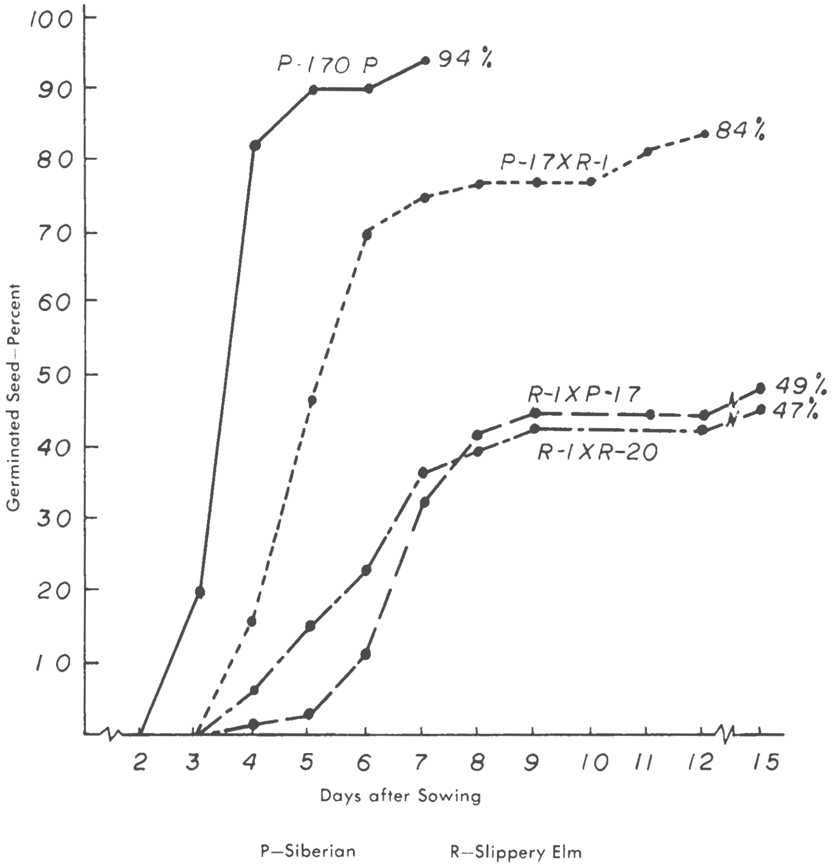


Figure 7. Germination of Seeds of Siberian Elm, Slippery Elm and their Hybrids (80 seeds per lot).

The trees were watered at planting and subsequently as needed. Insecticides were applied to control leaf defoliators and root feeders. The area was fenced to prevent rabbit injury. Trees that died in the planting were replaced by transplanting supply plants of the same age growing in adjacent rows. Replication number 10 was lost to residual action of simazine which had been applied four years earlier in an unrelated experiment.

Seeds from the controlled cross between two slippery elm trees failed to germinate promptly. Consequently, open-pollinated seedlings of slippery elm were planted as slippery elm trees. After a month of growth, it was apparent that open-pollinated seedlings of slippery elm were actually natural hybrids with Siberian elm. To rectify the situation, seeds of slippery elm x slippery elm, which had been placed in stratification in June,

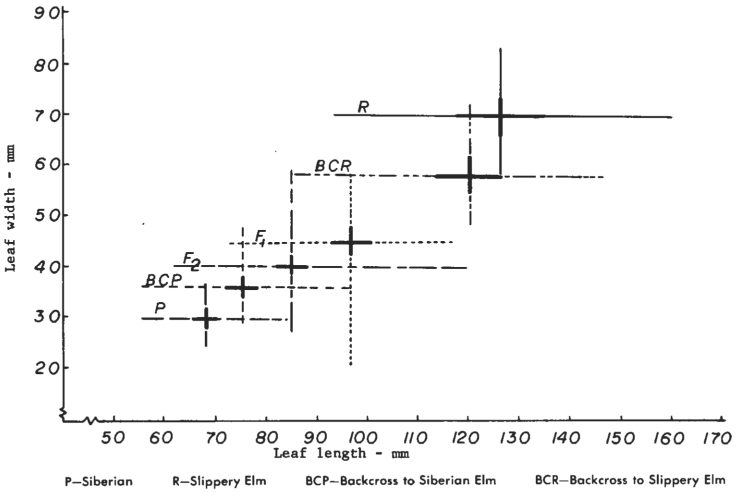


Figure 8. Ranges, Means and Two Standard Errors of Leaf Width and Leaf Length of Siberian Elm, Slippery Elm and their Hybrids.

were sown in August. They germinated satisfactorily and were kept in the greenhouse until natural growth cessation occurred in October. After a chilling treatment they were forced into growth in the greenhouse in March, 1965, and transplanted into the study plot in May, replacing one of the slippery elm open pollinated lots (F_1).

In the spring of 1966, all trees in the planting were undercut, lifted, and replanted in a new area. The trees were spaced 8'x12' and planted in a randomized complete block design with 4 tree plots and 9 replications. Height growth data and other observations have been taken since that time. Average height growth for each year is given in Table 7. In all years measured, the progeny group differences have been highly significant by the analysis of variance method. (See Table 8 for 1970 height growth data.) The Duncan multiple range test applied to the 1970 data shows the superiority of F_1 hybrids in height growth as compared to plants of the parent species and backcrosses. The tallest tree at the end of the 1970 growing season was an F_1 hybrid which had attained a height of 27 feet.

Growth Cessation

In mid-August, 1965, every tree in the test planting was staked with a 4-foot bamboo pole. The leading shoot was tied loosely to the stake. Beginning on August 30, increase in height growth was marked on the stake at two- to three-day intervals. A reference mark at the base of the stake and the tree insured constant alignment. The date of cessation of height growth was recorded for each tree.

Results are given in Table 9. The date on which most trees stopped growing is underlined. For most progeny lots this occurred on September 20. The most variable in growth cessation was slippery elm and the backcross to slippery elm. The least variable was Chinkota elm.Generally there were no marked differences between progenies of the two seed parents or their hybrids.

Seed Germination

Eighty seeds each of Chinkota elm (P-170P), Chinkota elm x slippery elm (P-17 x R-1), slippery elm x Chinkota elm (R-1 x P-17) and slippery elm (R-1 x R-20) were sown in greenhouse flats in June 1965, to obtain seedlings for mounting and measurement. Daily germination dates were recorded. Slippery elm seeds were stratified three months before sowing. The germination pattern of these seed lots is illustrated in Figure 7.

The influence of the seed parent on rate of germination was rather striking. Chinkota elm seeds germinated rapidly and reached germinative capacity in 7 days. Seeds of P-17 x R-1 began germination a day later, but they germinated rapidly in a pattern similar to Chinkota elm. F_1 hybrid seeds from the slippery elm seed parent and slippery elm seeds were markedly sluggish in their germination pattern. Only half of the latter two seed lots had filled embryos as verified by checking the non-germinating seeds after the test was completed.

Table 6. Hybridizations between Siberian Elm and Slippery Elm and the F_1 Hybrid in 1964.

Seed Parent	Pollen Source																										
Female Tree	Pm			P-17			R-1			R-20			H-1			H-17			P-30			P-32			P-35		
	B	TF	F	B	TF	F	B	TF	F	B	TF	F	B	TF	F	B	TF	F	B	TF	F	B	TF	F	B	TF	F
P-17	—	—	—	2	300	79	13	2000	300	—	—	—	5	500	68	—	—	—	—	—	—	—	—	—	—	—	—
R-1	7	600	400	6	1000	750	1	400	0	10	1300	1000	7	400	3	—	—	—	—	—	—	—	—	—	—	—	—
R-20	—	—	—	7	160	61	7	[illegible]	79	1	10	0	4	100	62	—	—	—	—	—	—	—	—	—	—	—	—
H-1	—	—	—	10	10,000	1	8	4000	0	—	—	—	12	10,000	0	15	10,000	0	—	—	—	—	—	—	—	—	—
H-17	—	—	—	1	400	0	1	400	1	—	—	—	8	10,000	0	—	—	—	—	—	—	—	—	—	—	—	—
P-30	—	—	—	—	—	—	6	[illegible]	81	—	—	—	3	500	88	—	—	—	3	300	20	—	—	—	—	—	—
P-32	—	—	—	—	—	—	14	[illegible]	15	—	—	—	8	5,000	172	—	—	—	—	—	—	3	300	0	—	—	—
P-35	—	—	—	—	—	—	3	500	0	—	—	—	2	400	130	—	—	—	—	—	—	—	—	—	5	500	0

B—number of bags; TF—total number of fruits (above 2000 estimated to nearest 1000)
F—filled fruits
P—Siberian "Chinkota" elm
R—Slippery elm
H—F_1 hybrid (slippery x Siberian)
Pm—mixture of pollen from several "Chinkota" trees

Production of Hybrid Seed

Siberian elm and slippery elm have flowering dates that overlap. Usually, Siberian elm flowers slightly earlier and is shedding pollen at the time the protogynous flowers of slippery elm are receptive. This offers an opportunity for natural hybridization to occur with slippery elm as the seed parent. In 1952, a planting was made in the Brookings area to explore this possibility. Chinkota elm and slippery elm trees were planted side by side in an isolated area. First flowering and fruiting occurred in 1964, and open pollinated fruit was collected from slippery elm trees which ripened ample quantities of samaras. In January 1965, 300 stored seeds from one slippery elm parent were placed in cold stratification at 40° F. By April, after 46 days of stratification, 90 sprouted seeds were removed and sown in flats. These seeds had little or no dormancy and had begun to grow slowly at the low stratification temperature. The resulting seedlings were left in flats until at least 4 true leaves had formed, at which time they were pulled, pressed and mounted.

In June, the remaining seeds were removed from stratification (142 days) and sown in flats. These were also grown to the same size and were mounted.

The seedlings were classified as hybrids (slippery elm x Siberian elm) or as slippery elm on the basis of leaf shape, presence of long hairs on the upper leaf surface, degree of sunkenness of main veins and seedling vigor. All seedlings that developed from early germinating seeds were hybrids; all but five seedlings from late germinating seeds were slippery elm which is consistent with stratification requirements of that species.

Approximately 45% of the seedlings from 300 seeds were hybrids. Furthermore, all seeds that had little or no dormancy produced F_1 hybrid seedlings. Dormant seeds produced almost all slippery elm seedlings.

This test verified that natural hybridization does occur when slippery elm grows in close proximity to Siberian elm. It also suggests a method by which commercial production of hybrid seed is possible. If selected slippery elm and Siberian elm trees are planted in adjacent rows or alternated in the row, seed can be collected from the slippery elm trees and sown in rows without prior stratification. Seeds that germinate promptly will produce F_1 hybrids; dormant seeds, most of which are slippery elm, will probably fail to germinate or germinate too late to cause any problem in the lifting and grading process.

Morphological Characteristics

An extensive study of the taxonomic characteristics of elms has been undertaken by Richens (1955, 1956, 1958, 1959, 1961a, 1961b) for the purpose of identifying elm species and hybrids growing in England. He measured several leaf characteristics including length, relative width (width/length), relative petiole length (petiole length/leaf length), basal asymmetry, number of teeth, a set of measurements on the marginal tooth, and the degree of scabrousness of the leaf surface. Melville (1937) noted that elm leaves developed different shapes depending upon the part of the crown and upon the kind of shoot on which they were growing. Leaves formed on short lateral shoots differed from those formed on a leading shoot, a proleptic shoot, an epicormic shoot or a sucker. He recommended that sample leaves be taken from short lateral shoots. Later he (1960) recommended that the third leaf from the apex on short lateral branches be taken for samples since these leaves are the least variable.

Leaves

In this study the third leaf from the apex on a short determinate lateral branchlet on the south side of the mid-crown was collected from several trees of the parent species and from the hybrids of the 1953 and 1954 crosses. When the third leaf was not usable because of malformation or mechanical injury, the fourth leaf was sampled. All leaves were dried, pressed and measured.

All sample leaves were measured for leaf length and width (at widest dimension), length of leaf from the widest point to the base, length of petiole, number of pinnate veins on the longest side of the leaf, number of bristles and/or hairs per $80mm^2$ on the upper leaf surface, number of hairs along 8mm of length of the longest vein on the leaf undersurface and leaf weight. Averages and standard errors of these measurements are presented in Table 10. Figure 8 illustrates the ranges, means and two standard errors of two leaf characteristics measured. Sample leaves of each progeny group are shown in Figure 9.

Table 7. Average Height Growth of Various Elm Progeny from 1965 through 1970.

Progeny	1965 inches	1966 inches	1967 feet	1968 feet	1969 feet	1970[1] feet
P x R	39	57	10.9	11.7	16.8	21.7a
R x P	49	66	11.5	12.2	16.6	20.7a
R OP	40	54	9.4	10.9	14.9	18.8 b
P	34	48	7.3	9.5	13.4	17.1 c
BCR	26	36	7.0	7.8	13.2	16.9 cd
R	22	44	7.3	7.6	11.8	15.4 de
BCP	32	43	6.9	8.6	11.9	14.9 e

P—Chinkota elm; R—slippery elm; RxP, PxR, R OP-F_1; BCR, BCP-backcrosses.

[1] Any means not followed by the same letter are significantly different at the 5 percent level.

Table 8. Analysis of Variance of Height Growth of 7-year-old Elm Progeny.

Source of variation	JF	SS	MS	F
Progenies	6	1441.25	240.20	22.61**
Replications	8	180.71	22.58	2.11*
Experimental error	48	509.52	10.62	.99
Sampling error	189	2023.69	10.70	
Total	**251**	**4155.17**		

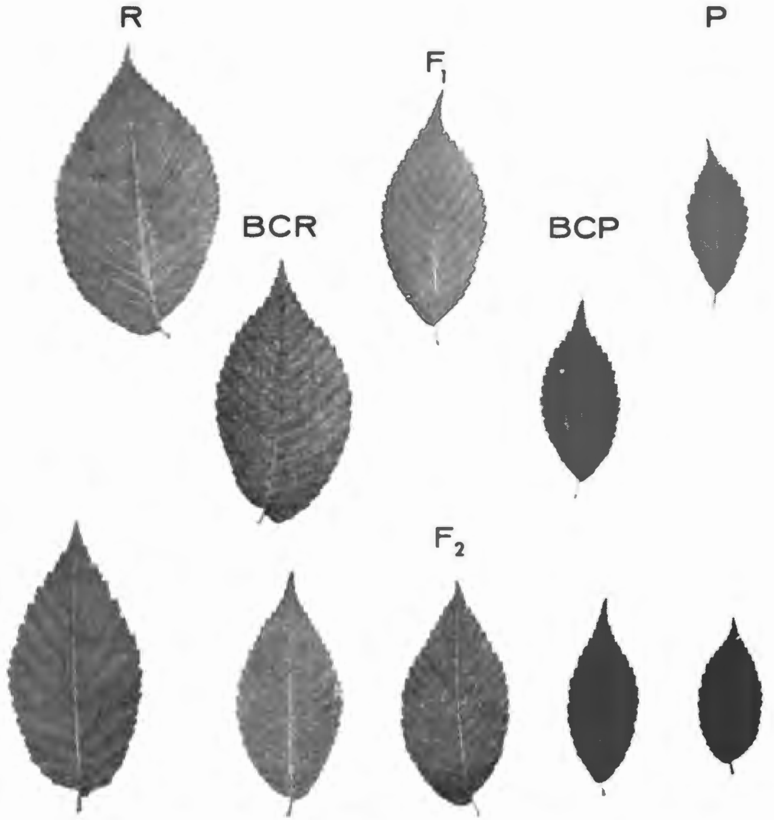
**Significant at 1% level.

*Significant at 5% level.

Table 9. Growth Cessation of Individual Trees within Each Ulmus Progeny Group by Frequency and Date of Cessation (1965)

	Progeny Groups							
Date	P-17	P-17 OP	P-17 x H-1	P-17 x R-1	R-1 x P-17	R-20 x H-1	R-1 x R-20	H-1 OP
Aug. 30							1	
Sept. 1			1			1	1	
3	2					2	2	1
8	3	1	2	1		1	2	1
10	3	3	3	1	1	2	3	1
13	9	8	3	2		7	6	4
15	7	9	5	3		7	3	11
17	1	1	1	1		2	1	
20	3	10	17	16	16	2	11	12
22		3	2	5	3	3		3
24		1			7	5	1	1
27			1	2	4	2	3	2
29			1	1	1			
Oct. 1				3	2	1	1	
4				1	2		1	
8						1		

P—Siberian elm ("Chinkota"); R—Slippery elm; H—Siberian x slippery elm



R—Slippery Elm P—Siberian BCP—Backcross to Siberian Elm
BCR—Backcross to Slippery Elm

Figure 9. Typical Leaves of Siberian Elm, Slippery Elm and their Hybrids (5/16 natural size).

The F_1 hybrid showed intermediate characteristics between the two parents in leaf length and width, number of veins per leaf, hairiness (both finer hairs and bristles) and weight. The F_1 was similar to Siberian elm in leaf width to length ratio, in leaf shape and in petiole to blade length ratio. The petiole length of the F_1 exceeded both parents.

Backcrosses also showed intermediate characteristics between the F_1 and the parent species in leaf length and width, number of veins per leaf and hairiness and to some extent in leaf weight.

The F_2 population tended to have mean characteristics similar to the F_1 and the backcross to Siberian elm. The 68 trees surviving at the time of leaf collection were numerically insufficient to produce the full array of segregates expected.

Seedling leaves of the parent species, of the Chinkota elm x Slip-

Table 10. Means and Standard Errors of Ten Leaf Characteristics of Siberian and Slippery Elm and their Hybrids

Progeny Group	Leaf Characteristics									
	Blade Length mm	Blade Width mm	Width/ Length ratio	E/L	Petiole Length mm	P/L[2]	V[3]	Pub[4]	HV[5]	Leaf Weight grams
P	69.0	30.4	.44	.44	8.6	.12	12.3	0.0	0.7	.1424
Std. Err.	1.44	.64	.009	.009	.33	.004	.26	....	.25	.0078
BCP	76.4	36.2	.47	.43	7.8	.10	12.4	8.5	8.0	.1425
Std. Err.	1.63	.91	.007	.008	.42	.005	.32	2.09	.83	.0094
F_1	97.1	44.9	.46	.44	10.4	.11	14.0	52.9	18.2	.2609
Std. Err.	1.84	1.39	.003	.005	.28	.003	.19	9.85	1.23	.0150
BCR	120.6	58.5	.48	.47	8.8	.07	16.3	220.1	35.6	.4369
Std. Err.	3.16	1.69	.01	.008	.40	.004	.40	24.09	2.16	.0252
R	126.5	70.1	.55	.47	7.7	.06	16.6	264.1	48.7	.6201
Std. Err.	4.35	1.80	.01	.009	.41	.002	.35	14.49	2.30	.0388
F_2	85.7	40.5	.47	.45	7.2	.08	13.1	132.6	16.8	.2268
Std. Err.	1.54	.75	.006	.005	.25	.003	.24	18.11	1.32	.0078

P—Siberian elm; BCP—Backcross to Siberian elm; BCR—Backcross to Slippery elm.
R—Slippery elm

[1] E/L—Ratio of length from base of blade to widest part to total length.

[2] P/L—Ratio of petiole length to blade length.

[3] V—Number of main pinnate veins on longest side of blade.

[4] Pub—Number of hairs on a 80 mm^2 area on upper surface of blade.

[5] HV—Number of hairs along 8 mm length of longest pinnate vein on under surface.

pery elm hybrid, and of the reciprocal cross were also compared. The first two true leaves formed showed the least variability and were the most useful as indicators of type of progeny. Leaf length and width and the distance from the widest portion of the leaf to the leaf base were measured on one leaf of each seedling.

The Chinkota elm seedling leaf was typically narrow and distinctly obovate. The slippery elm leaf was much wider than the Chinkota elm leaf and generally had a reticulate appearance on the upper surface due to sunken main and side veins. Pubescence was present on the upper surface of seedling leaves of both species, though some Chinkota elm leaves were glabrous. Hairs were much longer on leaves

Table 11. Means and Standard Errors of Four Leaf Characteristics of the First True Leaf of Seedling Elms

	Length mm	Width mm	E/L[1]	W/L[2]
P-17	15.6	6.5	.57	.42
Standard Error	.30	.14	.003	.010
P-17 x R-1	16.6	8.4	.48	.50
Standard Error	.25	.14	.007	.007
R-1 x Pm	19.1	10.2	.48	.54
Standard Error	.50	.35	.007	.013
R-1 x R-20	16.2	9.3	.48	.58
Standard Error	.48	.32	.012	.021

P—Siberian elm ("Chinkota")
R—Slippery elm
Pm—Mixed pollen of "Chinkota" elm

[1] E/L—Ratio of length of blade from base to widest part to length of blade

[2] W/L—Ratio of blade width to length

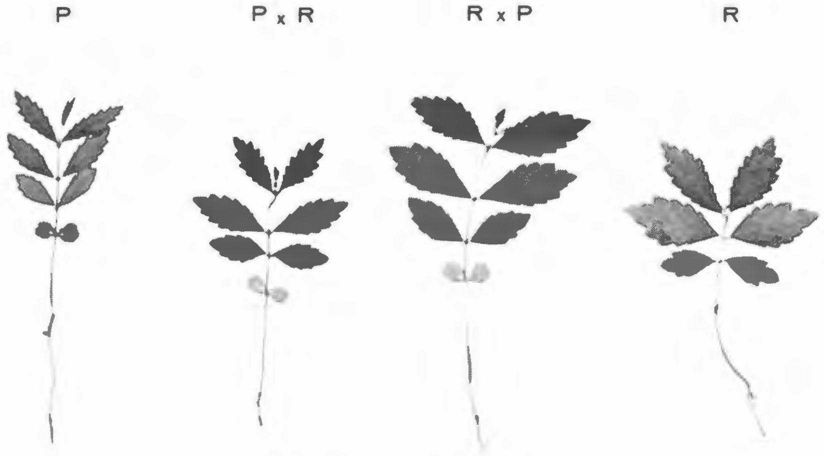


Figure 10. Typical Seedlings of Siberian Elm, Slippery Elm and their Hybrids.

of slippery elm seedlings than on leaves of Chinkota elm.

F_1 hybrid seedlings had leaves that averaged longer and wider than leaves of Chinkota elm seedlings. This was most striking where slippery elm was the seed parent. The F_1 hybrid seedlings grew more rapidly than slippery elm seedlings. The latter tended to grow so slowly that the first four leaves often showed a whorl-like arrangement; on the other hand, hybrid seedlings showed definite elongation of the internodal region between the first and second pairs of leaves. Averages and standard errors of seedling leaf measurements are given in Table 11. A sample of each seedling type is illustrated in Figure 10.

Fruits

Four samaras were collected from each fruiting tree of the various hybrid elm types and from the parent species in 1961, when a high percentage of the trees matured fruit. Each samara was measured in length, width, length from the base to the point of greatest width, length of fruit stalk (after freeing from the residual calyx), depth of the apical notch and length of the free portion of one of the residual stigma lobes at the apical end. In addition, the number of hairs on the seed cavity and on the main vein from the base of the samara to the seed cavity was counted. Each samara was weighed.

The means and standard errors of nine samara characteristics are presented in Table 12. The most obvious differences between populations were in pubescence counts, though the F_1 and F_2 samaras were somewhat more sparsely pubescent than anticipated. Apparently the glabrous condition of Siberian elm was somewhat dominant. Intermediate characteristics in the F_1 were also noted in the depth of the

Table 12. Means and Standard Errors of Nine Samara Characteristics of Siberian Elm, Slippery Elm and their Hybrids

Progeny Group	Length mm	Width mm	E/L[1]	N[2]	Fruit stalk Length mm	RS[3]	SC[4]	VH[5]	Samara Width gms.
P	12.4	12.0	.55	2.6	1.4	.3	0	0	.0069
Std. Edd.	.27	.34	.009	.13	.06	.03	....	....	.0003
BCP	12.0	11.6	.57	1.9	1.5	.5	1	1	.0058
Std. Err.	.23	.23	.006	.09	.02	.03	.30	.08	.0003
F_1	12.6	12.5	.59	1.4	1.8	.9	22	8	.0073
Std. Err.	.19	.17	.008	.05	.06	.04	1.7	.7	.0002
BCR	13.7	11.9	.57	1.6	2.4	1.0	134	29	.0086
Std. Err.	.32	.26	.009	.08	.03	.04	8.2	2.5	.0003
R	13.2	11.0	.60	.80	2.4	1.2	459	63	.0098
Std. Err.	.17	.25	.010	.04	.08	.04	4.3	3.1	.0003
F_2	11.7	10.7	.57	1.5	1.4	.5	18	5	.0078
Std. Err.	.12	.13	.004	.04	.05	.02	2.1	.5	.0002

P—Siberian elm; BCP—Backcross to Siberian elm; BCR—Backcross to slippery elm; R—slippery elm

[1] E/L—Length from base to widest part to total length ratio

[2] N—Depth of apical notch in mm

[3] RS—Length of free portion of residual stigma

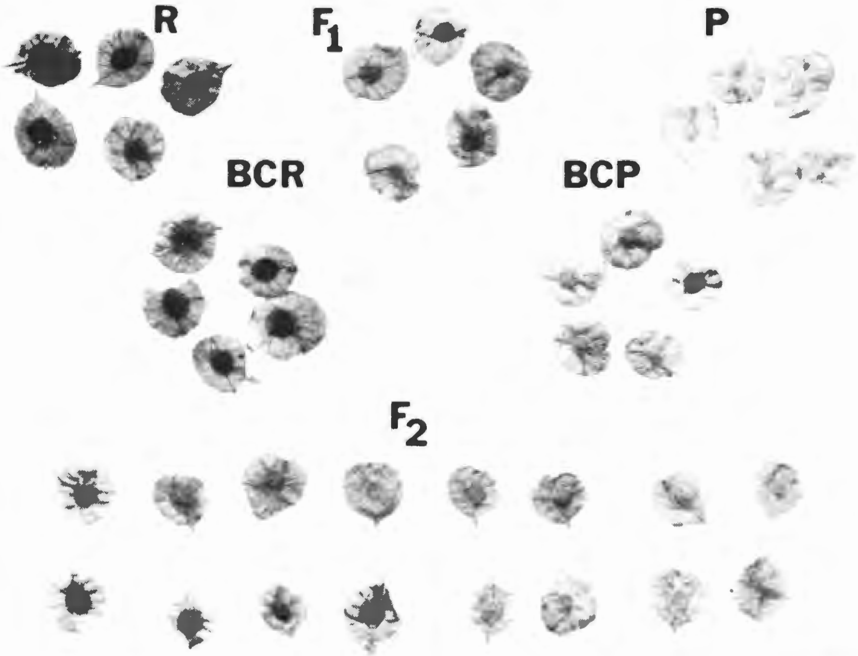
[4] SC—Number of hairs on the seed cavity

[5] VH—Number of hairs on main vein from base of seed cavity to base of samara

Table 13. Means and Standard Errors of Buds and Flower Characteristics of Siberian Elm, Slippery Elm and their Hybrids

Progeny Group	Vegetative Bud Length mm	Flower Bud Length mm	Floret Length mm	Floret Width mm	No. of Florets/ inflorescence
P	1.9	3.4	2.2	1.5	15.1
Std. Err.	.16	.13	.04	.04	.54
BCP	2.0	4.3			19.4
Std. Err.	.05	.03			.94
F_1	3.1	5.0	3.3	1.6	24.6
Std. Err.	.02	.04	.04	.05	.76
BCR	3.6	5.2			21.6
Std. Err.	.02	.07			.87
R	5.7	7.3	4.4	2.3	17.9
Std. Err.	.13	.13	.02	.04	.65
F_2	2.6	4.2			19.4
Std. Err.	.04	.02			.44

P—Siberian elm; BCP—Backcross to Siberian elm; BCR—Backcross to slippery elm
R—Slippery elm



R—Slippery Elm
BCR—Backcross to Slippery Elm

P—Siberian
BCP—Backcross to Siberian Elm

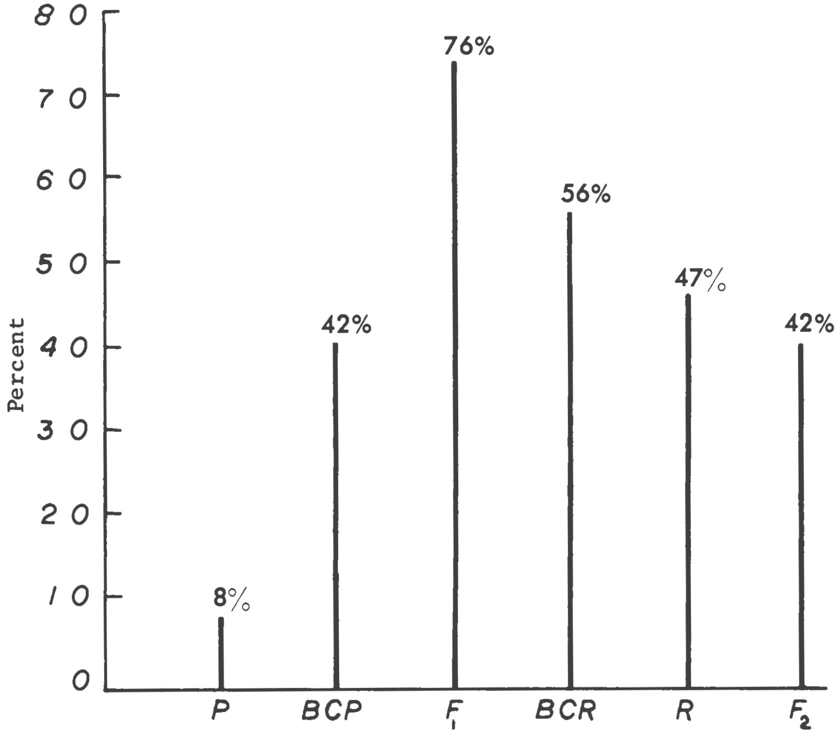
Figure 11. Typical Samaras of Siberian Elm, Slippery Elm and their Hybrids (about ¾ natural size.)

apical notch, fruit stalk length and fruit weight and length. F_2 samaras were very similar to the backcross to Siberian elm. Figure 11 is a photograph of samples of each progeny group.

Flowers and Buds

One twig which bore several flower buds was collected from each tree of the various progenies and parent trees. Every flower bud was dissected to determine the number of florets in each inflorescence. Ten per cent of the florets from each twig were dissected under magnification for counts of the number of stamens in each floret. Only 5% of the F_2 population fruited and several of those trees had poorly developed buds. Most trees in the other progeny groups bore flower buds. Later in the season, inflorescences were collected at the time of initiation of anthesis and were stored in alcohol for later measurement.

Means and standard errors of floret length and width as well as vegetative bud and flower bud lengths are recorded in Table 13. The F_1 floret was intermediate in



P—Siberian
BCP—Backcross to Siberian Elm

R—Slippery Elm
BCR—Backcross to Slippery Elm

Figure 12. Percent of Inflorescences Having 20 or More Florets in Siberian Elm, Slippery Elm and their Hybrids.

length between the two parent species, but the width was similar to Siberian elm.

The inflorescence of the F_1 contained more florets than either parent, apparently an expression of hybrid vigor. The frequency with which inflorescences having twenty or more florets present in each of the progeny groups is shown in Figure 12. The chi-square test of independence applied to these frequencies shows that they differ at a highly significant level. Some of the F_1 inflorescences had over 40 florets and 19 percent had 30 or more. Eight percent of the F_2 flower clusters had 30 or more florets, and one flower bud contained 56 florets, the maximum counted in any inflorescence.

The individual florets of each of the progeny groups also differed in the number of stamens present. In

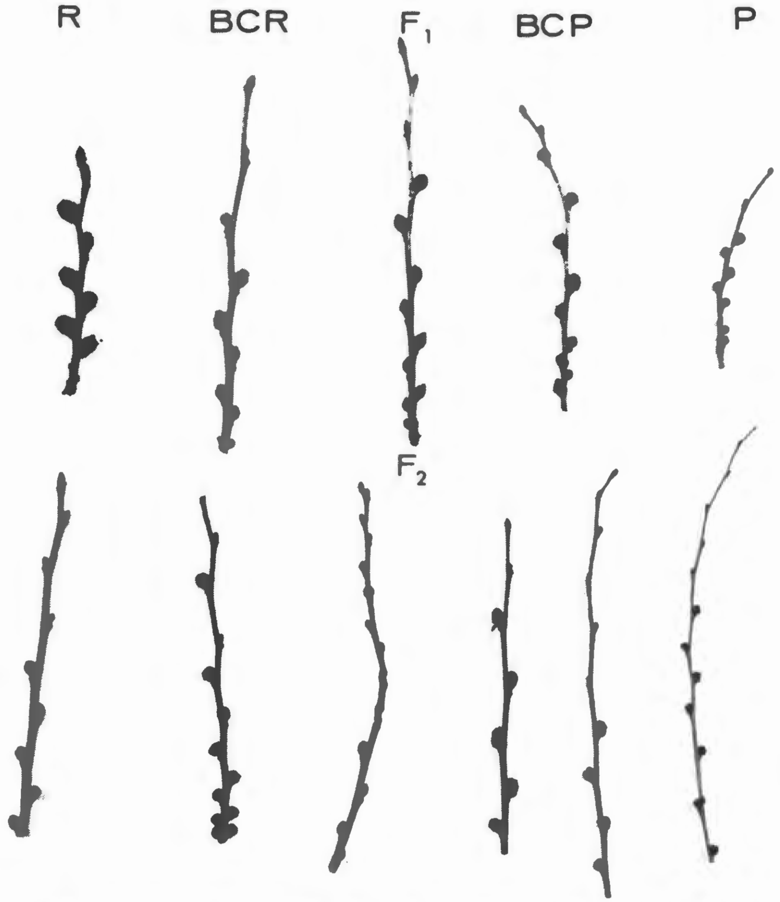


Figure 13. Typical Twigs of Siberian Elm, Slippery Elm and their Hybrids Showing both Vegetative and Flower Buds (about 1/4 natural size).

Siberian elm, four stamens per floret were most common. In slippery elm, most florets had seven stamens but the number varied from 5 to 8. Other progeny groups had stamen counts that were intermediate. The number of stamens in F_2 florets varied from 3 to 7 (Table 14).

Vegetative and flower bud measurements of F_1, backcrosses, and F_2 were intermediate between the parental types. These measurements were made on the first vegetative bud below the pseudoterminal bud and on the first flower bud from the apex on ten twigs from each tree. Typical twigs with both kinds of buds are illustrated in Figure 13.

Table 14. Percent of Occurrence of Stamens per Floret in Siberian Elm, Slippery Elm and their Hybrids

	No. of stamens per floret					
Progeny	3	4	5	6	7	8
	Percent of florets sampled					
Siberian elm	1	92	7			
Backcross to Siberian elm	3	63	33	1		
F_1 Hybrid		37	60	3		
F_2 Hybrid	1	21	55	21	2	
Backcross to slippery elm		5	53	42		
Slippery elm			2	28	51	19

Summary

The primary objective of this study was to produce hybrids between Siberian elm and slippery elm using a hardy seed source of Siberian (Chinkota) elm as one parent. Hybrids were backcrossed to the parents, and two F_1 hybrids were crossed to obtain a population similar to an F_2 population. Progenies resulting from these crosses were planted-out for growth performance and for morphological comparisons.

The first hybridization trials were made in 1953 and 1954, between slippery, Siberian, American and hybrid (slippery elm x Siberian elm) elm trees located in the Brookings area in South Dakota. Small populations were obtained from the cross between slippery and Siberian elm trees and from the reciprocal cross. American elm failed to cross with either of these species. Backcross progenies were obtained from the F_1 hybrid on both parent species, and a progeny resembling an F_2 population was obtained by crossing the two F_1 hybrid trees. The progeny were out-planted for morphological studies and general growth performance.

The self-compatibility of several slippery, Siberian, American and F_1 hybrid elm trees was tested in 1959. Selfing occurred in some of the individual trees of each species, but the per cent of filled seeds was less than 6% in all but two trees of slippery elm. None of the F_1 hybrid trees yielded any viable fruit.

In 1964, a randomized complete block design growth study was planted from crosses made in the spring. Included in the planting were progenies of both parents, of controlled crosses (slippery elm x Chinkota elm and reciprocal), and of backcrosses to both parents. A natural F_1 hybrid population which came from seed collected from a slippery elm tree in close proximity to Chinkota elm trees was also included in the planting. Height growth measurements were determined annually.

Highly significant height growth differences between the various progeny types were found by analyses of variance after each growing season. At the end of the 1970 season, the average heights of the three F_1 progenies were significantly different from the other types at the 5% level (Duncan's multiple range test). Some of the F_1 trees had an average annual height growth of almost 4 feet; mean height growth for the best F_1 averaged more than three feet per year. A severe windstorm in 1968 resulted in major stem breakage that affected the height growth ranking of progeny groups. Damage was particularly severe among the taller F_1 hybrid trees.

Height growth cessation of seedlings in 8 progeny groups was observed in the fall of 1965. Only minor differences were noted between progenies, though the range of cessation varied and was greatest in slippery elm.

Seeds having Chinkota elm as the seed parent germinated more rapidly than seeds having slippery elm as the seed parent.

Seed from an open-pollinated slippery elm tree growing adjacent to Chinkota elm trees produced only F_1 hybrid seedlings from promptly germinating seeds. Seeds of the same collection which required a cold strafication period before germination developed into seedlings that were mostly slippery elm. This suggests that quantity production of F_1 hybrid seedlings could be accomplished by establishing an isolated slippery and Chinkota elm planting and collecting seed from the slippery elm trees. The sequence of flowering in these species in the Brookings area is so timed that many of the protogynous flowers of slippery elm are receptive at the time Chinkota elm trees are shedding pollen.

Morphological comparisons of leaves, flowers, fruit and buds of the parent species, backcrosses, F_1 and F_2 were studied in progenies of the 1953, 1954 crosses. Since these various structures contrasted sharply between the parent species, it was anticipated that the F_1 would show several intermediate characteristics. This was true with respect to leaf size, number of veins, hairiness and weight. The F_1 samara was intermediate in amount of pubescence, depth of apical notch, stalk length and fruit width. The floret of the F_1 was intermediate in length and in the number of stamens. The number of florets in a single inflorescence of the F_1 exceeded those of either parent. Lengths of flower and vegetative buds in F_1 trees were intermediate in size to those of the two parents. Similarly flower and vegetative bud sizes in the backcrosses and in the F_2 population were intermediate between the parental types though the F_2 population was too small to show the full array of segregates. F_1 hybrid seedling leaves averaged longer than similar leaves of the parent species.

On the basis of height growth, F_1 hybrids between Chinkota elm and slippery elm have shown superiority to the parental species. Since quantity production of hybrid seed is feasible, the F_1 offers a source of fast growth and improved height of fast growing tries for windbreaks and shelterbelts in South Dakota. Life span, maximum height and reaction to environmental pressures such as drought, diseases and insects remain to be ascertained as test plantings of this hybrid are observed through the years.

Literature Cited

——— 1950. Sixty-third Annual Station Report, Agricultural Experiment Station, South Dakota State College.

——— 1954. Forest Tree Breeding in Canada. J. of For. 52:682-5.

Aljbenskii, A. V. 1951. (Results of Hybridization of Larch, Maple, Elm and Ash Trees). Trud. Inst. Lesa. 8:88-94, 205. PBA 25:558. (Original not seen).

——— 1956. (New Hybrids of Trees). Les. Hoz. (Forestry) 9:15-19. PBA 27:2260. (Original not seen.)

Anderson, M. L. Elm Disease. Nature Lond. 189:886-7.

Beattie, R. K. 1937. The Dutch Elm Disease in Europe. Am. Forests 43:159-161, 201.

Britwum, S. P. K. 1961. Artificial Hybridization in the Genus *Ulmus*. Proc. 8th Ntheast. For. Tree Impr. Cof., New Haven, Conn. 1960, pp. 43-7.

Clapper, R. B. 1952. Breeding and Establishing New Trees Resistant to Disease. Econ. Bot. 6:271-93.

——— and J. M. Miller. 1949. Breeding and Selecting Pest-resistant Trees. Yearbk. Agri. U. S. Dept. Agric. pp. 465-71.

Collins, Paul E. 1955. Chinkota Elm. South Dakota Farm and Home Res. 7:14-16.

Darlington, C. D. and A. P. Wylie. 1956. Chromosome Atlas of Flowering Plants. The MacMillian Company, New York, N. Y.

Dermen, H. and C. May. 1966. Colchiploidy of *Ulmus pumila* and Its Possible Use in Hybridization with *U. americana*. For. Sci. 12:140-6.

Ehrenberg, C. E. 1954. Almsjukan Historik och Atgardn for Framstallning av mot Sjukdomen Resistenta Alman. (Elm disease. History and measures for the production of elms resistant to the disease.) Svenska SkogsvForen. Tidskr. 52:35-41. PBA 14:3384. (Original not seen.)

Engstrom, Harold E. and Lewis S. Matthew. 1942. Effects of the 1940 Armistice Day Freeze on Siberian Elm in the Plains Country. J. of For. 40:704.

Gerhold, H. D., E. J. Schreiner, R. E. McDermott and J. A. Winieski. 1966. Breeding Pest - Resistant Trees. Pergamon Press. Oxford, Eng.

Goidanich, G. 1938. (Notes on Researches in the Selection of Elms Resistant to Elm Disease.) Ital.

Agric. 75:69-74. PBA 8:1347. (Original not seen.)

Graves, A. H. 1948. Forest-Tree Breeding. Econ. Bot. 2:284-305.

Harlow, W. M. and E. S. Harrar. 1968. Textbook of Dendrology. 5 ed. McGraw-Hill Book Co., New York, N. Y.

Hartley, E. P. 1927. Forest Genetics with Particular Reference to Disease Resistance. J. of For. 25:667-86.

Heybroek, H. M. 1962. Elm Breeding in The Netherlands. Silvae Gent. 6:112-7.

——— 1963. (The "Groeneveld" Elm.) Ned. Bosb. Tijdschr. 35:370-4. (Trans. in Plant Dis. Reptr. 48: 187.)

Johnson, L. P. V. 1939. The Breeding of Forest Trees. For. Chron. 15: 139-51.

——— 1946. Fertilization in *Ulmus* with Special Reference to Hybridization Procedure. Canad. J. Res. 24 (Sect. C) 1-3.

——— and C. Heimburger. 1946. Preliminary Report on Interspecific Hybridization in Forest Trees. Canad. J. Res. 24 (Sect. C) 308-12.

Larsen, C. Syrach. 1956. Genetics in Silviculture. Essential Books, Inc. Fair Lawn, N. J.

Maxon, Marcus A. 1951. Siberian Elm. South Dakota Farm and Home Res. 2:28-30.

Melville, R. 1937. The Accurate Definition of Leaf Shapes by Rectangular Coordinates. Ann. of Bot. N Series 1:673.

——— 1944. The British Elm Flora. Nature, Lond. 153:198-9.

——— 1960. A Metrical Study of Leaf-Shape in Hybrids: I. The Leaf-shape of some F_1 Hybrids and Their Parents. Kew Bull. 14:88-102.

Peace, T. R. 1939. The Resistance of Elms to the Disease Caused by *Ophiostoma (Ceratostomella) ulmi*. Inst. Leaflet No. 2, pp. 4. Imperial For. Insti., Oxford, Eng.

Rehder, Alfred. 1940. Manual of Cultivated Trees and Shrubs. 2nd Ed. The MacMillan Company, New York, N. Y.

Richens, R. H. 1945. Forest Tree Breeding and Genetics. Joint Pub. Imp. Agric. Bur. No. 8.

——— 1955. Studies on Ulmus I. The Range of Variation of East Anglian Elms. Watsonia 3:138-53.

——— 1956. Elms. New Biol. 20:7-29.

——— 1958. Studies on *Ulmus*: II. The Village Elms of Southern Cambridgeshire. For. 31:132-46.

——— 1959. Studies on *Ulmus*: III. The Village Elms of Hertfordshire. For. 32:138-54.

——— 1961a. Studies on *Ulmus*: IV. The Village Elms of Huntingdonshire and a New Method for Exploring Taxonomic Discontinuity. For. 34:47-64.

——— 1961b. Studies on *Ulmus*: V. The Village Elms of Bedfordshire. For. 34:181-200.

Rockwell, F. I. 1945. What Kind of Trees Shall I Plant? N. & S. Dak. Hort. 18:04.

Sax, Karl. 1933. Chromosome Numbers in *Ulmus* and Related Genera. J. of Arn. Arb. 14:82-84.

Schreiner, E. J. 1937. Improvement of Forest Trees. U. S. Dept. Agric. Yearbk. pp. 1241-79.

Smucker, S. J. 1941. Comparison of Susceptibility of the American Elm and Several Exotic Elms to *Ceratostomella ulmi*. Phytopath. 31:758-9.

Stockwell, P. and F. I. Righter. 1947. Hybrid Forest Trees. U. S. Dept. Agric. Yearbk., 1943-1947, pp. 465-72.

Swingle,R. U., B.S. Meyer and Curtis May. 1945. Phloem Necrosis Research during 1944. Phytopath. 35: 489.

Webb, W. E. 1948. A Report on *Ulmus pumila* in the Great Plains Region of the United States. J. of For. 46:274-78.

Went, J. E. 1938. Compilation of the Investigations on the Susceptibility of Different Elms to *Ceratostomella ulmi* Buis. in The Netherlands. Phytopath. Zeit. 11:181-201.

——— 1954. The Dutch Elm Disease. Tijdschr. o. PlZiekt. 60:109-27.

——— 1955. Verslag van de onderzoekingen over de iepenziekte en andere boomziekten, uitgevoerd op het Phytopathologisch Laboratorium "Willie Commelin Scholten" te Baarn, gedurende 1952 en 1953. (Report on investigations on Elm disease and other diseases at the "Willie Commelin Scholten" Phytopathological Laboratory, Baarn, 1952-53). Meded. Com. Ziekt. Boomsoorten 48. PBA 28:4752. (Original not seen.)

Wyman, Donald. 1951. Elms Grown in America. Arnoldia 11:79-93.