

ABSTRACT

VARIATION BETWEEN AND WITHIN NINE EURASIAN SPECIES OF *Ulmus*

By

Gary Long

The American elm, long the most popular shade tree in eastern North America, has been decimated over much of its range by the Dutch elm disease (*Ceratocystis ulmi*). This study represents the first step in a program to screen foreign species of *Ulmus* for possible replacements for the American elm. The objectives of this study are as follows:

1. Determine the occurrence and extent of variation in morphological characters of the samaras of nine Eurasian species of *Ulmus* available for study.
2. Determine the occurrence and extent of variation in morphology, physiology and resistance to Dutch elm disease of the seedlings grown from these samaras.
3. Combine the information gained under numbers 1 and 2 above and information from the literature into a basic set of data to be used in planning and carrying out future elm breeding research at Michigan State University.

Seed collections from 567 individual trees, representing 9 Eurasian species of *Ulmus* were included in this study. Twenty-six characters were studied on a four samara sample from each seedlot. Forty-nine additional characters were studied on the seedlings produced.

These characters were then analyzed to determine the differences between species and the occurrence and extent of genetic variability within species. There were highly significant differences (.01 level) between species in each of the 75 characters studied. Eight of the nine species included in the study were distinctly different from each other. There was very little difference between *U. glabra* and *U. elliptica*.

Very little of the within-species variation could be accounted for by the geographic origin of the seed. Only leaf size in *U. minor* showed a recognizable geographic trend.

Susceptibility to Dutch elm disease seemed to occur at random within the material studied. Selection for resistance will need to be on a family basis.

U. Ulmus minor and *U. japonica* showed the greatest potential for producing an acceptable substitute for the American elm.

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EURASIAN SPECIES OF *ULMUS*

By

Gary Long

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CHAPTER I

INTRODUCTION

The American elm (*Ulmus americana* L.) has been without question the most popular shade tree in the United States. Its ready availability, ease of transplanting, relatively fast growth rate and ability to withstand rough treatment have all added to its popularity. However, its unique vase-shaped form, not found in any other tree growing in this country, native or exotic, is the reason most often cited for it being the most planted ornamental species in the United States.

The introduction of Dutch elm disease (*Ceratocystis ulmi* (Buis.) Moreau) into the United States in the early 1930's drastically altered the value of elm plantings in this country. American elm has been almost completely eliminated from many areas and the planting of new elms has been curtailed in most regions.

The advance of Dutch elm disease through the native range of American elm has stimulated extensive research on disease transmission by insects, on the nature of pathogenicity and on methods of controlling the disease. The orientation of most of this work has been toward slowing the rate of loss of existing elms.

New elms will not be planted in most parts of the United States until tree planters can be given a guarantee that these trees have a high probability of living a normal life span. One way to provide such elms for future generations of Americans to enjoy is to develop cultivars which are genetically resistant to the disease.

In the spring of 1968 these ideas prompted research workers at Michigan State University to initiate a program to develop varieties of elm resistant to dutch elm disease. Three possible approaches to developing genetically resistant cultivars of elm were considered.

They were as follows: (1) Search for resistance in the existing populations of American elm; (2) Introduce resistance into American elm by crossing it with other species of known resistance; (3) Develop cultivars with desirable characteristics combined with a high degree of resistance to Dutch elm disease from other species of elm.

The first approach has been followed by several research organizations in the United States and Canada. They have shown that resistance to the disease does occur in American elm but in very limited quantities. The resistant trees discovered in these programs are often poor in other characteristics, which limits the possibility of using them directly as clones. More breeding work is necessary before this resistance can be of value to tree planters.

The second approach has received attention by elm breeders in this country for many years (Smucker, 1944). However, a strong compatability barrier prevents crossing American elm with other species. Attempts to overcome this barrier are being made (Derman and May, 1966). Unless this barrier can be effectively overcome, this approach offers little potential for elm breeders.

The third approach has been adopted by the elm breeding program at Michigan State University. Foreign species of elm are reported to contain a higher level of resistance to Dutch elm disease than American species (Went 1938, Heybroek 1968). They also show resistance to some of the other insects and diseases that plague American elm (Heybroek, 1969). Much information is available on the resistance of these species to Dutch elm disease. However, there has been little information on the variability in disease resistance or other characters within species.

The initial phase of the elm breeding program at Michigan State University was to obtain as much European and Asiatic *Ulmus* material as possible, screen this material for resistance to dutch elm disease and evaluate its potential for future improvement work. The study described in this thesis represents the first portion of this screening program.

The objectives of this thesis study are as follows:

1. Determine the occurrence and extent of variation in morphological characters of the samaras of nine Eurasian species of *Ulmus* available for study.
2. Determine the occurrence and extent of variation in morphology, physiology and resistance to Dutch elm disease of the seedlings grown from these samaras.
3. Combine the information gained under numbers 1 and 2 above and information from the literature into a basic set of data to be used in planning and carrying out future elm breeding research at Michigan State University.

CHAPTER II

TAXONOMY

A thorough taxonomic study is a valuable first step in any breeding program. This type of study allows the breeder to become familiar with available material, provides information on floral biology and reduces the chances of mistaken identification of parental material. It may provide insight into the evolutionary development of the group being studied, which will be valuable in planning and conducting research. If interspecific crosses are planned, it can provide worthwhile clues on the crossability pattern in the genus and will aid in authenticating any hybrids produced.

The Genus *Ulmus*

The genus *Ulmus* consists of about thirty species of trees widely distributed through the Northern Hemisphere. The genus is conspicuously absent from western North America today, but fossil evidence indicates that it was present during the Miocene when the genus reached its maximum distribution (Berry, 1923). The native ranges of several species of *Ulmus* seem to be decreasing at the present time (Staub, 1967). Central and northern Asia are generally considered to be the

center of distribution of the genus because the most species are native to that region. However, the elms of eastern North America are the most diverse group.

No comprehensive monograph of the genus has been published. Heybroek (1968) compiled a survey of the genus but did not include taxonomic descriptions. Richens (1956) did an interesting and original survey of the genus based on only three characters. Other pertinent sources of reference for the genus include: Bean (1951), Elias (1970), Rehder (1940, 1949), Schneider (1917), Sokolov (1958). Regional floras also serve as a source of information on particular species.

The Subgeneric Classification

The genus has been divided into various sections, subsections and series. The classification generally followed was proposed by Schneider (1916) and revised by Rehder (1949). Five sections are recognized in this classification. A sixth section, *Trichocarpus* Cheng was proposed in 1963.

The section *Ulmus* (Syn. *Madocarpus* Dum.) is the only section which has been subdivided into subsections and series. This section is by far the largest in the genus and the only one represented on all four continents. Schneider (1916) seemed to use this section to accommodate species that did not clearly belong elsewhere. Heybroek (1968) increased the naturalness of the group by transferring four species to other sections.

The subgeneric classification of *Ulmus* is shown in Table 1. The classification of species not previously classified was done with the aid of the key in Table 2.

Most of the subgeneric grouping is natural. However, some species which have recently become better known do not fit well into these groups. Heybroek (1968) stated that an accurate subdivision of the genus will not be possible until more information is available on several Asiatic species.

Phylogeny

Bechtel (1921) studied the floral anatomy and morphology of several genera of the *Ulmaceae* family and concluded that *Ulmus* was the most primitive. He described the flowers of *Ulmus* as highly reduced and specialized. Tippon (1938) showed data from wood anatomy which supports this arrangement.

Grudzinskja (1966) recognized three types of inflorescences: paniculiform in *Blepharocarpus*, racemose in *Chaetoptelea* and *Trichoptelea* and capitate in *Ulmus* and *Microptelea*. He concluded that evolution had passed from the first to the third type of varying degrees of reduction of flower number and shortening of main and lateral axes.

Richens (1963) compiled a list of parasites specific to elm. By studying the occurrence of these parasites in

Table 1. The subgeneric classification of the Genus *Ulmus* L.

Section	Subsection	Origin ¹
	Series	
	Species	
Blephocarpus Dum.		
	U. laevis	E
	U. americana	Am
Chaetoptelea (Leibm.) C. Schn.		
	U. mexicana	M
	U. thomasii	Am
	U. alata	Am
Ulmus (Syn. Madocarpus Dum.)		
Glabrae (Moss.) C. Schn.		
Fulvae C. Schn.		
	U. rubra	Am
	U. elliptica	E
Euglabrae C. Schn.		
	U. glabra	E
	U. laciniata	As
	U. bergmaniana	As
	U. uyematsui	As
Foliaceae C. Schn.		
Nitentes C. Schn.		
	U. wallichiana	H
	U. minor	E
	U. japonica	As
	U. wilsoniana	As
	U. chumila	H
	U. procera	E
Pumilae C. Schn.		
	U. pumila	As
Microptelea (Spach.) Pl.		
	U. parvifolia	As
	U. lanceaefolia	H
	U. crassifolia	Am
	U. monterreyensis	M
Trichoptelea C. Schn.		
	U. serotina	Am
Trichocarpus Cheng		
	U. kunmingensis	As
	U. davidiana	As
	U. macrocarpa	As
Insufficiently known to classify		
	U. villosa	H
	U. lesuerri	M
	U. divaricata	M
	U. multinervosa	M

¹Origins are American, Asia, Europe, Mexico and Himalayas and Southeast Asia.

Table 2. Key to the sections, subsections and series of
Ulmus L.

- A. Flowers vernal, appearing before or shortly after leaves.
- B. Flowers subsessile to very short pedicellate, not pendulous, samaras not ciliate on margins.
- C. Flowers produced in flower buds only.
..... *Section Ulmus*
- D. Nutlet separated from the apical notch of the wing by a suture.
..... *Subsection Glabrae*
- E. Samara pubescent over the locule.
..... *Series Fulvae*
- E. Samara glabrous.
..... *Series Glabrae*
- D. Nutlet near the apical notch of the wing.
..... *Subsection Foliaceae*
- F. Nutlet in the apical part of the elongated samara..... *Series Nitentes*
- F. Nutlet in the center of a round samara.
..... *Series pumilae*
- C. Flowers produced in mixed buds
..... *Section Trichocarpus*
- B. Flowers long pedicellate, often unequally so, becoming pendulous, samaras marginally ciliate.
- G. Flowers fasciculate, the floral axis only slightly elongating, branches without corky wings.
..... *Section Blepharocarpus*
- G. Flowers racemose, the floral axis slender and elongating, branches often with corky wings.
..... *Section Chaetoptelea*
- A. Flowers Autumnal, or appearing considerably after the leaves.
- H. Flowers fasciculate, not pendulous, leaves sub-persistent *Section Microptelea*
- H. Flowers in pendulous racemes, leaves deciduous.
..... *Section Trichoptelea*

different areas and on different species, he was able to show some interesting relationships. The American, European and Himalayan populations seemed to be more closely related to each other than to the Far East population. Five different elm populations occur in Europe. They are the Balkans, Central Europe, Italy, Scandinavia and England. The English population resembled the Central European population more than it did material from adjacent areas of the mainland. Evidence of trans-Atlantic migration of *Ulmus* was also shown.

Economic Importance

Elm wood is hard, heavy, durable resists splitting and will last indefinitely under water. The wood of American species of elm has been of minor economic importance but some European and Asiatic species produce valuable wood. The fact that the Dutch elm disease was imported into this country on elm veneer logs from Europe attests to their value. Today in the Netherlands veneer quality elm logs command the highest prices paid for any species grown in the country (Heybroek, 1963b).

Elm wood was used to make water pipes in many European cities before the manufacture of metal products was perfected. Its resistance to splitting made it the primary wood used to make hubs for wooden wheels. Because of its military value for making bows, gun carriages and below

water parts for wooden ships, planting of elm was encouraged in parts of Europe and existing stands were preserved for future military use.

The fibrous inner bark of elm trees was used to make cloth by people of Europe and Asia. It has also been used to make rope and twine in Europe, Asia (Heybroek, 1966a), and at a local level in the southern United States (Harrar and Harrar, 1946).

The bark of elm trees was considered a good human food in Scandinavia (Heybroek, 1963b), and elm was planted for this purpose in Norway. Chun (1921) reported that elm bark is still being used as a source of human food in mountainous areas of China. Bark, leaves and twigs of *U. pumila* were eaten in China in times of famine and the species was extensively planted for that purpose (Grudzinskja, 1961).

The mucilaginous inner bark has been used as a binding agent in making flat bread from barley in Scandinavia (Heybroek, 1966a), as a folk remedy to cure throat ailments by the Indians and early settlers in the United States (Fowells, 1965), and as an ingredient in the manufacture of incense in China (Chun, 1921).

In almost all parts of Europe and Asia, elm leaves have been used, and highly prized, as a source of livestock feed. They have a high nutritive value and are highly palatable to stock (Anon., 1947). Elms were planted in Europe since before Roman times for this purpose.

A recession of elms in Europe about 5,000 years ago discovered by pollen counts in peat formations, has been attributed to newly immigrated groups of farmers lopping the elm for fodder (Troels-Smith, 1960). This practice is still widespread in the Himalayan Region and elms face extinction in some areas if the practice is continued, because the constant lopping prevents the formation of flower buds and seed.

Elm trees have been indispensable in the growing of grapes in Italy for the past 2,000 years. Vines were trained on living trees and the foliage was cut in the summer to feed stock (Heybroek, 1966a).

In spite of all the interesting uses of elm, its chief value in most regions of the world has been for ornamental and shelter plantings. Elms have been planted in the parks and gardens of Europe and Asia since ancient times (Sokolov, 1958). Today, even in Holland where elm wood receives premium prices, it is still considered mainly as an ornamental. The planting of elm for shade trees in the United States began soon after the first settlements were established on this continent. Elm is an important component of shelterbelt plantings in the Great Plains of the United States and in the Steppes of Russia (George 1937; Collins 1955; Grudzinskja 1956; Albensky 1969).

The Species of *Ulmus*

The species of *Ulmus* included in the following discussion are listed in Table 1. Flora Europaea (Tutin et. al., 1964) was the authority used to determine the European species of *Ulmus* recognized. The Asiatic species follow Heybroek (1968). Five species of elm that have been described from Mexico have been included even though the validity of some of them is questionable.

Eastern North American Species of *Ulmus*

Six species of *Ulmus* are native to Eastern North America. They are very diverse and distinct from each other. Five recognized sections of the genus are represented, more than in any other elm growing region of the world. The species offer no special taxonomic problems.

U. americana L. American Elm

The native range of American elm covers almost the entire United States east of the Rocky Mountains and extends into southern Canada. It has been successfully planted in almost all parts of the United States. American elm is the only species of *Ulmus* that is regularly a polyploid ($4x=56$).

Florida elm (*Ulmus americana* var. *floridana* (Chapm.) Little) differs from the type variety only in degree of several quantitative characters (Kurz and Godfrey, 1962).

Fernald (1945) recognized four forms of American elm based on smoothness of leaf and branch pubescence. Elias (1970) stated that attempts to distinguish these forms can be frustrating since both smooth and rough leaves can be found on the same tree.

U. thomasi Sarg. Rock Elm

U. racemosa Thomas, non Borkh

Rock elm is native from western New England to Minnesota and Nebraska south to Tennessee. It can reproduce by root suckers but this reproduction is not believed to be important in the natural spread of the tree (Otis, 1931).

Rock elm produces the hardest, toughest wood of all the elms (Harlow and Harrar, 1958). Lumbering activities have seriously reduced the species over much of its range.

No races have been reported in the species. Natural hybrids with *U. rubra* are reported from Wisconsin (Fowells 1965) and Missouri (Hess and Dunn, 1967). Hess and Dunn (1967) suggest that an ecological isolation between the two species prevents hybrid seedlings from surviving under natural conditions.

U. alata Michx. Winged Elm

The distribution of winged elm is primarily within the humid region of southeastern United States. The species

is of no particular commercial importance except that it is occasionally cut as a substitute for rock elm (Harlow and Harrar, 1958). Its pleasing growth habit has made it a favorite ornamental of many southern communities. The inner bark is fibrous and has been used locally for baling twine (Harrar and Harrar, 1946).

U. rubra Muhl. Red or slippery Elm

U. fulva Michx.

The native range of red elm covers most of the eastern half of the United States. It is the only elm species that shows seed dormancy. Red elm can spread by interconnected rhizomes during the seedling stage (Fowells, 1965).

Natural hybrids of *U. pamila* X *U. rubra* have been reported from many locations where the two species have been growing together. Several of these hybrids have been selected and propagated for distribution by commercial nurserymen (Green, 1964).

U. crassifolia Nutt. Cedar Elm

The cedar elm is native from southwestern Tennessee to southern Texas. An isolated stand was recently reported from northern Florida (McDaniel and Swift, 1967). Standley (1922) believed that the species probably crossed the border

into Tamaulipas, Mexico. However, the species has never been definitely reported from Mexico.

Cedar elm is the common elm of Texas where it is used as a street and shade tree (Harrar and Harrar, 1946).

U. serotina Sarg. September Elm

September elm ranges from southern Illinois, Kentucky and Tennessee south to Alabama, Georgia, Arkansas and eastern Oklahoma. The species resembles American elm in general form, although it never gets as large. It has been used as a shade tree in Alabama and Georgia (Harrar and Harrar 1946).

The September elm is the least known of all the elms of eastern North America. No races or hybrids of the species have been reported.

The Elms of Mexico

Five species of *Ulmus* have been described from Mexico. Only one of these, *U. mexicana*, occurs abundantly anywhere in the country. The other four species are known only from their original descriptions based on a few herbarium samples (Muller 1936, 1937, 1942; Standley, 1936). More study is needed to determine the validity of these species.

U. mexicana (Leibm.) Planch.*Chaetoptelea mexicana* Leibm.

U. mexicana is a tropical species ranging from central Mexico to Honduras (Standley and Steyermark, 1946). It was originally described as a separate genus (*Chaetoptelea* Leibm.) because the fruit do not have true wings. However, this difference was not regarded as sufficient to establish a new genus and it was reduced to a section of *Ulmus*. Schneider (1916) put two other American species, *U. thomasi* and *U. alata* in the same section.

U. divaricata C. H. Mull.

This little known species was described in 1936 from near Monterrey, Nuevo Leon, Mexico. It was found growing commonly in the type locality. The species seems to be closely related to *U. americana*, differing only in the shape of the samara tip.

No information is available on the species except the original description. (Muller, 1936.)

U. multinervosa C. H. Mull.

U. multinervosa was described in 1937 from the mountains of Northern Coahuila, Mexico. At the time of collection, all of the trees were barren of flowers and fruits, but a single samara and some peduncles were found after a tedious search in some debris-filled crevices

(Muller, 1937). The vegetative characters of the species do not distinguish it from *U. divaricata*, so the species was described on the basis of this single fruit.

No additional information has been published on this species.

U. monterreyensis C. H. Mull.

U. monterreyensis, a fall blooming elm, was described from Nuevo Leon, Mexico in 1942 (C. H. Muller, 1942). It is the first definitive report of a fall blooming elm from Mexico, although Standley (1922) believed that *U. crassifolia*, common in southeast Texas, probably crossed the border into Tamaulipas. The author stated that the species is rare in the type locality.

Vegetatively the species is very similar to *U. crassifolia* (Elias, 1970). The type specimen had immature fruit. Mature fruit and additional flowering material are necessary to determine if this is a valid species.

U. lesuerrii Standley

This species is known only from the Rio Bonita area of Sonora (erroneously cited as Chihuahua under the original description) (Muller, 1942). The type specimen was sterile so the species is known only from vegetative material (Standley, 1936).

It is the only species of *Ulmus* reported from west of the Continental Divide in North America.

The Elms of Europe

The elms of Europe have been a source of considerable confusion for taxonomists. Several factors have contributed to this confusion. Elms hybridize easily; the hybrids are generally fertile and hybridize further to produce swarms of intermediates. In Europe, man has interfered with the native elms for thousands of years (Trols-Smith 1960; Heybroek, 1963b). As a result, in Europe today one can never be sure if a tree is native or not. This interference of man has added to the hybridization and the resulting confusion.

The difficult natural conditions have caused considerable confusion in the nomenclature which has hindered the understanding of the genus. This confusion dates back to Linnaeus who named only one European species, *U. campestris* L. This name was subsequently applied in most European countries to the most common, local form or species. Being a permanent source of error and confusion, the name was rejected as a "nomen ambiguum" (Melville, 1938).

Further confusion arose from botanists and horticulturists who described horticultural varieties (often clones) as botanical varieties or species. *Flora Europaea* (1964) recognized only five species of *Ulmus* in Europe.

Green (1964) compiled a list of cultivar names for *Ulmus*. These two publications should help to overcome much of the confusion in nomenclature.

U. minor Mill.

U. carpinifolia Gled. *U. foliaceae* Gilib.

U. stricta Lindl. *U. nitens* Moench.

U. glabra Mill. (non Huds.) *U. densa* Litv.

U. campestris L. (pro parte)

U. minor is native in central and southern Europe, from Spain to the Ural Mountains in the east and extending into North Africa and Asia Minor. It reproduces itself by root suckers as well as seed. The root suckering habit of the species enabled it to withstand lopping for fodder better than non-suckering species. It was planted for this purpose in many areas of Europe since ancient times (Heybroek, 1963b).

U. minor has been a source of considerable confusion for taxonomists. Rehder (1949) lists twenty three synonyms of the species. Many varieties and forms of the species have been described. However, the validity of some of these is questionable.

U. glabra Huds. Wych or Scotch Elm

U. scabra Mill. *U. montana* With.

The native range of *U. glabra* covers most of Europe. Its range extends north of the Arctic Circle in Norway and as far east as the Ural Mountains.

U. glabra has been planted extensively as a park and street tree since ancient times. It occurs naturally on well-watered, fertile soils and is very intolerant of salinity and drought (Sokolov, 1958). The roots of *U. glabra* do not produce root suckers. Because of this, it is the favorite understock used to propagate improved varieties of elm in Europe.

Natural hybrids between *U. glabra* and *U. minor* (*U. X hollandica*) Miller occur extensively in Europe. The hybrid seems to be more prominent in some areas than either parent. Many of the most desirable cultivated varieties of elm in Europe have been selected from these hybrids.

U. procera Salisb. English Elm

The origin of *U. procera* is unknown. In older books it is said to be native to Europe, introduced to England by the Romans (Bean, 1951). However, the tree seems to be distinctly different from *U. minor* growing on the continent and is not found growing wild anywhere except in southern England. It occurs in parks and gardens in Spain, but always as a planted tree. It is the dominant tree in many parts of southern England, especially in hedgerows. However, all of these trees seem to have come from root suckers, which the tree produces freely. The production of fertile seed is extremely rare in England, although it does produce

fertile seed in milder climates (Henry 1910). The tree may have originated as a hybrid from the other British elms (Bean, 1951).

Many horticultural varieties have been selected which indicates that genetic variability is present in the species (Green, 1964). Richens (1967) reported natural hybrids between *U. procera* and *U. minor* are common in southern England.

U. laevis Pall. European White Elm

U. pedunculata Foug. *U. effusa* Willd.

U. racemosa Borkh.

U. laevis is native from the Pyrenees to the Ural Mountains. The species has been cultivated since ancient times for shade and shelter in the U.S.S.R. (Sokolov, 1958) but it has received little attention from tree planters in the rest of Europe (Heybroek, 1968).

A variety *celtidea* (often regarded as a separate species) has been described from the U.S.S.R. Its general growth habit is reported to resemble *U. americana* (Heybroek, 1968; Sokolov, 1958).

U. elliptica C. Kock

U. elliptica is native in the broadleaved forests of the southern part of European U.S.S.R. This species is morphologically similar to the American species *U. rubra*.

U. elliptica has received little attention from tree planters, although Sokolov (1958) states that it is suitable for planting within its native range.

U. canescens Melville

The native range of *U. canescens* encircles the Eastern Mediterranean basin, it occurs sporadically where suitable site conditions exist. The species was first described in 1957 and is not well known. It is similar to *U. minor* in many respects (Tutin, et. al., 1964).

Elms of Eastern Asia

More species of *Ulmus* are native to Eastern Asia than any other region of the world. The taxonomy of many of these species is not completely known. As these species become better known, they should increase our understanding of the genus.

U. pumila L. Siberian Elm

U. androssowii Litv., *U. pinnato-ramosa* Dieck

U. Manchurica Nakai

The Siberian elm, often erroneously called Chinese elm, has a natural range extending almost completely across Asia from eastern China to Russian Turkestan, north to the Transbaikalian region. Grudzinskaja (1961) thinks that the

species may have originated in Sinkiang and was transported to the Far East and Russian Central Asia by man in ancient times.

The species was first introduced into the United States in the early 1900's by F. N. Meyers and others (Webb, 1948). The drought resistance, relatively fast growth rate and ease of propagation seemed to make this species the answer to tree planters' problems, especially in the Great Plains Region. The species was promoted by several government agencies and planting was begun on an extensive scale. By 1948 *U. pumila* was recognized as the most planted tree species of all time in the United States (Webb, 1948). The windbreaks and shelterbelts of the Great Plains Region made up the bulk of this planting.

The extensive planting of Siberian elm created a strong demand for planting stock. The source of the seed did not seem important and it was generally obtained from the most readily available source. Most of the seed was collected by students of Nanking University from trees growing around Nanking, China, which is about the same latitude as Houston, Texas. These southern sources were planted throughout the central and northern Great Plains Region. The problem of winter hardiness soon developed. The famous Armistice Day freeze of 1940 killed a high percentage of Siberian elm throughout the central and northern Great Plains.

(Engstrom and Matthew, 1942). This provided one of the best examples of the importance of seed source in the history of tree planting.

Hardy strains of Siberian elm have been developed in South Dakota (Collins, 1955), and Manitoba (Green, 1961). No one seems to like the species very much because of its susceptibility to ice damage, relatively short life span, and its prolific reproduction that have made it a weed in many areas. Some people have even advocated a ban on planting the species in certain areas (D. E. Hutchins, personal communication). However, no other species has been able to equal its fast growth rate, ease of establishment and drought resistance. Collins (1955) reported that it was still planted more than any other hardwood in the central and northern Great Plains region.

U. kunmingensis Cheng

U. kunmingensis was described from Yunnan province of mainland China in 1963. The original description is the only information available on the species (Cheng, 1963).

U. parvifolia Jacquin Chinese Elm

U. parvifolia is native to a wide latitudinal range from the island of Hainan to Korea. It is also native in Taiwan and Japan.

Southern sources of Chinese elm are evergreen and the leaves usually persist on northern sources until mid-winter. Chun (1921) reported that the autumn foliage often turns a brilliant red or yellow. The interesting, scaly bark adds to the ornamental value of the species.

The Chinese elm is a small tree that should not be considered as a replacement for the American elm. However, it is a fine ornamental in its own right and should be planted more in this country (Wyman, 1965).

U. davidiana Planchon

U. davidiana is native to northern China, Mongolia, Korea and the Amur region of far eastern U.S.S.R. The species is reported to be one of the hardiest of all elms (Weikoff, 1941). Very few specimens of this species have ever been planted outside the native range of the species.

U. macrocarpa Hance

U. macrocarpa is native to northern China, Manchuria, Korea, Mongolia and the southern part of far eastern U.S.S.R. Komorov (1936) stated that the tree is a rare relic of an earlier vegetation type. The species is almost unknown as a cultivated tree, but its broad spreading crown and shiny foliage make it an attractive tree, especially when fruiting (Sokolov, 1958).

U. wilsoniana Schneider

U. wilsoniana is native to Central China. Schneider (1917) reported that the species is not common in the type locality.

U. wilsoniana is growing in Arnold Arboretum from scionwood sent from Central China in 1910. Grafted specimens of this tree have been planted in other arboretums and botanic gardens.

The glossy green foliage of this tree makes it an attractive ornamental. It is of interest to elm breeders because it is resistant not only to Dutch elm disease, but also to elm bark beetle and elm leaf beetle.

U. uyematsui Hayata

U. uyematsui is native to the central part of the island of Taiwan at elevations of 1500-2500 meters. The species is of no economic importance and has received little attention from researchers.

U. laciniata (Trautv.) Mayr.

U. laciniata is native to Japan and eastern China as far north as the Sakhalin peninsula. Seed germination for the species is very low.

Komorov (1936) states that this species is very similar to *U. glabra*. It seems to be a far eastern race replacing *U. glabra* after considerable geographic gap.

Features typical of *U. laciniata* may be found in Ural Mountain populations of *U. glabra*. The shape of mature specimens of *U. laciniata* is reported to resemble *U. americana* (Heybroek, 1968).

U. bergmanniana Schneider

U. bergmanniana is a fairly common tree in western Hupeh and eastern Szechuan provinces of Central China. The species is cultivated in its native range (Schneider, 1917). Very few specimens of the species have been grown outside the native range.

U. japonica Sarg.

U. propinqua Koidz. *U. davidiana* var
japonica Nakai

U. japonica is native to northern China, Korea and Japan extending into the Transbaikal Region of the U.S.S.R. It is one of the hardiest of all elm (Weikoff, 1941).

Komorov (1936) described five variations of the species based on combinations of leaf smoothness, twig corkiness and growth habit. He stated that these five forms are not strictly delimited geographically but they are clearly differentiated ecologically.

The wood of the tree furnishes valuable lumber in Japan. Chun (1921) stated that the tree sometimes assumes

the characteristic vase shape of the American elm and should be useful as a street tree because of its rapid growth, ornamental character and hardiness.

Elms of the Himalayas and
Southeast Asia

The elm flora of this part of the world is still not completely known. Most of the elm trees occur in remote areas that have not been fully explored botanically. Three species have been described from the region and at least one more is waiting to be described (Heybroek and Melville, in press).

The destructive practice of lopping trees for livestock fodder has made it difficult to find naturally occurring elms except in parks or in very inaccessible regions.

U. wallichiana Planch

U. wallichiana is native in the western Himalayas from Nepal to Kashmir at altitudes of 3,500-10,000 feet. It is often planted in its native range and the branches lopped every other year for cattle fodder (Brandeis, 1911). The practice of lopping all young branches for livestock fodder has made it very difficult to collect seed from this species except in a few protected areas (Heybroek, personal communication).

The Dutch have used this species extensively in their breeding program in recent years. It seems to cross easily with other members of the section *Ulmus*.

U. 'chumila'

This is a new species from the western Himalayas. Heybroek (1968) used the name but a valid taxonomic description of the species has not been published. *U. X brandisiana* is reported by Heybroek to be a natural hybrid between this species and *U. wallichiana*.

U. lancifolia Roxb.

U. lancifolia is a tropical species native to southeast Asia. It is the only species of *Ulmus* with a native range that extends south of the equator.

The dormant period of the species coincides with the seasonal rainfall pattern. The species usually blooms in midwinter and has been classified by authors as both spring and fall blooming. The species is closely related to the fall blooming *U. parvifolia* (Touw and Van Steenis, 1968). Hybrids between the two species have been reported from the island of Hainan (Heybroek, 1968).

U. villosa Brandeis

U. villosa is native to the northwest Himalaya region from the Indus to the Jumna rivers. The wood of this species is of no particular value but the branches are lopped for fodder.

This species produces root-suckers to an extraordinary extent and probably reproduces itself in this way. The seed is reported to fall off the tree before it is ripe.

Cytology

The base chromosome number of *Ulmus* is $x=14$ (Sax, 1933; Leliveld, 1934; Krijthe, 1939). All species of *Ulmus* in which the chromosomes have been counted are regularly diploid ($2n=28$) except *U. americana* which is a tetraploid ($2n=56$) (Sax 1933, Darlington and Wylie, 1955). Sax (1933) believed that the species was probably an autotetraploid. Staub (1968), after studying all the evidence available, concluded that more data is needed to determine the origin of the polyploid condition.

Krijthe (1939) reported that *U. pumila* var. *pinnato ramosa* sometimes showed 28 chromosomes in the haploid metaphase stage of the pollen grain. The Swedish Forest Tree Breeding Association at Kalltorp produced triploid and tetraploid forms of *U. glabra*. These forms proved to be

just as susceptible to Dutch Elm Disease as normal *U. glabra* and it was considered useless to include them in a hybridization scheme (Went, 1954).

Ehrenberg (1949) studied asynapsis (decreased chromosome pairing at first metaphase) in *U. glabra*. A high degree of sterility resulted when asynaptic X asynaptic elms were crossed. Only 19 seedlings were produced from 1636 seeds obtained in the crossing. Fifteen of these were tetraploid and the remaining four triploids. Asynaptic X normal showed a higher fertility level. Seedlings from this cross were all triploids. All seedlings obtained from normal X normal crosses were normal diploids.

The triploid seedlings produced by Ehrenberg (1949) were slightly more vigorous than diploids while the tetraploids grew only about half as fast. Stomate size of the triploid seedlings was intermediate between the larger tetraploid and the diploids.

Grudzinskja and Zakharyeva (1967) studied the karyotypes of seventeen forms of six species of elm native to the U.S.S. R. Individual chromosomes were similar in all forms studied and they concluded that karyotypes are of no diagnostic value in *Ulmus* taxonomy.

Polyploids have been induced in normally diploid species of *Ulmus* by colchicine application (Heimbürger, 1966; Derman and May, 1966; Heybroek, 1968). Most of this work has been aimed at overcoming the crossability barriers

between the tetraploid *U. americana* and diploid species (Heimbürger, 1966; Derman and May, 1966). Heybroek (1968) reports that tetraploids have been made of some of the best clones produced in the Dutch breeding program. When this material reaches flowering age it will be crossed with diploid varieties in an attempt to produce vigorous triploids.

Lester (1968) attempted to produce polyhaploids (haploids doubled) in American elm. Flowers of American elm were pollinated with non-viable, irradiated American elm pollen and with pollen of the diploid species, *U. pumila* and *U. rubra*, which normally do not cross with American elm. Over 300 filled seed and 168 seedlings were produced from the crosses. All of the seedlings proved to be tetraploid. Lester stated that the pollination seemed to increase the amount of selfing in the American elm parents.

Counting the chromosomes of all seedlings to determine the success of attempts to produce polyhaploids has been very time consuming. An attempt is now being made to develop a screening technique using marker genes that will make it possible to divide seedlings into groups of high and low probability of reduced chromosome number (Lester, 1968).

CHAPTER III

HYBRIDIZATION IN *ULMUS*

Natural Hybrids

Natural hybrids have been reported many times in *Ulmus*. However, only about a third of the species have been involved and only a few of the possible combinations between these species are reported. Natural hybrids that have been reported in the literature are shown in Table 3.

In almost all cases natural hybrids have been the result of man interfering with the native vegetation. The most classical example of this is in southern England where there is evidence that man has imported and planted elm for the past 2,000 years (Richens, 1955).

The elms of southern England reproduce mainly by root suckers. However, about every ten years a crop of viable seed is produced (Richens, 1955). New genetic combinations are formed in these occasional flurries of reproductivity and then propagated asexually. As a result of this, the population of elms of southern England has evolved into a group that have confused taxonomists for the past 300 years (Melville, 1946).

Table 3. Natural interspecific hybrids (=X) of *Ulmus*.
Reported in the Literature.

[illegible]

Richens (1955, 1958, 1959, 1961a, 1961b, 1965, 1967) compiled a series of papers on the local elm flora of England based on historical and morphological data. Jeffers and Richens (1970) combined the morphological data from the earlier studies into a multivariate analysis. The results of these studies show that four groups of elms occur in England. They correspond with *U. procera*, *U. minor*, *U. glabra* and *U. minor* X *U. glabra* hybrids. *U. glabra* is the only elm native to England.

Hybridization Techniques

Flowers of *Ulmus* are minute, only about one-eighth inch across. Each flower contains 4 to 8 stamens. The flowers in a single cluster do not develop simultaneously. As much as two weeks may elapse between the emergence of the first and last flowers. Pollination bags need to be removed daily during this period to inspect the flowers and remove any newly emerged stamens.

Emasculation is time-consuming and limits the number of pollinations that can be accomplished. Recent hybridization work in *Ulmus* has depended on self sterility to prevent selfing. A marked protogyny that prevents selfing has been reported in *U. americana* (Shattuck, 1905), *U. minor* and *U. glabra* (Henry, 1910).

Went (1954) reported on ten years of selfing studies involving 189 trees. Self fertility ranged from 0 to

100%. In addition to the large difference among individuals, she also found a large year to year variation within a tree. Of the 189 trees involved, 12% produced over 10% fertile seed. She concluded that emasculation was the only sure method of knowing the parents of a seedling produced from controlled pollination.

Lester (1968) reported that the amount of selfing in *U. americana* was apparently increased by pollination with non-viable irradiated American elm pollen or pollen of diploid species of elm. He also found a wide variation in the amount of selfing among individual trees.

Cut branches of elm placed in water can be forced to flower and produce fruit in the greenhouse. The historical development of this technique was reviewed by Pauley (1949). Wright (1949) studied the effect of time of collection, branch size and greenhouse environment on the production of elm seed on cut branches. One to three foot branches, three fourths of an inch in diameter, gave the best results. Branches collected shortly before the natural flowering time flowered more quickly and produced more fruit than earlier collections, unless flower buds had been damaged by cold weather. Greguss (1970) showed a tree to tree variation in the dormancy required before a tree could be forced to flower in *U. minor* and *U. glabra*. One *U. minor* tree produced normal pollen from branches cut immediately after natural defoliation.

Collins (1967), Ozolin (1958) and Went (1954) stated that production of seed on cut branches gives erratic results. The method is not used extensively in most elm breeding work. However, the forcing of cut branches to collect pollen is commonly used. Greguss (1970) reported that pollen collected in this way was more fertile than pollen produced naturally on the tree in *U. laevis*, *U. minor* and *U. glabra*.

Collins (1967) improved on the cut-branch technique by grafting scionwood from mature flowering trees onto potted seedlings. The potted grafts maintained their small size, flowered the first year after grafting, and those that survived were still flowering after eleven years. However, the production of seed on this grafted material was erratic.

Crossability Patterns of *Ulmus*

Knowledge of the crossability pattern in *Ulmus* is far from complete. Most crosses reported in the literature have not been authenticated or are poorly authenticated. More detailed hybridization studies in the genus are needed, especially studies using rigorous rules for certification of hybridity.

Differences in flowering time form an obvious crossability barrier between the spring and fall blooming

elms. No effort to overcome this barrier through pollen storage or other techniques has been reported.

A strong crossability barrier seems to isolate *U. americana* from the rest of the genus. The nature of this incompatibility is not known. Sax (1933) theorized that it might be due to unequal chromosome pairing at meiosis between the tetraploid *U. americana* and diploid species of elm. This theory is generally accepted by most elm workers and efforts to overcome the incompatibility by inducing tetraploids of other species is in progress at several places. Tetraploid *U. pumila* produced by the U.S.D.A. (Derman and May, 1966) and growing at the Shade Tree Research Center, Delaware, Ohio, has now reached flowering age and it should be known in a few years if the increase in ploidy level will overcome the compatibility barrier.

Heybroek (1968) suggested that part of the incompatibility may be due to genic differences between sections. *U. laevis*, the other well known member of the section *Blephocarpus*, is difficult to cross with other species. *U. americana* X *U. laevis* has been reported at least four times in the literature, but only one of the reports states that the progeny showed characters intermediate between the two parents (Collins, 1967). Sax (1933) reported abundant seed set and high germination from this cross, but was unable to find any triploids in the progeny.

Graft compatability may parallel pollination compatability. Collins (1967) presented data that suggests a compatability barrier to grafting may exist between the sections *Blepharocarpus* and *Ulmus*. He reported a high degree of success grafting scions of *U. laevis* on *U. americana* rootstocks. Complete failure resulted from grafting the same material on *U. pumila* rootstock. *U. pumila*, *U. rubra*, and *U. pumila* X *U. rubra* hybrids were all successfully grafted on *U. pumila* rootstocks. Attempts to graft this material on *U. americana* rootstocks showed little success.

Weaker compatability barriers may be present between the other sections of *Ulmus*. All crosses reported between sections have either not been authenticated, or resulted in poor seed set and low survival except *U. laevis* X *U. brandisiana* (a little known species from China) reported by Collins (1967).

It is interesting to note that Went (1938) reported that *U. brandisiana* could only be grafted on *U. laevis* rootstock. Attempts to graft it on *U. glabra* and *U. minor* rootstocks were unsuccessful.

The hybrid combinations reported in the literature are shown in Table 4. A list of the references in which elm hybrids have been reported is given in Appendix B.

Table 4. *Ulmus* hybrid combinations produced by controlled pollinations.

[illegible]

- | | |
|-------------------------------|---|
| 1. Easy cross | 4. Very difficult cross |
| 2. Intermediate in difficulty | X. Cross has been re-
ported in the litera-
ture but no indica-
tion of the difficulty
was given. |
| 3. Difficult cross | |

CHAPTER IV

THE DUTCH ELM DISEASE

History

The story of how the Dutch Elm Disease was introduced into the New World on elm veneer logs imported from Europe in the early 1930's is well known. These logs brought both the deadly fungus and its main insect carrier, the European elm bark beetle. On their way to sawmills in the midwest, these logs gave rise to several centers of infection. An eradication program launched by the U.S.D.A. was able to stamp out some centers, but others soon spread out of control. Today the disease has covered almost the entire native range of the American elm.

The origin of the disease in Europe has never been determined. Eastern Asia is generally believed to be the ultimate source of the disease. It is the only area of the world where a significant number of elm species show at least a moderate degree of resistance to the disease. The disease has never been reported from eastern Asia, but most of the area where it might occur has never been investigated by scientists interested in the disease. Another possible theory is that a harmless saprophytic fungus mutated into the deadly parasite we now know.

The disease was first reported from Tilburg, Holland in 1919, hence its name. The first possible occurrence of the disease dates back to 1917 in northern France and even 1912 in England. The history of the discovery of the disease and isolation of the causal organism has been reviewed by Westenburg (1932) and Elgersma (1969).

The disease spread rapidly over Europe, reaching Italy and Yugoslavia in 1929 and Tashkent in Uzbekistan, U.S.S.R. beyond the Urals in 1939. This amounted to an average advance of 150 miles per year. The disease is now spread over most of Europe and western Asia (Heybroek, 1966a).

Description of the Fungus and the Disease

Dutch elm disease is caused by the fungus *Ceratocystis ulmi* (Buis.) Moreau. The fungus develops in the living wood as a parasite and in dead elm wood as a saprophyte. In living trees the fungus occurs in the water conducting vessels of the xylem. Yeast-like spores are produced by the fungus by budding. These spores are carried through the tree by the flow of sap. Gum and tyloses produced by the fungus are deposited in the vessels interrupting the flow of water and causing wilting and death of the tree (Walter, et. al., 1943).

Production of toxin by the fungus in culture has been demonstrated by Zentmeyer (1942), Dimond (1947), and Santamour and French (1958). Toxin has not been isolated from diseased trees and the importance of it in the pathogenicity of the fungus is not known. Zentmeyer (1942) and Dimond (1947) believe that the toxin formed by the fungus is the main cause of abnormalities in the tree. They point out that it is unlikely that tylose and gums could completely block a large trunk. The rapidity with which the fungus develops lends support to their concept (Tchernoff, 1965). Kerling (1955) injected cultured toxin into a tree. The tree developed symptoms similar to those produced by inoculation with a spore suspension.

After its host dies, the fungus, growing as a saprophyte, produces spores under the loosened bark and in insect galleries formed between bark and wood. The spores are produced in sticky masses which can cling to the outside of an insect and be carried from diseased to healthy trees.

The main insect vector involved in the spread of the disease in America is the European elm bark beetle *Scolytus multistriatus*. In Europe the larger *Scolytus scolytus* is probably the main vector, but *Scolytus multistriatus* and *Scolytus laevis* are important in the spread of the fungus. The native American elm bark beetle (*Hyluroyopinus rufipes*) may also spread the disease in

America. The beetles feed in the small twig crotches of healthy elm trees, but they breed only on recently cut, dead or dying elms. In the spring the adult beetles emerge from infected wood and fly to nearby living elm trees to feed. When the feeding injuries penetrate through the bark of the wood, the disease organisms may be introduced into the vascular system of healthy trees. Adult beetles may fly several miles in search of suitable breeding places and, thus, transport the disease from one area to another.

Elm trees killed by the disease provide breeding areas for the beetles. This results in an increased population of beetles in the area which increases the spread of the disease. This vicious cycle continues until something breaks the causal chain or until the population of elms available for feeding declines until it affects the beetle population.

Development of the Disease After Artificial Inoculation

Elm bark beetles were used in the first attempts to artificially inoculate elm trees with *Ceratocystis ulmi* fungus. Contaminated beetles were placed on the tree in cheese cloth cages and allowed to feed for five days to insure inoculation. Later investigations showed that infection could be obtained more easily by introducing a spore suspension directly into the xylem with a syringe (Went 1938). Tchernoff (1965) was able to obtain more

uniform infection by placing a drop of spore suspension on the stem and then wounding the stem with a sharp pointed knife. Positive results could be obtained only when the xylem had been cut followed by active absorption of the suspension.

The number of spores in the inoculum seems to have little affect on the success of inoculations. There was no marked difference in severity of symptoms between trees inoculated with 200,000 spores per tree and trees inoculated with only 200 spores (Tchernoff, 1965).

Age of spores does affect the success of inoculation. As spores get older they lose their virulence with no apparent change in morphology. Tchernoff (1965) recommends that spore suspensions less than 10 days old be used for comparative inoculations.

Strains of *C. ulmi* which vary in virulence have been reported many times. Therefore, it is recommended that several isolates of *C. ulmi* be mixed in the spore suspension to insure virulence of the inoculum. If possible, the virulence of the inoculum should be checked on material of known susceptibility.

The way in which test plants are raised may determine their reaction to inoculation. Trees should be growing vigorously when inoculated. If growth is inhibited, fewer symptoms will be shown. After transplanting, trees need at least one growing season to become established

before they will exhibit typical symptoms. Hot weather and direct sunlight after inoculation are most favorable for expression of disease symptoms. Watering plants before or directly after inoculation is favorable for obtaining best results (Tchernoff,1965).

Environmental Factors Affecting the Disease

The spread of Dutch elm disease depends upon a rather close cooperation between the fungus and its insect vector. The fungus is not very dangerous if the insect vector is not present. The population of beetles may fluctuate widely under the influence of weather and availability of dead elms for breeding places. Even the percentage of fungus-carrying beetles in a newly hatched population will fluctuate with weather conditions and the presence or absence of mites in the galleries (Franzen,1939).

The Netherlands forest service kept a record of all elms in the country that had to be removed because of the disease between 1930 and 1944. Not only was the total number counted, but also, the number of diseased trees on different soil types (Went,1954). Between 1932 and 1937, 34% of the elms on peat soil and 37% of those on sandy soil became diseased. During this same period, only 8% of the elm on clay soils became infected.

Vazda (1952) found that centers of infection were in groups of elms growing on sites where soil moisture had

undergone a sudden unfavorable change in moisture content. The affect of soil moisture on expression of the disease was studied by Kais,et. al., (1962). Soil type, moisture-holding capacity and water availability influenced both degree of infection and duration of susceptibility to the disease in *Ulmus americana*.

Burger (1938) found that elms growing near the Dutch coast were relatively unaffected by the disease. The line drawn to denote the area where large elm plantations still occurred in 1938 shows a striking conformity with lines denoting an equal mean wind velocity of 4.5 meters per second during summer (Heybroek, 1957). This suggests that wind has a strong influence on the severity of the disease. Went (1954) believed that this influence was primarily on the insect that carried the disease. Heybroek (1957) stated that the cause of this influence is not known. It may be that the wind decreases tree growth which makes them less susceptible. A high relative humidity would be maintained in this area by the wind which blows from the sea. This would avoid a vapor pressure deficit which may hasten the development of a wilt disease like the Dutch elm disease. Went (1938) stated that artificially inoculated seedlings exhibit few symptoms in cool moist growing seasons.

Although a high relative humidity during the growing season seems to inhibit the expression of symptoms in

diseased trees, there is ample evidence that a high relative humidity is necessary at the time of inoculation. Tyler, Parker and Pope (1940) studied the affect of relative humidity on young elm trees in the greenhouse. Plants grown in a moist chamber for a time and then transferred to the greenhouse developed more symptoms than trees grown in the greenhouse for the entire period. Kais, Smalley and Riker (1962) found that inoculation of susceptible elm seedlings with dry spores resulted in infection only when moisture loss was prevented by covering the wounds with masking tape. Under field conditions they found that in spite of a high relative humidity during the entire susceptible period, the incidence of infection in uncovered inoculated wounds was consistently lower than in similar taped wounds. A suspension of spores in water gave a higher incidence of infection than dry spores. The highest rates of infection were obtained using a spore suspension in combination with taping the wounds.

Temperature also affects the expression of the disease. Tyler (1945) reported that a temperature of 15 to 29°C. favored disease development. He found that trees exposed to 26°-29°C. wilted in three to five days after inoculation. Temperatures of 9.5° to 12°C. and 32° to 37°C. inhibited wilt expression. Kais, et. al., (1962) studied the interaction of soil and air temperature on the development of Dutch elm disease. Maximum infection occurred at air

temperatures of 24°C. with soil temperature of 26°C. Soil temperatures seemed to affect disease development more than air temperature.

Physiological Factors Affecting Dutch Elm Disease

Vigorously growing trees are more susceptible to the disease than slow growing ones (Went, 1954; Heybroek, 1957; Peace, 1960). Tchernoff (1965) stated that any factor which tends to increase the vigor of a susceptible tree will enhance the development of disease symptoms after inoculation.

Transplanted elm generally do not show symptoms when inoculated until they have had at least one growing season to recover (Went, 1954; Heybroek, 1957; Smalley, 1963; Tchernoff, 1965). Grafted material also needs at least one year to become established before it can be successfully inoculated.

Vigorous trees have a better chance of recovering from an infection than slow growing trees (Peace, 1960). The fungus is generally confined to the large vessels of springwood. It seldom penetrates the denser summerwood. If the tree can survive the initial attack long enough to lay down a new layer of wood it has a good chance of recovery if not reinfected (Banfield, et. al., 1947). Fungus was isolated from recovered elms in Great Britain after a period of up to 7 years (Peace, 1960). In recovered trees

the fungus becomes confined to vessels invaded during the year of symptom expression and is buried by subsequent rings of healthy tissue (May, 1935; Pope, 1943; Banfield, 1968).

Peace (1960) found that spraying trees to prevent insects from reinoculating them greatly increased their chance of recovery. He also found a difference between varieties in ability to recover. Manka (1953) reported that *U. laevis* was better able to recover from the disease than *U. minor*.

Smalley and Kais (1966) found a large difference between and within species in the time and duration of maximum susceptibility during the growing season. The dissolution of the end walls of the earlywood vessels has been closely correlated with initiation of the period of susceptibility in American elm. Pomerleau (1965) observed a close relationship between early cambial activity and the beginning of susceptibility. The increase in resistance during the growing season is closely related to the beginning of latewood production (Banfield, 1968).

Branched seedlings generally develop fewer symptoms than plants with a single stem (Arisumi and Higgs, 1961). Smalley (1962) believed this difference to be due to the shortened period of elongation of multi-branched seedlings. The period of maximum susceptibility can be extended by the application of nitrogen fertilizers (Smalley, 1962).

Heybroek (1957) stated that 2-year-old seedlings are not susceptible to the disease. Three-year-old seedlings develop symptoms of the disease upon inoculation only if they are extremely well grown. He observed that when a group of seedlings are inoculated year after year additional individuals become infected. He interpreted this to mean that susceptibility of the disease increases with age. In most clones a jump in susceptibility has been observed at about the same time as a tree begins to flower.

Smalley (1962) studied the susceptibility of young American elm seedlings in the greenhouse. He found that seedlings of American elm were susceptible during their first growing season from the time the first true leaves emerge until the cessation of terminal growth. There was no evidence of juvenile resistance. Tchernoff (1965) studied the effect of seedling age on susceptibility. Age of seedling did not affect susceptibility. In another experiment he compared two groups of plants of the same age, belonging to the same clone, one group in the juvenile and the other in the adult stage of development. This is possible in elms because stem cuttings maintain the adult character while callus cuttings from the same tree are in the juvenile stage (Tchernoff, 1963). No difference in degree of susceptibility was observed between the two groups.

Smalley and Kais (1966) showed that the duration of susceptibility in American elm decreases with age if trees are inoculated in the crown. However, age did not affect susceptibility if all trees were inoculated in the trunk.

Internal Mechanisms of Resistance
to Dutch Elm Disease

McNabb, et. al. (1971) hypothesized two possible mechanisms of resistance. First, resistant hosts limit establishment of the pathogen and prevent the systemic development of the disease. Second, external symptoms of disease are limited but systemic establishment of the pathogen takes place. The host-parasite relationship is more neutral than pathogenic.

Experimental evidence suggests that localizing of pathogen establishment is the primary mechanism involved in most cases. McNabb, et. al. (1971) proposed four possible host factors that could regulate this general mechanism of resistance. They are: (1) vessel size and grouping in the functional xylem; (2) relative time required for tylose growth response in parenchyma cells adjacent to invaded vessels; (3) gross nutrient of xylary fluid for fungus growth, reproduction and toxin production, and (4) inhibition or promotion of fungus growth reproduction and toxin production by hormone like host metabolites. These factors may work singly or in combination.

Pope (1943) compared the vascular anatomy of *U. pumila* and *U. americana* and suggested a possible anatomical mechanism. He thought that early initiation and subsequent production of latewood isolated the fungus in the portion of the wood where inoculation occurred and shortened the period of susceptibility. However, Buisman (1936) stated that wood structure had no affect on the movement of spores through either resistant or susceptible elms. Dimond, et. al. (1949) found no difference in vessel length and vessel diameter between *U. americana* and *U. pumila*.

Elgarsma (1969) did an extensive study of factors affecting the resistance of elm to *C. ulmi*. He found that vessel diameter strongly influenced water movement through the xylem in the material studied. He concluded that vessel diameter is a primary factor in determining susceptibility or resistance in elms.

McNabb, et. al. (1971) measured the vessel diameter and area of contiguous vessel-groups (product of average vessel diameter and average number of contiguous vessels) in twenty-three different selections or clones of European and American elms of known resistance. They found that vessel-group size was more highly correlated with susceptibility than individual vessel size.

Sinclair, et. al. (1970) found resistance in *U. americana* was closely correlated to vessel size diameter. Vessel diameter is now used as one of the criteria of

selection in their elm breeding program at Cornell University. New candidates for selection are included in the program for further study if the average vessel diameter is less than 60 microns.

Smalley (1962) was able to increase the resistance of susceptible American elms for up to two years by treatment with trichlorophenyl acetic acid (T.C.P.A.). Formation of tyloses in the vessels of treated trees seemed to be the main factor involved in the increased resistance.

The plugging of vessels by the growth of tyloses (Banfield 1968) and accumulation of gums (Elgarsma, 1967) has been suggested as a mechanism of localizing the spread of the fungus. However, McNabb, et. al. (1971) found that many vessels in a group are not adjacent to parenchyma cells. They suggest that these vessels do not become plugged with tyloses.

Elgarsma (1967) could find no significant difference between resistant or susceptible elms in the sugar content of the sap. He did report a higher concentration of free amino acids in the sap of resistant elms. However, after a more extensive study (Elgarsma, 1969) he concluded that there was no direct relationship between amino acid content and resistance.

CHAPTER V

THE GENETIC IMPROVEMENT OF *ULMUS*

Improved varieties of elm have been selected and propagated by tree planters for several hundred years. Green (1964) in his "Registration of Cultivar Names in *Ulmus*" lists over 400 named cultivars of elm. Undoubtedly many other cultivars have been grown that were never named. Many of these were never accepted by tree planters and were planted only on a very limited scale. However, some were very successful and were planted extensively over a wide range.

Almost all elm cultivars have resulted from informal selection by nurserymen of chance seedlings or mutations. Only a few have been produced as a result of formal selection and breeding studies. The first such program was begun in Holland in 1928.

Any new selections that are released to the public will need to incorporate resistance to Dutch elm disease with other desirable characteristics. Most progress will be made through formal selection and breeding programs. The following chapter summarizes the progress of formal studies aimed at the genetic improvement of *Ulmus*.

Europe
Netherlands

Elm was the most important tree grown in the Netherlands before Dutch elm disease invaded the country (Heybroek, 1957). Over 95% of the elms planted in the country belonged to a single clone (*U X hollandica* cl. belica). This clone proved to be highly susceptible to the disease and the entire elm population of the country was threatened. An elm-disease committee was established to study the problem and make recommendations. They concluded that no other tree species could replace elm in many sections of the country, and the most practical method of combating the disease was to develop new genetically resistant varieties of elm. As a result of this decision, an elm breeding program was established in 1928. The progress of this program has been reviewed by Went (1938, 1954) and Heybroek (1957, 1966b).

The initial phase of this program consisted of screening *Ulmus* material for possible sources of resistance. Three groups of elms were included in the screening program. The first group consisted of cultivated varieties of *Ulmus* which had been developed in Europe. Both asexually propagated clones and seedlings from these clones were collected and tested. About 10,000; 1 or 2 year-old seedlings of European species of *Ulmus* made up the second group. These seedlings were obtained from nurseries throughout Europe. The

third group was made up of seed collections of *Ulmus* species native to North America and Asia. Most of this seed was obtained from arboretums and botanical gardens.

Differences in susceptibility were exhibited between clones included in the study. However, none of the cultivars contained enough resistance to be recommended for general planting (Went, 1938). *U X hollandica* cl. 'vegeta' was one of the clones that showed some resistance to the disease. Later, this clone was considered to be acceptable for planting in areas of the country where the disease had not been very severe (Heybroek, 1957).

Screening of the seedlings was more successful. A number of resistant individuals were obtained in this way. However, the percentage of resistant individuals in a population was very low. Only seven resistant individuals were selected out of 5,700 *U. minor* seedlings tested in the first 10 years of the program. Six of these seedlings were selected from a group of elms from Spain. The other selected seedling originated in France.

One selected Spanish seedling was released to growers in 1936 under the name 'Christine Buisman'. Although this clone is highly resistant to Dutch elm disease, it proved to be very susceptible to another disease caused by the fungus *Nectria cinnabarina* (Tode) Fr. Because of this susceptibility, its planting was soon stopped in Holland. The clone has been grown successfully in Italy

and the United States where *Nectria* disease is not a problem (although it is present in both areas).

In 1946 a selected seedling from France was released under the name 'Bea Schwartz'. This selection was resistant to both Dutch elm disease and *Nectria cinnabarina*, but it had a poor growth form and was never accepted very well by tree planters.

All eastern North American species of elm screened in the program were very susceptible to the disease. The Asiatic material ranged from very susceptible to highly resistant.

In 1937 hybridization was started between the various species and varieties that remained from the original collections after screening. After the disappointing results of their first two introductions, the Dutch developed a set of eight criteria to be used in selection. They are as follows:

1. Resistance to Dutch elm disease
2. Resistance to *Nectria cinnabarina*
3. Resistance to frost
4. Resistance to wind
5. Fast growth
6. Good form
7. No epicomic shoots or suckers
8. Valuable timber

If any of these characteristics were missing they considered the tree to be of little value (Heybroek, 1957).

As a result of the hybridization and selection program, the clone 'Commelin' was released in 1961. This clone has good form but only moderate resistance to Dutch elm disease (Heybroek, 1961, 1963). The clone 'Groenveld' was released in 1963. It is highly resistant but rather slow growing. More new hybrid varieties are now being tested for possible future release.

Future elm breeding work in Holland will concentrate on incorporating Himalayan species of *Ulmus* into the breeding program. An attempt to produce fast growing triploid varieties is also being made (Heybroek, 1968).

Several organizations in the United States have been interested in importing the resistant Dutch varieties and growing them in this country. Heybroek (1966a) pointed out that elms in Holland are grown primarily for lumber, ornament and for protection from the wind. The less shade a tree produces the better, since the sun does not shine very much in Holland. Trees selected for Dutch conditions would probably not be accepted in this country where elm is grown primarily for shade.

The elm disease committee of Holland has made both seed and scionwood of their most promising material available to research workers in this country. This material is presently being tested at several locations in the United States and Canada.

England

The British policy toward the control of Dutch elm disease is to do nothing about it except occasionally remove dead trees (Heybroek, 1966). This official policy was adopted as early as 1929 and has proved to be quite effective. Peace (1960) found that the disease, though widespread in England, has killed only 10 to 20% of the British elm population in the past thirty years. After the peak years of 1931 and 1936-1937 the disease has exhibited a gradual decrease in the country.

The reason the disease has been less serious in England than on the continent or in America is not completely understood. The elms of England are generally more resistant to the disease than the elms of the rest of Europe or America. However, this difference alone is not sufficient to account for the difference in severity of the disease.

The maritime climate of Britain may limit development of the disease. Heybroek (1957) stated that the disease has not been as serious in areas of Holland near the seacoast as further inland. In some cases a clone that is highly susceptible in a more continental climate has not been attacked in these areas.

Recovery of diseased trees is common in England (Peace, 1960). Apparently, it is unpredictable whether a

diseased tree will be healthy or diseased again next year. Trees with three-fourths of their crowns dead from the disease have been known to recover (Heybroek, 1966a).

One factor that is well known is that far fewer elm trees would grace the English countryside today if the early policy of removing trees as soon as they showed symptoms of the disease had been continued (Peace, 1960).

Selection and testing clones of *U. procera* resistant to Dutch elm disease has been carried out for several years by the Forestry Commission, Alice Holt Lodge, Wrecclesham England (Jobling, 1969). Methods of asexual propagation of selected clones are also being studied.

Italy

The growing of grapes in Italy has depended upon the use of elm trees to serve as props since ancient times. *U. minor* was the species used for this purpose before Dutch elm disease invaded the country about 1929.

An elm breeding program to develop varieties resistant to the disease was reported by Goidanich (1938) and Goidanich and Azzarolli (1938, 1939). Both artificial inoculation and hybridization were used in the program. As a result of this research *U. pumila* var. *pinnato-ramosa* largely replaced *U. minor* for use in the grape growing industry. Castellani (1966) reported that new resistant strains of *U. minor* from Spain have now largely replaced

the less desirable *U. pumila* var. *pinnato-ramosa*. Italian research is now concentrated on the selection of *U. minor* and *U. minor* X *U. pumila* hybrids that combine disease resistance with useful agricultural characteristics.

U.S.S.R.

A Russian program to develop elms resistant to Dutch elm disease began in 1946. Experiments were conducted in 22 locations in southwestern Siberia. In these areas almost all of the elm trees had been affected by the disease (Ozolin 1958, 1959). The first step in the program was to locate surviving trees in areas heavily infected by the disease. Attempts to inoculate these trees in the field to determine resistance were not successful (Ozolin, 1959). Later experiments concentrated on seedlings from the selected trees. Selections were in open-pollinated and control-pollinated seed lots.

Results of studies on species resistance to the disease reported by Ozolin differ from the results reported from other countries. The largest difference is that the Russians rated *U. pumila* as highly susceptible to the disease. Elm researchers in other countries usually regard *U. pumila* as the most resistant species. The *U. pumila* material used in the Russian study came from Kharobovsk, in the Transbaikal a region probably not sampled in other elm research projects. The source difference may account

for the unusual results. *U. pumila* var. *pinnato-ramosa*, which is native to the region where the study was conducted, was rated as highly resistant to the disease. In addition to species resistance, the Russians also found individual resistance in otherwise susceptible species.

Controlled pollination was carried out on mature trees in the field and on cut branches in the greenhouse. Blossoms were emasculated in the control pollinations. Studies of the inheritance of disease resistance, tree form, and seedling vigor were reported by Ozolin (1958).

In addition to disease resistance, vegetative propagation and seed storage was studied. *U. laevis* seed stored in a paper bag two years under room conditions still germinated but germination time was doubled. Grafting gave better results than cuttings.

Studies on the biochemical nature of resistance included amylase activity and carbohydrate concentration. Ozolin (1959) stated that results of these studies were highly contradictory and do not allow for conclusions to be drawn.

Two thousand trees resistant to the disease were distributed to nurseries in 1958. No information on the success of this material is available.

Portugal

Selection of *U. glabra* for resistance to Dutch elm disease has been conducted for the past eleven years at the Estacao De Biologia Florestal, Oeiras, Portugal. Five clones which showed resistance to five different Portuguese strains of the fungus have resulted from this work.

The resistance of foreign clones to Portuguese strains of the fungus is also being investigated. Resistant clones produced by the Netherlands elm breeding program are being utilized in this study (Natalina F. dos Santos de Azevedo, personal correspondence).

United States

University of Wisconsin

A program to obtain and screen world-wide seed collections of elm for resistance to Dutch elm disease was begun by the Department of Plant Pathology, University of Wisconsin in 1957. To date almost 500 seed collections and clones from all over the world have been screened. (Dr. Eugene Smalley, personal communication.) These collections include species of other genera in the *Ulmaceae* family as well as *Ulmus* (Smalley and Riker, 1962).

As a result of this testing over 1,000 resistant individuals representing eight species and several hybrids of elm are now growing in the elm arboretum near Madison, Wisconsin.

In 1966 an elm genetics and breeding program was developed jointly between the Department of Forestry and Plant Pathology to determine patterns of inheritance for disease resistance and ornamental traits (Lester, 1969).

The material now being studied at Wisconsin can be divided into two groups. One group is made up of *U. americana* and the other includes the three diploid species, *U. pumila*, *U. japonica* and *U. rubra*. The objective of the Wisconsin work includes clarification of crossability patterns in *Ulmus*, estimation of self compatability and determination of the extent to which desirable characters can be transferred among species and individuals. Screening of established and newly obtained progenies for resistance to Dutch elm disease is being continued. Anatomical and biochemical studies of resistant and susceptible individuals and selection of resistant individuals for desirable ornamental characteristics are also being conducted (Lester, 1969).

Agricultural Research
Service of U.S.D.A.

The U.S. Department of Agriculture began studying the possibility of selecting American elms resistant to Dutch elm disease shortly after the disease was discovered in Ohio in 1930. It has been a major project since 1937 (Smucker, 1944). In the initial phase, 35,000 elm seedlings collected from throughout the natural range of the species

were grown in test nurseries and inoculated with the fungus. Only two seedlings remained after three consecutive seasons of inoculations. These later proved susceptible to new strains of fungus (Clapper, 1952).

In the 1930's a U.S. financed field laboratory was established in England to compare resistance of American elm with European species. American elm was the most susceptible of all species tested. The English-American program was closed out when it became threatened by World War II (L. R. Schreider, personal correspondence).

One of the original objectives of the U.S.D.A. program was to combine the resistance of Dutch elm disease and phloem necrosis of *U. pumila*, the high quality lumber of *U. thomasi* and the beauty of *U. americana* all into one variety. Compatibility barriers stopped this program in the first stages (Smucker, 1944).

Several thousand seedlings were collected by elm breeders in the Department of Agriculture from mixed plantings of *U. pumila*, *U. rubra* and *U. americana* in the Great Plains Region. They were looking for natural hybrids that might be resistant to the disease (Smucker, 1944). All *U. pumila* hybrids proved to be too susceptible to Dutch elm disease for recommended use (Swingle, 1961).

Swingle (1961) reported that over 200,000 American elm trees have been tested for resistance to the disease, of which 19 were moderately resistant. Most of the

selections were carriers of one or more viruses that make them difficult to propagate. The viruses may have influenced their reaction to inoculation with Dutch elm disease fungus.

Tests for resistance to phloem necrosis were more encouraging. Individuals that had survived in areas heavily infected by the disease were selected. Resistance tests on seedlings and clones of these survivors showed positive results (Swingle, 1945). Clapper (1952) stated that 2,000 American elm had been selected for their resistance to phloem necrosis.

In later research, seedlings were first screened for their resistance to Dutch elm disease. If they showed resistance, they were subjected to phloem necrosis. The results of this work have not been published.

Present research at Delaware, Ohio, and at the U.S. National Arboretum is devoted to elm hybridization and further selection in American elm for resistance to Dutch elm disease (Egolf, 1968).

Cornell University

Selection of American elm for resistance to Dutch elm disease was begun by Cornell University in 1934 in cooperation with Boyce Thompson Institute for Plant Research. Elm seed and seedlings were collected from

throughout the northern half of the range of American elm (Welch, 1949). Fifty-five collections of material involving over 21,000 individual trees were included in the study.

In the early stages of the program, all seedlings that exhibited external symptoms after artificial inoculation were discarded. This standard was later relaxed and modified as the number of trees diminished and it became apparent that American elm displays a variable syndrome after inoculation. The criteria of selection used in later stages of the program allowed retention of a tree if (a) it survived infection and recovered from external symptoms, (b) and was not successfully attacked by elm bark beetles, (c) and displayed potential for growth rate and form characteristic of American elm (Sinclair, et. al., 1968).

The first inoculations confirmed the low level of resistance of American elm; 94% of the seedlings wilted so badly that they were discarded. Only in 9 of the 55 collections were more than 10% of the trees alive after the first inoculation.

By 1967, 17 survivors had been selected by one or more of the criteria listed earlier. Of these, six survived infection but were very slow growing trees; and, one did not have the typical form of *U. americana*. Only one was considered promising and it later developed elm leaf mosaic, a virus disease and was withdrawn from possible release (Sinclair, 1970).

Selection was not as rigid in the Cornell program as it was in other American programs where all trees that showed symptoms were discarded (Oullett and Pomerleau, 1965; Smucker, 1944). Sinclair suggested that if the stern selection criteria used in other programs had been employed at Cornell, they might not have recognized any natural resistance in *U. americana*. Whether the apparent resistance exhibited by the selected trees is a strongly heritable character remains to be determined.

Present work at Cornell involves selection of new material from areas infected by the disease for a long period of time. New selection techniques are being developed.

University of Massachusetts

Several years of research on the resistance of elms to Dutch elm disease have been conducted by the Shade Tree Laboratory of the University of Massachusetts. Attempts to induce mutation of American elm seed in hopes of finding resistance to the disease has been a major part of the program.

During the past ten years over six million elm seeds have been irradiated. From this material 110 trees survived two or three inoculations. From 4,573 trees inoculated in 1970, 68 were apparently wilt free. Reciprocal crosses of resistant elm trees are being attempted (McKenzie, 1970).

South Dakota State University

A serious weakness of Siberian elm in the northern Great Plains has been its lack of winter hardiness. In 1944, workers at South Dakota State University began a program to develop hardier strains of the species. Two sources of seed, from Manchuria and one of unknown origin from a nursery in Washington, were included in the study (Maxon, 1951). A source from Harbin, Manchuria, proved to be the best adapted to South Dakota conditions. The seedlings of this source became dormant early in the fall and were not subject to damage by sudden freezes. In 1952 the strain was named "Chinkota" and released to the public.

The seedlot used to develop "Chinkota" elm was also used to develop the "Harbin," "Manchu," and "Dropmore" strains in Canada and many people consider them all to be the same. The one major difference is that the research workers in South Dakota realized the importance of maintaining a source of high quality seed and developed a seed orchard to produce it. Since it was first introduced "Chinkota" elm has been produced under certification standards of the Seed Stocks division of South Dakota State University and only certified seedling stock has been sold to growers (Collins, 1955).

Collins (1967) did an extensive study of *Ulmus* hybridization and hybridization techniques. He also did an intensive study of *U. pumila* X *U. rubra* hybrids. Backcross

progenies showed characteristics intermediate between the F_1 and the recurrent parent. No studies on resistance to Dutch elm disease were included in the project.

Syracuse University

In 1957 the genus *Ulmus* was added to existing forest tree improvement programs at the State University College of Forestry at Syracuse University. The objective of this project was to:

1. perfect the hybridization methods using cut branches in the greenhouses
2. determine the crossability pattern within available *Ulmus* species
3. determine the best possible grafting method for each species
4. provide hybrid seed and test material resistant to Dutch elm disease

Four American elms from the city of Syracuse, that had been infected with the disease and apparently recovered, and eight resistant clones from the Cornell University project were included in the study. Selection of other *Ulmus* species was based on assumed resistance or on known successful crosses (Anon., 1962).

The results of the hybridization study were published by Wineski (1960) and Britwum (1961). No attempt to certify the authenticity of the hybrids produced in the study has been published.

Canada

The Canada Department of Agriculture began an elm breeding program at the L'Assomption Experiment Station, L'Assomption, Quebec, in 1948. Three years of crossing work with *U. americana* and *U. pumila* resulted in one triploid seedling (the only authenticated case of a triploid seedling resulting from a controlled cross between the two species) (Heimbürger, 1966). The triploid seedling resisted artificial inoculation of *Ceratocystis ulmi* for several years, but finally succumbed.

Screening of *U. americana* for resistance to Dutch elm disease was begun in 1952. From 1952 to 1956, 43,000 seedlings were inoculated. After four annual inoculations only two seedlings remained.

Irradiation of elm seed to induce mutation as a possible method of finding resistance was done in 1955. In 1956 thermal neutrons were used for the same purpose. Since 1955, 20,000 seedlings, from seed subjected to induced mutation, have been inoculated. Three of these plants have escaped infection after three inoculations. According to a newspaper release, the 'Quebec' elm, a slow growing but highly resistant clone of American elm, was released to the public in 1970.

CHAPTER VI

RATIONAL AND CONDUCT OF THE MICHIGAN STATE UNIVERSITY ELM BREEDING PROJECT

The elm breeding project at Michigan State University is part of a comprehensive Dutch elm disease research program developed jointly by the Departments of Entomology, Plant Pathology and Forestry. The heavy loss of native Michigan elm to the Dutch elm disease was the primary reason for initiating this program. The biology and control of the insect vector and the potential value of systemic fungicides for controlling the disease in existing elm trees are being investigated by the Departments of Entomology and Plant Pathology respectively. The selection and breeding of elms for resistance to Dutch elm disease was undertaken by the Department of Forestry with assistance from the campus Parks and Planning office.

A number of tree species from other genera have been suggested as possible replacements of the American elm. However, none of these species contain all of the desirable characteristics of American elm. There is still a need for elm genetically resistant to Dutch elm disease.

Developing varieties of elm with the desirable characteristics of American elm combined with an acceptable level of resistance to Dutch elm disease is the objective of the elm breeding program.

After considering the possible alternatives, it was decided that these objectives could be most easily obtained by working with the foreign species of *Ulmus*. American collections of *Ulmus* are limited. Therefore, it was decided that the most efficient approach to the problem would be to obtain as much foreign material as possible and screen it for disease resistance and other ornamental traits.

Development of varieties of elm that have a broad genetic base and can be produced from seed is the goal of the Michigan State University elm breeding program. This is the main difference between the M.S.U. program and other elm breeding programs.

Materials and Methods

Seed Procurement

In the spring of 1968, Dr. George Parmalee, Campus Curator of Woody Plants, and Dr. J. W. Wright, Professor of Forestry, wrote personal letters to cooperators in Europe and Asia asking for collections of seed from elm trees growing in their vicinity. They received 576

individual tree collections of *Ulmus* seed in response to these requests; 516 arrived during the spring and summer of 1968 and the remainder during the following year.

Nine species of *Ulmus*, representing three sections of the genus are included in the collection. Seven of these species are from the section *Ulmus*. They include: *U. elliptica* of the series *Fulvae*; *U. glabra*, and *U. laciniata* of the series *Glabrae*; *U. wallichiana*, *U. minor* and *U. japonica* of the series *Nitentes*, and *U. pumila* of the series *Pumilae*. The other two species are *U. laevis* of the section *Blepharocarpus* and *U. parvifolia* from the section *Microptelea*.

Open pollinated seed collected from the most promising hybrid clones developed in the elm breeding program at Wageningen, Netherlands are also included in the collection. The number of seed collections of each species is summarized by country of origin in Table 5.

As soon as it was received, each seedlot was given an accession number (MSFG, Michigan State Forest Genetics number) and a description of the seedlot was entered in the permanent accession record maintained by the Department of Forestry.

Cultural Practices

Elm seed is reported to lose its viability rapidly in storage. Therefore, all seed was planted as soon as possible after it arrived. To insure against loss, a

Table 5a. Number of collections of the four European species of *Ulmus* represented in the M.S.U. collection summarized by country of origin.

Country of origin	<u>Species</u>					Dutch Hybrids	Total
	U. minor	U. elliptica	U. glabra	U. laevis			
1. Austria	7		18	3			28
2. Czechoslovakia	17		25	17			59
3. England	3		20	2			25
4. Germany	10		13	8			31
5. Greece	9						9
6. Hungary	12		2	13			27
7. Italy	27		16				43
8. Netherlands	1			2	27		30
9. Poland	6		10	22			38
10. Romania	1		7	2			10
11. U.S.S.R.	42	7	20	42			111
12. Yugoslavia	7		7	4			18
13. United States	9						9
	<u>151</u>	<u>7</u>	<u>138</u>	<u>115</u>	<u>27</u>		<u>438</u>

Table 5b. Number of collections of the five Asian species of *Ulmus* represented in the M.S.U. collection summarized by country of origin.

Country of origin	<u>Species</u>					Total
	U. japonica	U. laciniata	U. parvifolia	U. pumila	U. Wallichiana	
1. England		1				1
2. Italy				11		11
3. Japan	46	8	10	4		68
4. Korea			3	4		7
5. Netherlands		1			6	7
6. Pakistan					1	1
7. U.S.S.R.				18		18
8. United States			6	5		13
	<u>46</u>	<u>10</u>	<u>19</u>	<u>42</u>	<u>7</u>	<u>125</u>

portion of each seedlot was planted in the greenhouse. The remaining seed was planted directly in the nursery at the Tree Research Center on the Michigan State University Campus.

Seedlings germinated in the greenhouse were potted in two inch clay pots when they were 2-3 weeks old and transplanted to outdoor beds 2-3 weeks later when they were 4-6 inches tall.

In the spring of 1969 the nursery-grown seedlings were transplanted to a nursery study consisting of four replications of 10 tree plots. A modified randomized complete block design was used. All accessions of a species were randomized and grouped together. These species groups were randomly distributed through each of the four replications. This made it easier to detect differences both within and between species.

Not all accessions were included in all replications. An accession was included if it contained at least 20 seedlings, enough for two replications. In a few cases where a species was represented by only a few accessions, it was included in the test if only 10 seedlings were available.

In the spring of 1970 every seedling in the replicated test was inoculated with a suspension of *Ceratocystis ulmi*: (Dutch elm disease) spores using the method described by Tchernoff (1965). A drop of spore suspension was placed

on the stem of each seedling and the stem was wounded, allowing the spore suspension to penetrate into the stem.

Dr. John Hart of the Department of Plant Pathology prepared the spore suspensions and supervised the inoculations. All 7,800 seedlings in the replicated test were inoculated within 48 hours. To test the effectiveness of the spore suspension 10 young American elm trees 10 to 15 feet tall were also inoculated. All of these trees developed symptoms and three died completely.

Measurement of Characters

The choice of characters used in this study was based on three things: review of the literature, study of the material itself, and ease and rapidity of measurement. For convenience, the study was conducted in three parts. The first part was the study of a 4-samara sample which had been selected from each seedlot before it was planted. Study of a 10-leaf sample collected from each accession in the nursery at the end of the first growing season was the second part. Characteristics of seedlings in the nursery were studied in the third part.

Some collectors removed the wings from the seed before it was shipped. In other cases, the samaras were too badly damaged for measuring so that all accessions were not included in the samara study. Leaf measurements were made only on accessions that produced at least 5

seedlings. Accessions that were received during the second year or late in the first growing season were not included. Not as many accessions were included in the leaf study as in the samara study. The nursery study included only those accessions that produced enough seedlings to be included in the replicated nursery test. The number of accessions included in each part of the study are summarized in Table 6.

Table 6. The number of accessions included in each part of the study, summarized by species.

Species	Number of accessions included in:		
	Samara Study	Leaf Study	Nursery Study
<i>U. minor</i>	132	92	65
<i>U. elliptica</i>	7	1	0
<i>U. glabra</i>	140	48	12
<i>U. japonica</i>	39	16	10
<i>U. laciniata</i>	10	2	1
<i>U. laevis</i>	112	90	78
<i>U. parvifolia</i>	18	1	1
<i>U. pumila</i>	38	33	29
<i>U. wallichiana</i>	6	4	4
Total	519	303	233

Samara Characters

Four undamaged samaras were selected from each seedlot and mounted for further study. Twenty-six different

characters were measured, estimated or computed on these samaras. Characters that were present on every samara of one species and not shown by any other were not used. These include the ciliate samara margins of *U. laevis* and pubescence over the locule of *U. elliptica*.

Eight different measurements of size were made on each samara. Since these measurements are dependent on overall samara size, they are also expressed as ratios of total length or width.

Nine other characters of size, shape or color were scored on a scale of one to five. Each character was scored by choosing five samaras to represent the five grades of the character and comparing all others to these samples. A complete list and description of all characters studied is given in Appendix C.

Leaf Characters

A leaf collection was made in the fall of 1968 by collecting the largest leaf from five different trees in each accession. A similar collection was made in 1969 by collecting the third leaf from the terminal in each tree. If the third leaf was damaged, the next lower undamaged leaf was taken.

Seventeen different characters were measured, estimated or computed for each sample. Thirteen of these

were variables that depended on overall size and were also expressed as a ratio of leaf length making a total of 29 leaf characters.

The same characters were measured on 60 accessions in 1969. There was a high correlation between years ($r = .70$ to $.90$). Since this material did not seem to add any new information, the measurements were discontinued. A complete list and description of all leaf characters studied is given in Appendix C.

Nursery Characters

In the fall of 1968 four different characters were scored on each accession in the unreplicated nursery planting. Sixteen additional characters were studied during the next 2 years in the replicated planting. A list and description of the twenty nursery characters studied is given in Appendix C.

Susceptibility to Dutch elm disease was recorded as the number of trees in each plot that showed branch die-back from the disease (few died completely). In August of 1970, there was a large difference exhibited among species in damage by a leaf-eating insect. Although the insect was not identified, damage was scored as the number of trees attacked in each plot.

CHAPTER VII

RESULTS

Germination and Growth

Although this study was not designed to test differences in germination, several factors were observed that may be of value to future studies of this type. For example, there was no significant difference in the number of seedlings produced from seedlots shipped moist and those shipped dry. The best evidence of this comes from 12 seedlots representing three species from Austria. Each seedlot was divided into two equal parts by the collector. One half was shipped moist and the other half dry. The method of shipping had no significant effect on the number of seedlings produced. Comparison of other seedlots shipped moist and dry also failed to show any significant difference. However, the seed shipped dry was the easiest to handle.

The time of year that the seed was planted seemed to be one of the major factors affecting germination and growth. In almost all cases seeds planted early in the growing season produced the most seedlings. *Ulmus pumila* and *U. laevis* were the only species that showed a significant amount of germination when the seed was planted after the middle of July.

The average number of seedlings per seedlot and the percent of seedlots that produced some seedlings are summarized by species in Table 7.

Five seedlots of *U. glabra* from Riga, Latvia, were collected June 20, 1968 and shipped by surface mail. They arrived in East Lansing, September 17th and were planted September 19th. The seed did not germinate until the following spring, but the percentage of germination was the highest of any *U. glabra* in the study. One seedlot of *U. pumila* var. '*Chinkota*' from South Dakota had been stored for three years by the collector. This seedlot also showed a high percentage of germination.

These results indicate it may not be as necessary to plant elm seed as soon as possible after maturation as is generally believed. In a study of this type there are obvious advantages to storing the seed and planting it all at the same time.

In spite of the southern origin of many of the accessions, there was very little winter injury to the nursery grown seedlings. Almost all injury was confined to accessions that had been planted late in the growing season and did not have time to harden off before winter. The only exception was *U. wallichiana*, a species native to the Himalayan region, which was killed to the ground both of the first two winters.

Table 7. The average number of seedlings per seedlot and the percentage of seedlots producing at least 1, 10 or 20 seedlings, summarized by species.

Species	Average number of seedlings per seedlot	Percentage of seedlots that produced		
		1 seedling	10 seedlings	20 seedlings
U. minor	55	87	70	63
U. elliptica	3	67	0	0
U. glabra	5	53	15	9
U. japonica	9	90	40	10
U. laciniata	2	22	10	0
U. laevis	75	92	69	53
U. parvifolia	47	72	55	55
U. pumila	85	92	84	73
U. wallichiana	24	83	67	33
Dutch Hybrids	25	90	70	55

The potted seedlings produced in the greenhouse did not grow as well after transplanting as did the nursery grown stock. Data from this material was not used in any of the analyses. The roots of the potted stock were curled in the soil ball transplanted with them. They were slow to grow into the coarse textured nursery soil. As a result, these seedlings were subject to frost heaving during their first winter and suffered unusually high mortality. These results indicate that the work involved in germinating and transplanting greenhouse seedlings was not worthwhile.

All seedlings transplanted in 1969 showed high survival except *U. wallichiana*. The poor survival of this species was probably due to winter injury. *U. laevis* seedlings were severely attacked by a leaf spot disease (*Gnomium ulmi*) which affected their growth. All other seedlings grew well after transplanting.

Variation Between Species

There were highly significant (.01 level) differences between species for every character studied. The high level of significance obtained (less than .0005 for all characters but two) indicates that the differences are real in spite of the differences in sample size.

The percent of total variance accounted for by differences between species varied greatly among characters. Samara characters were easiest to recognize, but samara,

leaf and nursery characters were of almost equal value statistically in distinguishing between species, as is shown in the following tabulation.

<u>Character</u>	Variance accounted for by differences among species	
	<u>Range</u>	<u>Average</u>
Samara characters	11 to 93%	55%
Leaf characters	17 to 75%	47%
Nursery characters	11 to 86%	56%

Species were divided into three groups (high, medium, or low) for each character depending on the species mean. Tukey's W. procedure was used to determine which species belonged in each group. There was slight overlap between groups, but the groups differed significantly (.01 level). This arrangement makes it possible to see which species could be distinguished from one another for each character. The species groups are shown in Table 8a, 8b, and 8c for samara, leaf and nursery characters respectively.

The use of a factor analysis or other multivariate technique to determine which characters were of most diagnostic significance was considered. However, Jeffers and Richens (1969) tried several of these techniques in a study of the elms of southern England. They obtained the same results as earlier studies using simpler techniques. The

Table 8a. Species means rated low, medium or high for each samara character and the percent of total variance accounted for by differences among species.

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
% of total				
1. Base length	64	lv,pa,pu	ja,lc,wa	mi,el,gl
2. Seed length	38	ja,lc,pa,wa	lv,pu	mi,el,gl
3. Seed-notch	84	mi,ja,lv,pa, pu,wa		el,gl,lc
4. Notch length	11	lc,pa,wa	ja,lv	mi,el,gl,pu
5. Samara width	72	ja,lv,pa,pu, wa	mi,lc	el,gl
6. Widest point to base	70	lv,pa	ja,lc,pu,wa	mi,el,gl
7. Seed width	58	ja,lv,pa	lc,wa	mi,el,gl,pu
8. Samara length	74	ja,pa,wa	lc,lv,pu	mi,el,gl
9. Base length/samara length	62	lv,pa,pu	el,gl,lc,wa	mi,ja
10. Seed length/samara length	53	el,gl,lc	mi,ja,pu,wa	lv,pa
11. Seed notch/samara length	92	mi,ja,lv,pa, pu,wa		el,gl,lc
12. Notch length/samara length	31	el,gl,lc,pa, wa	mi,ja	lv,pu
13. Samara width/samara length	47	el,gl,lc,pa, wa	mi,ja	lv,pu
14. Widest point to base/ samara length	29	el,gl,lv	pa,pu	mi,ja,lc,wa

Table 8a. (cont'd.)

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
% of total				
15. Seed width/samara length	41	el,gl,ja	mi,lc,wa	lv,pa,pu
16. Seed width/samara width	55	mi,el,gl,pu,wa	ja,lc,lv	pa
17. Tip shape	93	lc,lv,pa	mi,el,gl,ja	pu,wa
18. Base shape	38	el,ja	mi,gl,lc,pa	lv,pu,wa
19. Openness of notch	58	el,gl,lc,pa	mi,pu	ja,lv,wa
20. Style length	43	pa,wa	mi,lc,lv	el,gl,ja,pu
21. Style shape	57	pu	mi,el,gl,ja	lc,lv,pa,wa
22. Wing color	54	mi,ja,pu,wa	el,gl,lc	lv,pa
23. Seed color	44	pu,wa	mi,lc	el,gl,ja,lv,pa
24. Greeness of samara	47	mi,lv,pa,pu		el,gl,ja,lc,wa
25. Persistent calyxes	71	pa,wa	pu	mi,el,gl,ja,lc,lv
26. Contrast between seed color and wing color	49	lc,lv,pa,pu,wa	mi,el,gl	ja

*Species designations are el=*elliptica*, gl=*U. glabra*, ja=*U. japonica*, lc=*U. laciniata*, lv=*U. laevis*, mi=*minor*, pa=*U. parvifolia*, pu=*U. pumila*, wa=*U. wallichiana*.

Table 8b. Species means rated low, medium or high for each leaf character and the percent of total variance accounted for by differences among species.

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
% of total				
27. Leaf length	72	mi,ja,pa,pu	el,lv,wa	gl,lc
28. Leaf width	64	mi,el,pa,pu	ja,lv,wa	gl,lc
29. Number of veins	62	mi,pa,pu	el,ja,lv	gl,lc,wa
30. Number of major serrations	25	mi,el,ja,lv pa,pu		gl,lc,wa
31. Total number of serrations	59	lv,pa,pu	mi,el,ja,wa	gl,lc
32. Widest point to tip	70	mi,ja,pa,pu	el,lv,wa	gl,lc
33. Serration depth	60	mi,el,pa,pu	ja	gl,lc,lv,wa
34. Serration length	64	mi,pa,pu	el,ja,wa	gl,lc,lv
35. Serration width	34	mi,pa,pu,wa	el,ja	gl,lc,lv
36. Major-minor serration	61	mi,pu,wa	el,ja,pa	gl,lc,lv
37. Major-major serration	46	mi,pa,pu	el,ja,lv,wa	gl,lc
38. Obversity	50	mi,el,ja,pa	gl	le,lv
39. Petiole length	25	el,ja,lc,pu	mi,pa	gl,lv,wa
40. Pubescence of upper leaf surface	75	mi,ja,lv,pa, pu	el,wa	gl,lc

Table 8b. (cont'd.)

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
% of total				
41. Pubescence of lower leaf surface	72	lv,pa,pu	mi,el,gl,lc	ja,wa
42. Number of veins/number of major serrations	31	lv	mi,el,ja,pu wa	gl,lc,pa
43. Number of major serra- tions/total number of serrations	39	lv,pa,pu	el,lc,wa	mi,gl,ja
44. Leaf width/leaf length	36	el,pu	gl,lc,wa	mi,ja,lv,pa
45. Number of veins/leaf length	59	gl,lc	el,ja,lv,wa	mi,pa,pu
46. Number of major serra- tions/leaf length	57	el,gl,lc, lv,wa	ja	mi,pa,pu
47. Total number of serra- tions/leaf length	70	el,gl,lc, lv	pa,pu,wa	mi,ja
48. Widest point to tip/ leaf length	17	mi,gl,ja, lv,pu,wa	lc	el,pa
49. Serration depth/leaf length	28	el,gl,lc, pu	ja	mi,lv,pa,wa
50. Serration length/leaf length	26	gl,lc,pu, wa	mi,el,ja	lv,pa

Table 8b. (cont'd.)

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
% of total				
51. Serration width/ leaf length	21	el,gl,lc, pu,wa	mi,lv	ja,pa
52. Major-minor serra- tion/leaf length	30	el,gl,lc, pu,wa	mi,ja	lv,pa
53. Major-major serra- tion/leaf length	22	el,gl,wa	pu	mi,ja,lc,lv, pa
54. Obversity/leaf length	40	el,gl,lc, wa	mi,ja,pa	lv,pu
55. Petiole length/leaf length	50	el,lc,pu	gl,ja	mi,lv,pa,wa

Table 8c. Species means rated low, medium or high for each nursery character and the percent of total variance accounted for by differences among species.

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
	% of total			
56. Percent opposite leaves	57	gl,lc,pa,wa	el	mi,ja,lv,pu
57. <i>Gnomium ulmi</i> injury, 1968	40	el,mi,gl,ja, lc,pa,pu,wa	el	lv
58. Red fall color	11	mi,gl,ja,lc, lv	el	mi,ja,lv
59. Frost injury	46	gl,lc,pa,wa	el	mi,ja,lv
60. <i>Gnomium ulmi</i> injury, 1969	80	mi,gl,ja,pa, wa,pu		lv
61. Corky twigs	70	gl,lc,lv,pa, pu	mi,wa	ja
62. Fall color	65	gl,lc,pa,wa	mi	ja,pu
63. Long shoot-short shoot	72	gl,lv,wa	mi,ja,lc	pa,pu
64. Frost injury	52	pa	mi,ja,pu	gl,lc,lv,wa
65. Green leaves	30	ja,lv,wa	mi,gl,lc	pa,pu
66. Stem color	69	mi,pa,pu	gl,ja,lc	pa,pu
67. Twig color	64	pa,pu	mi	gl,ja,lc,lv wa

Table 8c. (cont'd.)

Character no. and name	Between species variance	Species with means of		
		Low	Medium	High
% of total				
68. Number of branches	75	gl,lv,wa	mi,ja,lv	pa,pu
69. Secondary branching	39	gl,lc,lv,wa	mi	ja,pa,pu
70. Branch angle	18	gl,ja	mi,lc,lv,pu	pa
71. Leafing out	64	mi,lc,wa	gl,ja	lv,pa,pu
72. Average height	56	lv,pa	mi,pu,wa	gl,ja,lc
73. Susceptibility	86	lc,pa,pu,wa	mi,gl,ja	lv
74. Insect attack	67	ja,lv,wa	mi,gl,lc,pa	pu
75. Contrast between stem and twig color	41	pu,wa	mi,gl,lv	ja,lc,pa

percent of variance due to between species differences given in Table 8 is a good indicator of the discriminating ability of various measured traits.

Results of the artificial inoculations are summarized in Table 9. These results are very similar to results obtained at the University of Wisconsin (E. B. Smalley, personal communication) in a similar study. The Dutch hybrid seedlings were grown from open pollinated seed from clones of known resistance produced in the elm breeding program at Wageningen, Netherlands. The results obtained from artificial inoculation of these seedlings was closely correlated to the resistance rating of the parent.

Table 9. Results of artificial inoculation with *Ceratocystis ulmi*.

Species	Percent of seedlings showing symptoms	Range in percent	Total number of seedlings tested	No of accessions tested
U. minor	50	6 to 90	2934	93
U. glabra	51	32 to 70	226	11
U. japonica	24	0 to 78	122	11
U. laciniata	14	14	7	1
U. laevis	86	40 to 100	2629	80
U. parvifolia	3	3	40	1
U. pumila	8	0 to 40	1016	37
U. wallichiana	6	0 to 8	34	4
Dutch hybrids	12	0 to 44	388	15

Species means for each character were converted to units of standard error to make comparison between species. The average differences between species was then computed as the sum of the differences between characters divided by the number of characters. The average differences are presented in Table 10 to show the relationship between species.

Table 10. The average difference per trait between nine Eurasian species of *Ulmus*.

1. <i>U. elliptica</i>	<u>1.</u>							
2. <i>U. glabra</i>	0	<u>2.</u>						
3. <i>U. laciniata</i>	3	2	<u>3.</u>					
4. <i>U. wallichiana</i>	3	3	3	<u>4.</u>				
5. <i>U. minor</i>	3	3	4	4	<u>5.</u>			
6. <i>U. japonica</i>	5	3	5	3	1	<u>6.</u>		
7. <i>U. pumila</i>	9	4	7	6	3	5	<u>7.</u>	
8. <i>U. laevis</i>	8	5	6	4	3	5	7	<u>8.</u>
9. <i>U. parvifolia</i>	10	7	8	7	4	6	7	4

One unit of difference = .66 standard error.
 Standard error= Square root $\frac{\text{Seedlot within species mean square}}{\text{average number of seedlots per species}}$

Since size measurements of samaras and leaves are highly correlated with overall size, the length and width

of samaras and leaves were the only size measurements included in the calculating of these differences. Fifty-five characters were used in computing the differences except for comparisons involving *U. elliptica*. Since this species was not included in the replicated nursery study, only 39 characters were used in computing the average difference between it and other species.

The species are arranged in Table 10 according to taxonomic grouping. The seven species of the section *Ulmus* are grouped by series. *U. laevis* of the section *Blepharocarpus* and *U. parvifolia* of *Microptelea* are separated from the other species.

Although the relationships in this table are not clear cut, there is generally more similarity between species within a group than between groups. The relationships agree with the taxonomic arrangement even though only one of the characters, the distance between the seed and notch of the samara, used by taxonomists to recognize these groups was included in the study. *Ulmus parvifolia*, the only fall blooming elm included in the study, shows the greatest difference from the other species.

Variation Within Species

U. minor

The number of accessions of *U. minor* included in each part of the study is listed by geographic region in

Table 11. In addition to the material listed, 12 accessions from outside the native range of the species were studied--3 from England and 9 from Cass County, Michigan. These accessions were not included in the analysis of variance but they were compared with the other material to see if their original source could be determined from this data. A complete list of the accessions studied is given in Appendix E.

Table 11. The number of accessions of *U. minor* included in each part of the study.

Region	Number of Accessions in		
	Samara study	Leaf study	Nursery study
West Central Europe	10	3	1
East Central Europe	37	24	22
Italy	27	18	16
Balkans	16	15	12
Central European U.S.S.R.	11	11	3
Southern European U.S.S.R.	<u>31</u>	<u>27</u>	<u>11</u>
TOTAL	132	92	65

The percent of variation due to differences between region and the regional averages are given in Table 12 for each character that was significantly different between regions. The regions in Table 12 are grouped in north-south

Table 12. The percent of total variance within *U. minor* accounted for by differences between regions and regional averages for each distinctive character.
H, M, L= high, medium and low respectively.

Character number and name	Between region variance	West Cent. Euro.	Regional averages			
			Italy	East Cent. Euro.	Balk. USSR	Cent. Euro. USSR
% of total						
<u>Samara Characters</u>						
1 Base length	10*	M	M	H	H	L
4 Notch length	11*	M	H	M	H	L
7 Seed width	20**	L	M	H	H	M
8 Samara length	11*	L	M	M	H	L
10 Seed length/samara length	14*	L	M	M	L	H
11 W.P.-Base/samara length	13*	H	M	M	M	M
16 Seed width/seed length	13*	M	H	M	M	H
<u>Leaf Characters</u>						
27 Leaf length	31**	H	M	H	L	L
29 No. of veins	27**	H	H	M	L	M
30 No. major serrations	44**	H	L	H	L	L
31 Total no. serrations	17*	H	M	H	L	L
32 Widest point to tip	48**	H	L	M	L	M
34 Serration length	35**	H	M	H	M	L
35 Serration width	31**	H	L	H	L	M
36 Maj.-min. serration	43**	H	M	M	L	L
37 Maj.-maj. serration	35**	H	L	H	L	M
40 Pub. of upper surface	17*	H	M	M	L	L
44 Leaf width/leaf length	23*	H	L	H	M	M
46 No. of maj. serrations/leaf length	29**	L	M	H	H	H

Table 12 (cont'd.)

Character number and name	Between region variance	Regional averages				
		West Cent.	Italy	East Cent.	Balk.	South Euro.
		Euro.		Euro.	USSR	USSR
% of total						
<u>Nursery Characters</u>						
56 % opposite leaves	24**	L	L	H	M	L
63 Long shoot-short shoot	39**	L	H	H	L	M
65 Green leaves 12/12/69	60**	M	H	M	L	M
68 No. of branches	20*	H	L	L	M	L
72 Height	45**	H	H	L	H	L
75 Contrast between stem and twig color	37**	L	H	L	H	L

*, ** means significant at .05 and .01 levels respectively.

pairs and arranged in a west to east order across the table. This makes it easier to detect any geographic trends that may be present.

Four of the seven samara characters that were significantly different between regions were size measurements and three were ratios. The overall variation in *U. minor* samara characters seemed to be random.

Nine of the twelve leaf characters that were significantly different between regions were size characters. Only two were ratios. This indicates that the *U. minor* leaves studied vary more in size than shape. Leaf size decreased from west to east and from north to south.

Time of planting varied for seedlots. At least part of the difference in leaf size may be due to differences in planting time. In the western and central regions seedlots from southern origins were planted before northern ones. All material from Russia was planted within two weeks. The fact that the northern origins produced larger leaves than southern origins in the western and central regions indicates that the true differences may have been underestimated. The difference in leaf size between the two Russian regions should not have been affected by planting time.

The decrease in leaf size from north to south seems to be true differences. However, the west to east trend is questionable.

The six significant nursery characters do not show any particular patterns except that the eastern regions were consistently low.

The relationship between seed sources was shown by computing the average difference between each source. These differences are shown in Table 13.

The English material seemed to be more closely related to the sources from the southern part of the West Central Europe region. However, both the English and American populations showed a closer relationship to all other sources than any of the material from within the native range of the species. The seed for these two sources may have been obtained from an area where trees from several different parts of the native range had been brought together and allowed to hybridize with each other. Southern England, where *U. minor* was first introduced before Roman times, seems to be just such an area. There is evidence that the *U. minor* of southern England has resulted from several very early introductions (Richens, 1955). The American material might easily have originated from southern England.

There was no significant difference in susceptibility to Dutch elm disease, either between regions, or locality within regions. There were, however, differences among the offspring of different individual trees. Simple correlations were computed between susceptibility to Dutch

Table 13. The average differences among 26 geographic origins of *U. laevis*. The underlined numbers refer to specific localities which are defined in Appendix D.

England																									
<u>30</u>	Eng.	30																							
West central Europe																									
<u>40</u>	Ger.	1	<u>40</u>																						
<u>42</u>	Ger.	1	<u>1</u>	<u>42</u>																					
<u>41</u>	Ger.	1	2	<u>0</u>	<u>41</u>																				
Italy																									
<u>71</u>	Ita.	0	1	1	1	<u>71</u>																			
<u>72</u>	Ita.	0	2	1	1	<u>0</u>	<u>72</u>																		
<u>73</u>	Ita.	1	3	2	1	1	<u>1</u>	<u>73</u>																	
East central Europe																									
<u>115</u>	Pol.	1	2	1	1	1	2	2	<u>115</u>																
<u>116</u>	Pol.	2	3	2	2	2	3	3	<u>2</u>	<u>116</u>															
<u>117</u>	Pol.	1	3	2	2	2	2	2	2	<u>1</u>	<u>117</u>														
<u>20</u>	Cze.	1	1	1	1	1	2	1	1	<u>1</u>	<u>2</u>	<u>20</u>													
<u>25</u>	Cze.	1	1	1	1	1	1	1	2	2	2	<u>1</u>	<u>25</u>												
<u>10</u>	Aus.	1	1	2	1	0	1	1	1	2	2	1	<u>1</u>	<u>10</u>											
<u>60</u>	Hun.	1	1	0	0	1	1	1	1	2	1	1	0	<u>1</u>	<u>60</u>										
<u>65</u>	Hun.	1	3	1	1	1	1	1	2	2	1	1	1	<u>1</u>	<u>65</u>										
<u>122</u>	Rom.	1	1	1	1	1	1	2	2	3	2	2	1	1	<u>1</u>	<u>122</u>									
Balkans																									
<u>155</u>	Yug.	0	1	1	1	0	1	2	2	3	3	1	1	0	2	1	<u>155</u>								
<u>157</u>	Yug.	0	1	1	1	1	2	2	2	3	3	1	2	1	1	2	2	<u>1</u>	<u>157</u>						
<u>50</u>	Gre.	0	0	1	1	0	1	2	2	3	3	1	2	0	1	2	1	0	<u>1</u>	<u>50</u>					
Central European U.S.S.R.																									
<u>135</u>	Rus.	0	1	1	0	0	1	1	1	2	2	1	1	0	1	1	1	1	2	1	<u>135</u>				
Southern European U.S.S.R.																									
<u>130</u>	Rus.	0	2	1	1	0	1	1	2	2	2	1	0	1	1	1	0	1	2	1	1	<u>130</u>			
<u>134</u>	Rus.	0	2	2	2	1	2	2	2	3	2	2	1	1	1	1	0	1	3	1	1	<u>0</u>	<u>134</u>		
<u>138</u>	Rus.	1	2	2	2	1	1	1	3	2	2	1	1	1	1	1	1	1	2	1	1	<u>0</u>	<u>138</u>		
<u>139</u>	Rus.	0	1	1	1	0	1	1	1	2	2	1	0	1	1	1	0	1	2	1	1	<u>0</u>	<u>139</u>		
<u>146</u>	Rus.	1	2	2	2	1	1	1	2	3	1	2	1	1	1	1	1	1	2	1	1	<u>0</u>	<u>146</u>		
<u>170</u>	USA.	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	1	1	0	0	1	<u>0</u>	<u>170</u>		

elm disease and each of the other 74 characters studied to see if any relationships existed. Only three characters, seed length, samara width and samara tip shape, were significantly correlated with susceptibility. Since you would expect 3 out of 74 characters to be correlated by chance alone at the 5% level, these correlations were considered meaningless.

U. laevis

The numbers of accessions of *U. laevis* included in each part of the study are summarized by region of origin in Table 14.

Table 14. The number of accessions of *U. laevis* included in each part of the study.

Region	Samara study	Leaf study	Nursery study
West Central Europe	21	19	19
East Central Europe	46	37	32
Balkans	4	2	2
Northern European U.S.S.R.	13	8	5
Central European U.S.S.R.	7	5	3
Southern European U.S.S.R.	5	4	4
Eastern European U.S.S.R.	16	15	12
TOTAL	112	90	78

In addition to the material listed, two accessions from England, which is outside the native range of the species, were compared to the other material to see if their original source could be determined.

The number of characters in each part of the study that were significantly different between regions or source within regions are shown in Table 15.

Table 15. The number of characters in each part of the *U. laevis* study that were significantly different between regions or source within region.

	Region		Locality within region	
	.05 level	.01 level	.05 level	.01 level
Samara study	4	10	8	3
Leaf study	6	6	6	1
Nursery study	3	5	2	7
TOTAL	13	21	16	11

The percent of total variance accounted for by difference between regions and the rating of the region averages for each character that was significantly different between regions is shown in Table 16. The percent of variance accounted for by differences in region and sources within region is given for each character in Appendix E.

The regions in Table 16 are grouped into North-South groups and arranged in an East-West order across the table.

Table 16. The percent of total variance within *U. laevis* accounted for by differences between regions and regional averages for each distinctive character.
H, M, L= high, medium and low respectively.

Character number and name	Between region variance	West Cent. Euro.	Regional averages				
			East Cent. Euro.	North Cent. Euro.	South East Euro.	USSR	USSR
% of total							
Samara Characters							
1 Base length	28**	M	L	M	H	H	
2 Seed length	17*	L	M	M	H	H	
4 Notch length	44**	L	M	H	L	M	
5 Samara width	30**	L	M	M	M	H	
7 Seed width	16*	L	M	H	M	M	
8 Samara length	24**	L	L	L	L	H	
12 Notch length/samara length	41**	L	M	H	L	L	
16 Seed width/samara width	25**	M	H	H	M	H	
17 Tip shape	25**	M	L	L	H	L	
18 Base shape	40**	H	M	L	L	L	
19 Openness of notch	30**	M	M	H	L	H	
21 Style shape	69**	H	M	H	H	L	
23 Seed color	22*	L	L	H	M	L	
24 Samara greenness	15*	H	H	L	M	H	
Leaf Characters							
27 Leaf length	18*	M	M	M	L	L	
28 Leaf width	29**	H	H	H	L	L	
29 Number of veins	19*	M	H	M	M	L	
31 Tot. no. serrations	17*	H	H	M	M	L	
32 Widest point to tip	25**	H	H	M	M	L	
34 Serration length	25**	L	H	H	L	L	

% of total

Table 16 (cont'd.)

Character number and name	Between region variance	Regional averages				
		West Cent. Euro.	East Cent. Euro.	North Cent. Euro. USSR	South East Euro. USSR	East Euro. USSR
	% of total					
39 Petiole length	19*	H	M	H	M	M
43 No. of maj. serr./total no. of serr.	23**	L	H	M	L	L
47 Total no. serr./lf. length	23**	H	M	H	H	H
50 Serr. len./leaf length	17*	M	L	M	M	H
51 Serr. width/leaf length	15*	L	M	M	L	M
53 Maj.-maj. serr./lf. length	42**	L	M	H	L	L
<u>Nursery Characters</u>						
57 <i>Gnomium ulmi</i> injury, 1968	32*	H	M	H	M	H
60 <i>Gnomium ulmi</i> injury, 1969	41**	M	L	H	M	H
66 Stem color	61**	H	H	H	H	H
68 No. of branches	62**	H	H	M	M	L
69 Second. branching	33*	M	H	L	L	L
72 Average height	41**	H	H	M	L	L
75 Stem twig color contrast	64**	M	M	L	H	L

*, ** means significant at .05 and .01 levels respectively.

No strong geographic patterns were exhibited by any of the significant characters. The pattern of variation seems to be random.

The average differences between sources was computed to show the relationship between seed sources. These differences are shown in Table 17.

The northern European population showed the greatest resemblance to the English material. However, there was enough difference to make it seem unlikely that they originated in this area. The *U. laevis* population of northern France and Germany, a likely source of the trees growing in England, was not sampled in the study.

Simple correlations were computed between susceptibility to Dutch elm disease and each of the other 74 characters. Two samara characters, greenness of samara and contrast between seed color and wing color, showed a significant positive correlation to susceptibility. No biological explanation of these results was available.

Leaf length, leaf width, number of veins, number of major serrations, total number of serrations and the distance from the widest point of the leaf to the tip were also positively correlated to susceptibility. These characters all measure leaf size and they are all positively correlated with each other. These six correlations show that leaf size is correlated with susceptibility.

Table 17. The average differences among geographic origins of *U. minor*. Underlined numbers refer to specific localities which are defined in Appendix E.

England																						
<u>30</u>	Eng.	<u>30</u>																				
West central Europe																						
<u>40</u>	Ger.	1	<u>40</u>																			
<u>41</u>	Ger.	4	<u>4</u>	<u>41</u>																		
East central Europe																						
<u>10</u>	Aus.	1	0	0	<u>10</u>																	
<u>20</u>	Cze.	2	0	0	<u>1</u>	<u>20</u>																
<u>118</u>	Pol.	1	0	3	0	0	<u>118</u>															
<u>117</u>	Pol.	1	0	2	0	0	0	<u>117</u>														
<u>116</u>	Pol.	2	0	2	0	0	0	0	<u>116</u>													
<u>115</u>	Pol.	2	1	2	1	1	0	0	0	<u>115</u>												
Balkans																						
<u>60</u>	Hun.	2	0	3	1	0	2	1	1	2	<u>60</u>											
<u>65</u>	Hun.	3	1	3	2	1	1	1	2	1	<u>2</u>	<u>65</u>										
<u>122</u>	Rom.	3	2	4	2	2	2	2	1	2	1	<u>4</u>	<u>122</u>									
<u>155</u>	Yug.	4	3	2	3	2	2	2	2	2	3	2	<u>3</u>	<u>155</u>								
<u>157</u>	Yug.	4	3	1	2	2	2	1	1	1	2	2	3	<u>1</u>	<u>157</u>							
Northern European U.S.S.R.																						
<u>137</u>	Rus.	2	1	3	1	1	1	1	1	1	1	1	2	3	2	<u>137</u>						
<u>133</u>	Rus.	2	2	4	2	2	2	3	3	2	2	3	4	4	3	<u>1</u>	<u>133</u>					
Central European U.S.S.R.																						
<u>132</u>	Rus.	2	1	5	1	1	2	1	2	2	1	3	3	3	3	2	2	<u>132</u>				
<u>144</u>	Rus.	5	2	4	2	2	3	2	2	3	2	4	1	3	3	4	3	<u>3</u>	<u>144</u>			
<u>140</u>	Rus.	4	3	4	3	1	3	3	2	3	3	5	1	3	4	4	3	3	<u>1</u>	<u>140</u>		
Southern European U.S.S.R.																						
<u>149</u>	Rus.	4	1	3	0	1	1	1	1	1	2	1	3	2	1	3	1	2	3	4	<u>149</u>	
Eastern European U.S.S.R.																						
<u>142</u>	Rus.	3	2	5	2	1	3	3	2	3	1	4	3	3	4	3	2	2	1	3	3	<u>142</u>
<u>143</u>	Rus.	5	3	3	2	1	2	3	2	2	2	3	1	2	3	5	2	4	1	2	3	2

0 indicates no significant difference between localities.
 5 indicates the greatest difference.

Two nursery characters, *Gnomium ulmi* injury and average tree height, had significantly positive correlations with susceptibility to Dutch elm disease.

The average height was significantly correlated with each of the leaf size characters. Leaf size and seedling height both indicate seedling vigor. Tchernoff (1965) reported that vigorous seedlings are more susceptible to Dutch elm disease than slow growing ones.

The correlation between susceptibility and *Gnomium ulmi* injury may have been due to mistakes in scoring Dutch elm disease symptoms. Seedlings that had been severely attacked by *Gnomium ulmi* were almost defoliated, which made it difficult to recognize Dutch elm disease.

U. glabra

Out of 143 seedlots of *U. glabra*, only 48 produced enough seedlings to be included in the leaf study and only 12 in the nursery study. The numbers of accessions included in each phase of the study.

Three of the leaf characters; widest point to the tip, serration depth and ratio of the number of veins to leaf length, were significantly different (.05 level) between regions. The English, East Central Europe and Balkan had the highest values in those three traits West Central European and Italian trees were the lowest values.

Because of the small number of accessions in the nursery part of the study no statistical analysis was attempted. Six of the twelve accessions studied were from Judenberg, Austria. The amount of variation in these six accessions was almost as great as the amount of variation in all 12 accessions.

U. pumila

Suwon, Korea and Alma Ata in central Asiatic U.S.S.R. are the only localities within the native range of *U. pumila* represented in the M.S.U. collection. Because of this, the *U. pumila* accessions were divided into two groups, an eastern group represented by four seedlots each from Japan and Korea and a western group consisting of 18 seedlots from European and western Asiatic U.S.S.R.

The 11 seedlots from Italy showed evidence of hybridization with both *U. minor* and *U. glabra* and were not included in the analysis. Five seedlots from the United States were also excluded from the analysis.

Only two samara characters, ratio of widest point to base to samara length and persistent calyxes, were significantly different between regions. The highest values for both of these traits was from the western region.

The number of veins, total number of serrations and distance from widest point to leaf were all significantly greater in the western region.

Accessions from the western region showed significantly less injury from autumn frost but were slower growing than the eastern material.

U. japonica

All but 5 of the 49 collections of *U. japonica* seed came from the island of Hokkaido, Japan. These other five seedlots were from central Honshu island. Only 11 seedlots, all from two localities on Hokkaido, produced enough seedlings to be included in the leaf and nursery parts of the study.

None of the samara characters showed any significant differences between islands. In fact, there was more variability within the Hokkaido material than between Honshu and Hokkaido.

The two Hokkaido locations tested in the leaf and nursery parts of the study did not differ significantly in any character.

U. parvifolia

Eighteen seedlots of *U. parvifolia*, the only fall blooming elm studied, are included in the M.S.U. collection. One seedlot, MSFG 6323, was collected in the early spring of 1968 from seed persisting on the tree. The other 17 accessions were not received until the fall of 1968 or the winter of 1968-1969. The seedlot received in the spring of

1968 was the only one included in the leaf and nursery parts of the study. Therefore, the only within species comparisons that could be made are on samara character.

Nine of the eighteen seedlots were from the island of Honshu, Japan, one from the island of Kyushu, Japan, two from Suwon, Korea and six were collected from trees growing on the M.S.U. campus. The Korean accessions had narrower seeds and a lower seed width/samara width ratio than the other accessions. These were the only characters that showed a significant difference (.05 level) between sources.

U. laciniata

Eight of the ten seedlots of *U. laciniata* in the study came from Japan. Six of these seedlots were from Hokkaido, one from northern Honshu and one from central Honshu. The other two seedlots came from England and the Netherlands. They were the only seedlots that produced any seedlings.

No analysis of the variation within species was attempted, but a comparison was made of the samara data from the five different sources. The Japanese sources resembled each other more than they did either of the other two sources, but there was more similarity between the samaras from England and the Netherlands than between any of the Japanese sources.

U. elliptica

Four of the seven seedlots of *U. elliptica* were from Leningrad, which is outside the native range of the species. The other three seedlots were from the Caucasus Mountain region of the U.S.S.R.--two from Yerevan and one from Tbilisi. Two of the seedlots from Leningrad produced enough seedlings to be included in the leaf study, but neither produced enough for the nursery study.

No analysis of the within species variation was attempted because of the small amount of material. However, a comparison of samara characters was made between the Leningrad material and the other two sources. The same similarity was shown between the Leningrad and Tbilisi, and Tbilisi and Yerevan. A comparison of Leningrad and Yerevan material showed almost twice as much difference as the other two comparisons.

U. wallichiana

Six of the seven accessions of *U. wallichiana* were obtained from the Netherlands elm breeding program. The wings had been removed from seeds from Pakistan, the only seedlot from within the native range of the species. None of the Pakistan seed germinated, so there was no material available for making comparisons within species.

Summary of Within-Species Variability

Five species--*U. minor*, *U. laevis*, *U. glabra*, *U. pumila* and *U. japonica*--were represented by enough material to make studies of within-species variation of samaras possible. Two of these species--*U. laevis*, and *U. minor* showed significant differences among regions in samara size characters. *U. laevis* was the only species that showed significant differences in samara shape and color characters.

Within species variation of leaf characters was studied in four species--*U. glabra*, *U. laevis*, *U. minor* and *U. pumila*. Significant differences between regions were shown in nine *U. minor*, two *U. glabra*, seven *U. laevis* and two *U. pumila* leaf characters. Petiole length and pubescence of upper leaf surface was significantly different between regions in *U. laevis* and *U. minor* respectively.

Only three species contained enough material for a study of within-species variation of nursery characters. None of the characters showed significant between-region differences in all three species. The number of branches per seedling and the number of seedlings with secondary branching were significantly different between regions in *U. laevis* and *U. pumila*. Average height was significantly different between regions in *U. minor* and *U. pumila*. Six characters did not show significant between region differences in any of the species. Susceptibility to Dutch elm disease was one of these characters.

The only character that showed any recognizable pattern of geographic variation in any of these species was leaf size in *U. minor*. The lack of geographic variation within species is surprising. There had to have been enough isolation and natural selection at one time to allow speciation to occur.

Part of the uniformity within species may have been due to man's activities in planting. However, it seems unlikely that there would have been enough movement of material between regions within the native range of the species to have affected the overall genetic pattern. It seems likely that there was not a great amount of geographic variability within species before man started moving trees around.

CHAPTER VIII

THE POSSIBILITIES OF BREEDING ELMS RESISTANT TO DUTCH ELM DISEASE

Ulmus americana has proved to be the most susceptible to Dutch elm disease in every test that has compared it with other species. Smalley and Kais (1966) found that seedlings from localities where the disease had been present for many years contained a higher level of resistance than seedlings from areas recently invaded by the disease. This indicates that some natural selection for disease resistance has taken place. The importance of this factor in a tree breeding program is obvious. However, it is doubtful if the disease has been present in Michigan long enough for natural selection to have had a significant effect on the American elm population.

The American elm is also susceptible to phloem necrosis, a virus disease. This disease is reported to have killed more American elms in some parts of the species range than Dutch elm disease. Phloem necrosis has not been reported in Michigan, but it is present in Ohio and Illinois and it would be unwise for an elm breeder to ignore the disease. Incorporating resistance to this disease into

varieties resistant to Dutch elm disease would take at least one additional generation of breeding and testing, which would add 15 to 20 years to a breeding program.

Ulmus americana and the closely related species *U. laevis* are the only species of elm susceptible to phloem necrosis. Both of them are also susceptible to *Gnomium ulmi*. The degree of susceptibility of *U. americana* to *G. ulmi* has not been reported. However, the high degree of susceptibility of *U. laevis* observed in this study would limit its value in future breeding work. These factors indicate that it would be much easier to develop desirable cultivars of elm from other species of *Ulmus* than from either *U. americana* or *U. laevis*.

Ulmus pumila is highly resistant to Dutch elm disease but has other undesirable characteristics. To utilize this resistance, an extensive interspecific hybridization program would be necessary to combine it with desirable characteristics of other species.

Ulmus wallichiana possesses many desirable characteristics in addition to Dutch elm resistance. However, it probably does not contain sufficient winter hardiness to be grown in Michigan.

Ulmus parvifolia is highly resistant to Dutch elm disease but the species develops into a small tree which would not be acceptable as a substitute for American elm.

U. laciniata and *U. glabra* both possess the desirable characteristics of leaf size, growth rate and form. There is also evidence that selections containing an acceptable level of resistance to Dutch elm disease could be obtained from these species. However, unless the poor germination, exhibited by material in this study, can be overcome, future work in either of these species will be limited.

Based on the information obtained in this study, *U. minor* and *U. japonica* have the most potential value for future breeding work. Seed from either of these species can be readily obtained from within their native ranges. The seed of *U. minor* is more easily germinated than *U. japonica*, but the latter species shows a higher degree of resistance to Dutch elm disease. Selection in either of these species would need to be on a family basis.

An eight acre planting of *U. minor* at the Fred Russ Experimental Forest in southwestern Michigan is a potentially valuable source of material. This planting, which is owned by Michigan State University, is about 25 years old. Few of the trees in the planting have been lost to Dutch elm disease even though mortality of American elm in the vicinity is nearly complete. Progeny of nine trees from the planting included in this study ranged from 40 to 70% susceptible to Dutch elm disease. However, more resistant families may be discovered with further screening work.

If parent trees that produce a high percentage of resistant progeny could be located in this planting, it could be easily developed into a seed orchard. A source of resistant material could be available within a few years.

Open pollinated seed from the best Dutch clones showed a low level of susceptibility in this study. The degree of susceptibility exhibited by the seedlings was closely correlated to the rating received by the parent clone in the tests in the Netherlands. Further screening work with this material would probably be rewarding.

The native ranges of potentially valuable Chinese species, not included in the present study, are isolated either politically or geographically. It would be very difficult to obtain seed from them at the present time. Every effort should be made to obtain this material if the political situation becomes more favorable in the future.

All of the material in the Michigan State University program has been reinoculated in the 1971 growing season. The data obtained in this study and the results of the 1971 inoculation will be used to select the most promising families. This material will be planted in a planting designed to insure a maximum amount of crossing between families.

When these trees reach flowering age, progeny tests will be used to evaluate possible parents. If these results

are encouraging, the planting may be developed into a seed orchard. Additional seed of some of the most promising material will be requested from the original collector. An attempt will also be made to obtain additional collections of seed from species not well represented in the present study.

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Vita

Final Examination--July 12, 1971

Guidance Committee--J. H. Hanover, M. W. Adams,
J. H. Beaman, J. W. Wright (Chairman)

Dissertation--Variation Between and Within Nine
Eurasian Species of *Ulmus*

Biographical Data--Born May 4, 1940, Edwards
County, Kansas
Married Elaine Miriam Stickney,
December 24, 1968

Education--Dodge City College A.A. 1960
Kansas State University B.S. 1963
University of Nebraska M.S. 1965
Michigan State University Ph.D. 1971

Experience--Graduate Assistant, University of
Nebraska 1963-1965
Instructor, University of Nebraska 1965-1968
Graduate Assistant, Michigan State University
1968-1970

APPENDICES

Appendix A
Species of Ulmus

Table A1. Authoratative references for the species of Ulmus

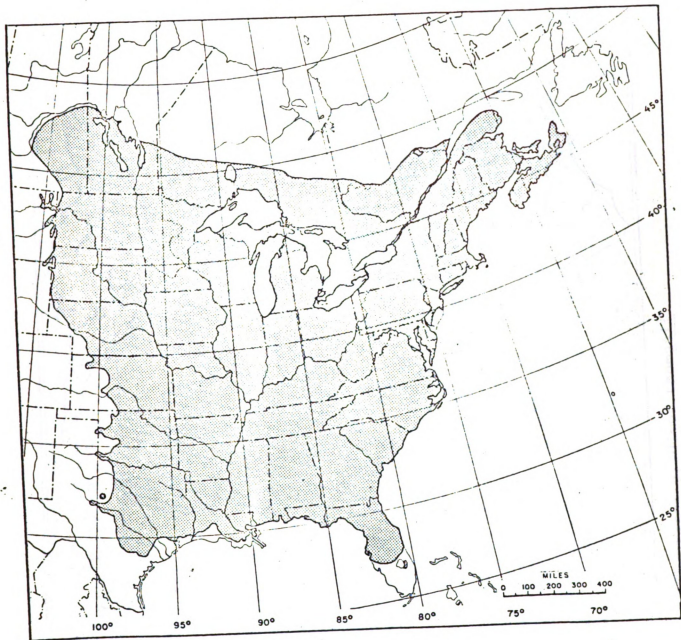
Species	Authoratative reference	
	Botanical description	Range
U. laevis	Bean 1951 Komorov 1936 Rehder 1940	Sokolov and Cvajezeva 1965, Schreiber 1957
U. americana	Rehder 1940 Harrar & Harrar 1946	Fowells 1965
U. mexicana	Standley & Steyermark 1946	Standley & Steyermark 1946 Staub 1967 Miranda 1952
U. thomasii	Rehder 1940	Fowells 1965
U. alata	Rehder 1940 Harrar & Harrar 1946	Fowells 1965
U. rubra	Rehder 1940 Harrar & Harrar 1946	Fowells 1965
U. elliptica	Komorov 1936 Bean 1951	Sokolov & Cvajezeva 1957
U. glabra	Bean 1951 Rehder 1940 Komorov 1936	Sokolov & Cvajezeva 1965 Tutin et al. 1967
U. laciniata	Komorov 1940 Bean 1951	Sokolov & Cvajezeva 1965 Ohwi 1965 Nakai 1932

Table A1. (Con't.)

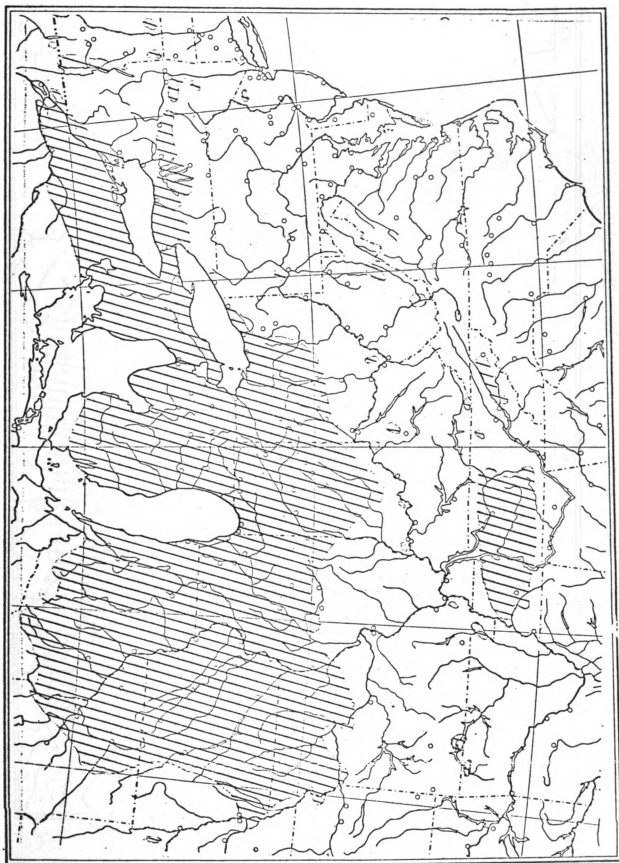
U. bergmaniana	Rehder 1940 Schneider 1917	Schneider 1917
U. uyematsui	Li 1963	Li 1963
U. wallichiana	Hooker Brandis	Hara 1966 Pearson & Brown 1932
U. minor	Rehder 1940 Bean 1951 Komorov	Schreiber 1957 Sokolov & Cvajezeva 1965
U. japonica	Nakai Komorov	Rehder 1923, 1924 Sokolov & Cvajezeva 1965 Nakai 1932 Ohwi 1965
U. wilsoniana	Bean 1951 Schneider 1917	Schneider 1917 Rehder 1923, 1924
U. procera	Bean 1951	Bean 1951
U. pumila	Rehder 1940 Komorov 1936	Sokolov & Cvajezeva 1965 Rehder 1923, 1924 Wang 1961
U. parvifolia	Rehder 1940	Nakai 1932 Wang 1961 Li 1963 Ohwi 1965
U. lanceaefolia	Kurz 1877	Pearson & Brown 1932 Merrill 1934 Touw & VanSteenis 1968
U. crassifolia	Rehder 1940 Harrar & Harrar 1946	McDaniel & Swift 1967
U. monterreyensis	Muller 1942	Muller 1942

Table A1. (Con't.)

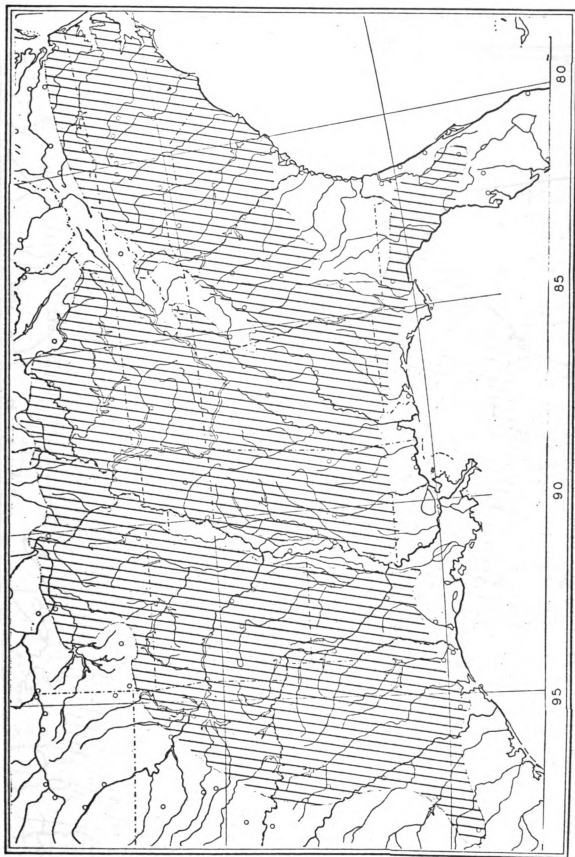
U. serotina	Rehder 1940 Harrar & Harrar 1946	Staub 1967
U. kunmingensis	Cheng 1963	Cheng 1963
U. davidiana	Nakai 1932	Rehder 1923, 1924 Wang 1961
u. macrocarpa	Komorov 1936 Nakai 1932	Sokolov & Cvajezeva 1965 Wang 1961 Schneider 1917
U. villosa	Bor 1953 Hooker 1885	Bor 1953 Hara 1966
U. lesuerri	Standley 1936	Standley 1936
U. divaricata	Muller 1937	Muller 1937
U. multinervosa	Muller 1936	Muller 1936



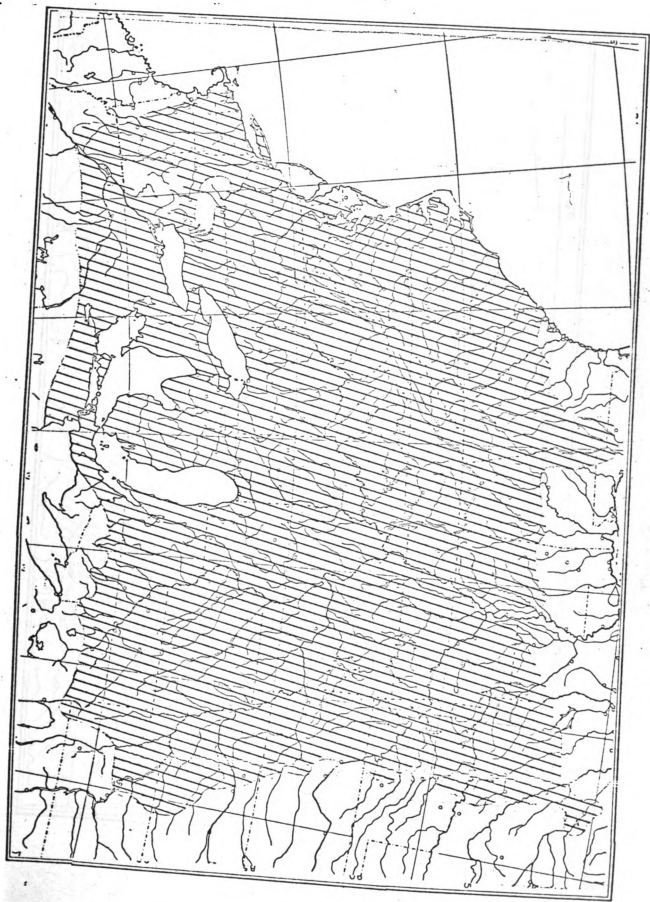
The range of *Ulmus americana*



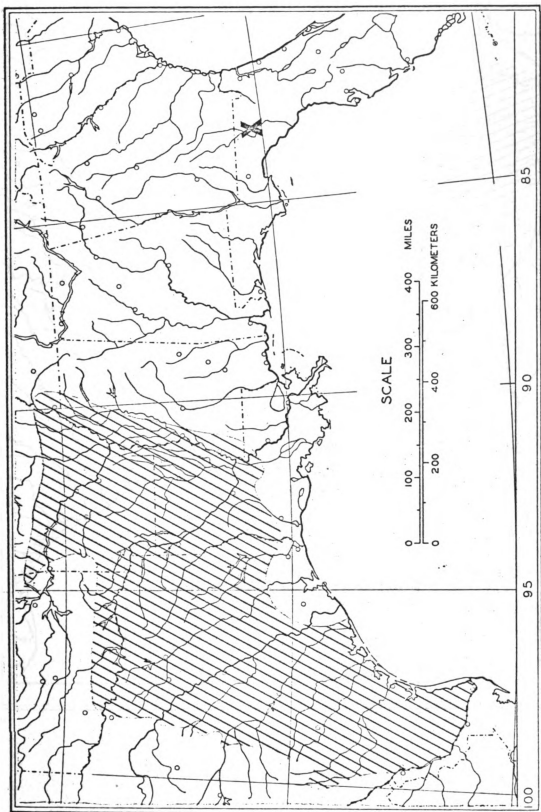
The range of Ulmus thomasi



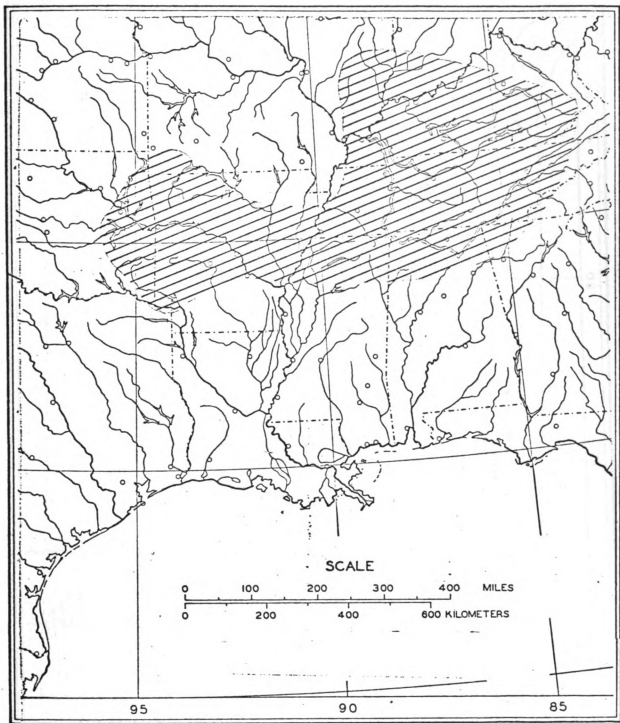
The range of *Ulmus alata*



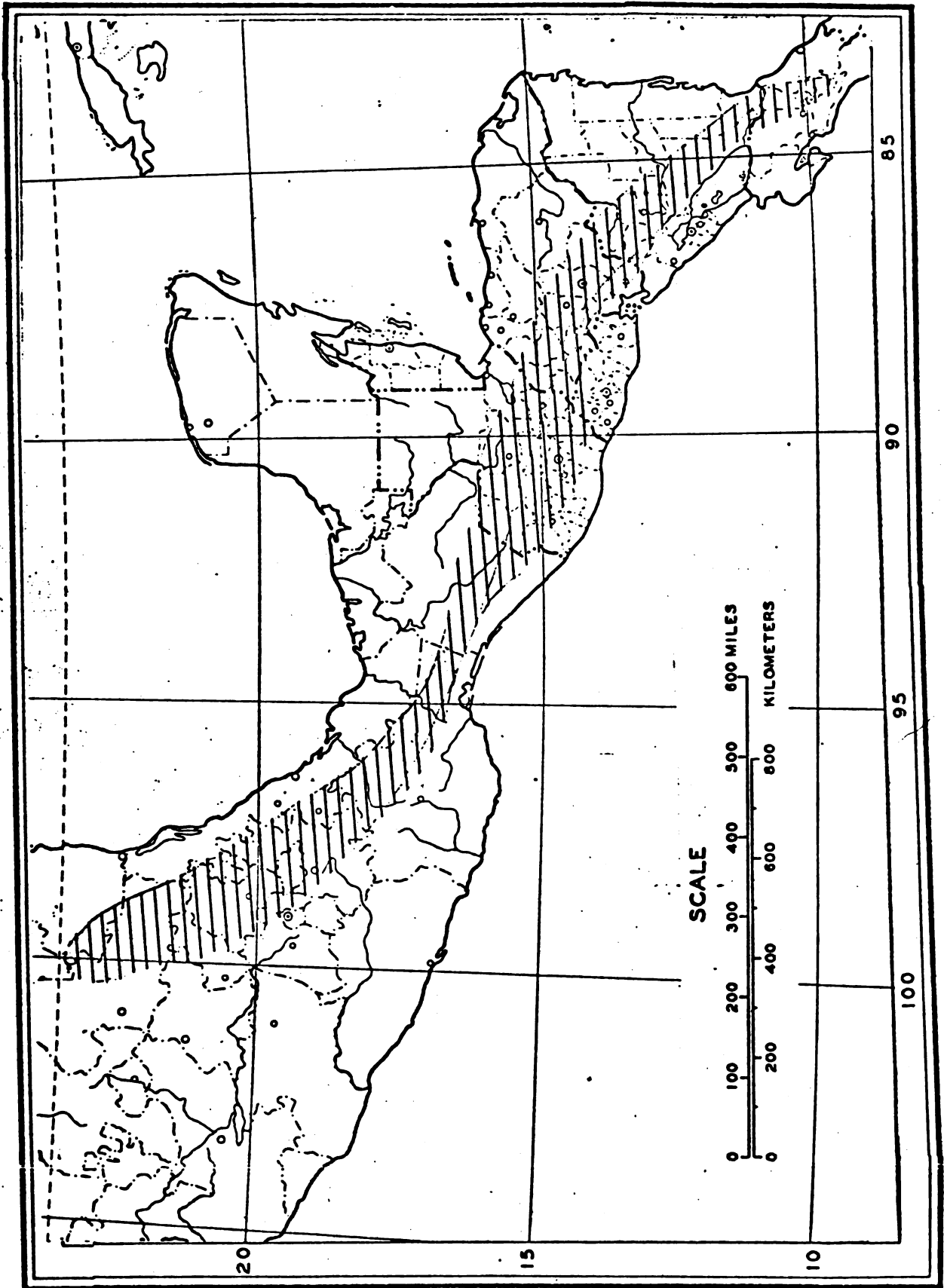
The range of Ulmus rubra



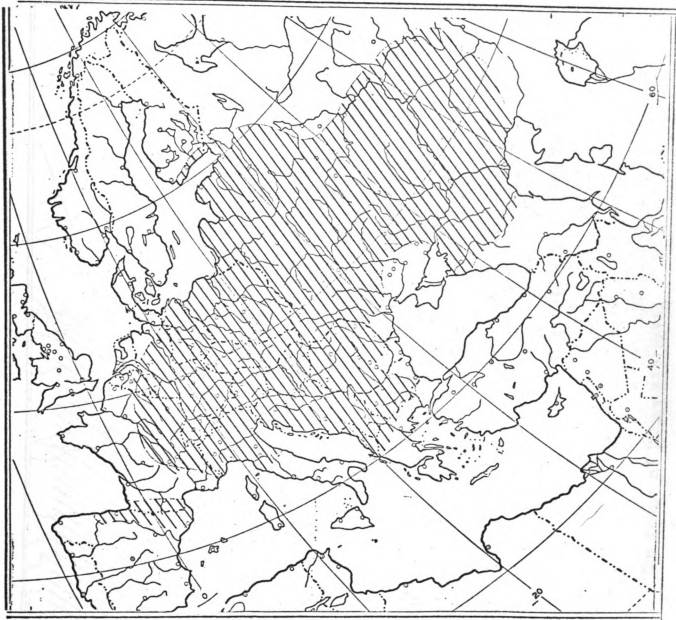
The range of *Ulmus crassifolia*
X- isolated occurrence



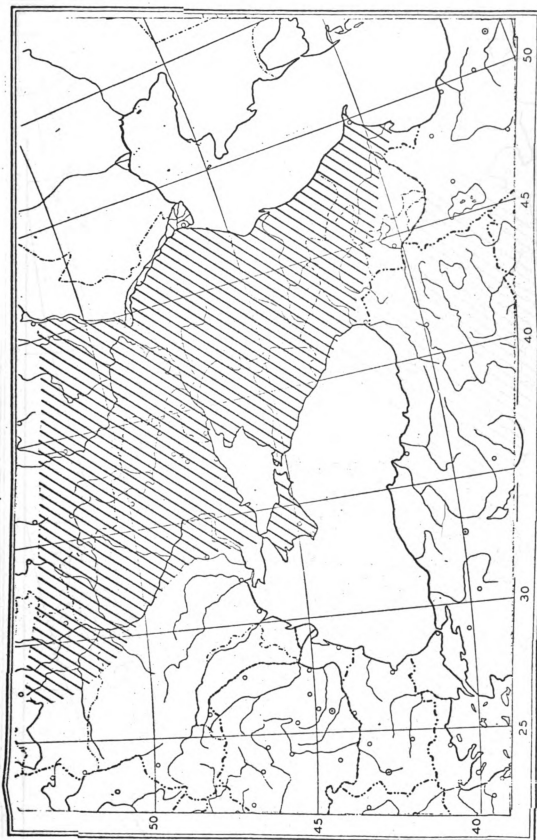
The range of *Ulmus serotina*



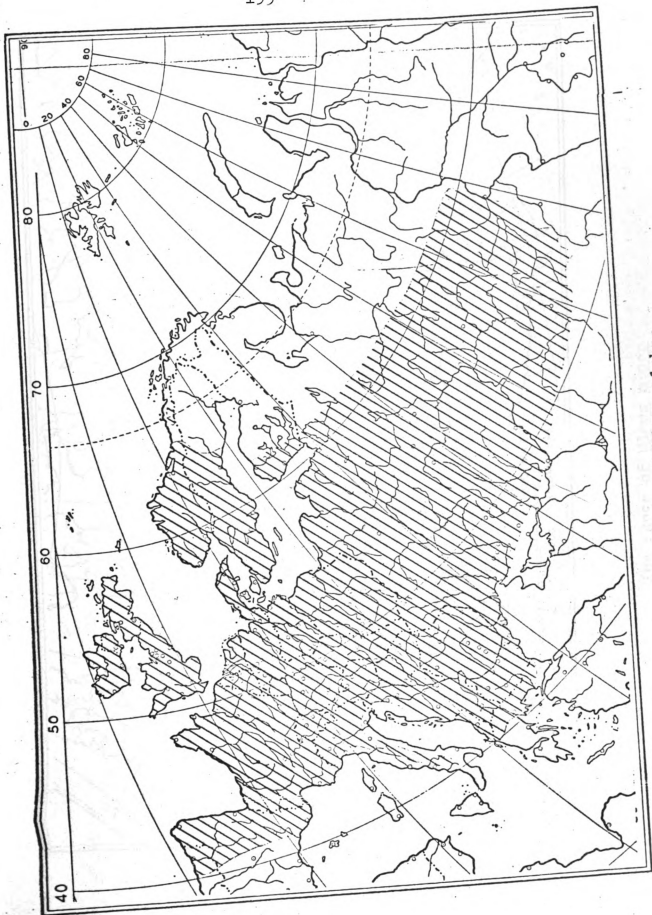
The range of *Ulmus mexicana*



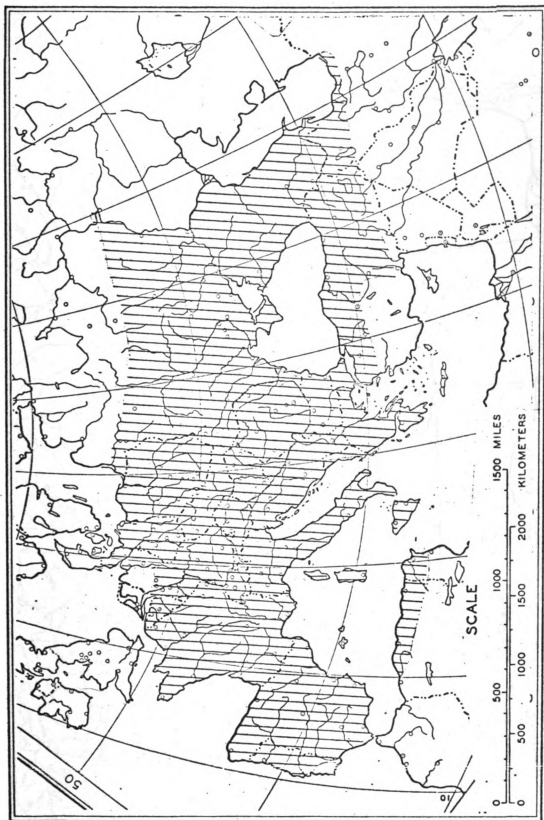
The range of Ulmus laevis



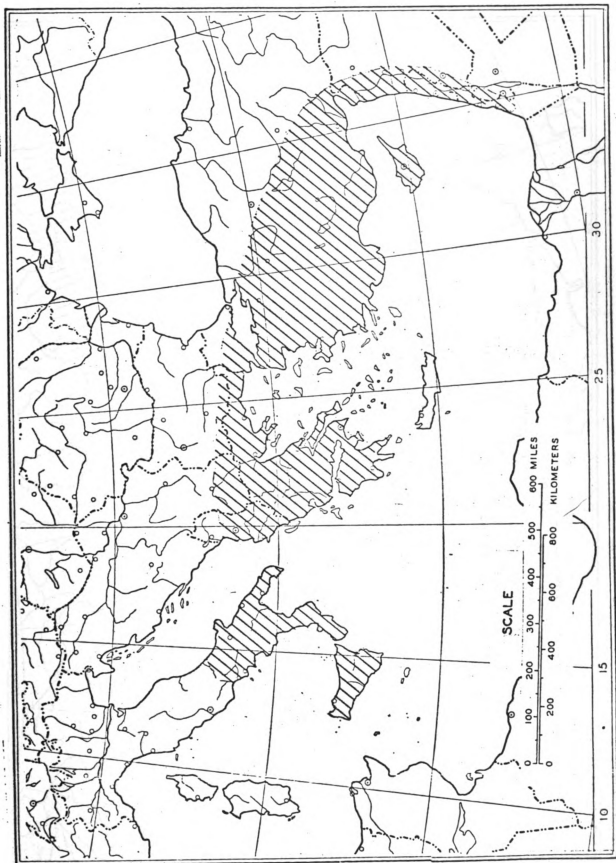
The range of Ulmus elliptica



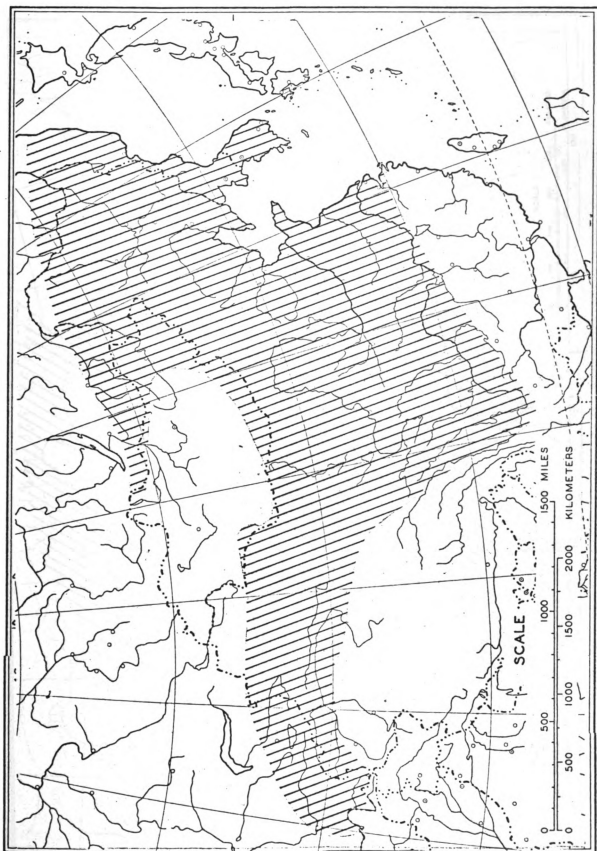
The range of *Ulmus glabra*



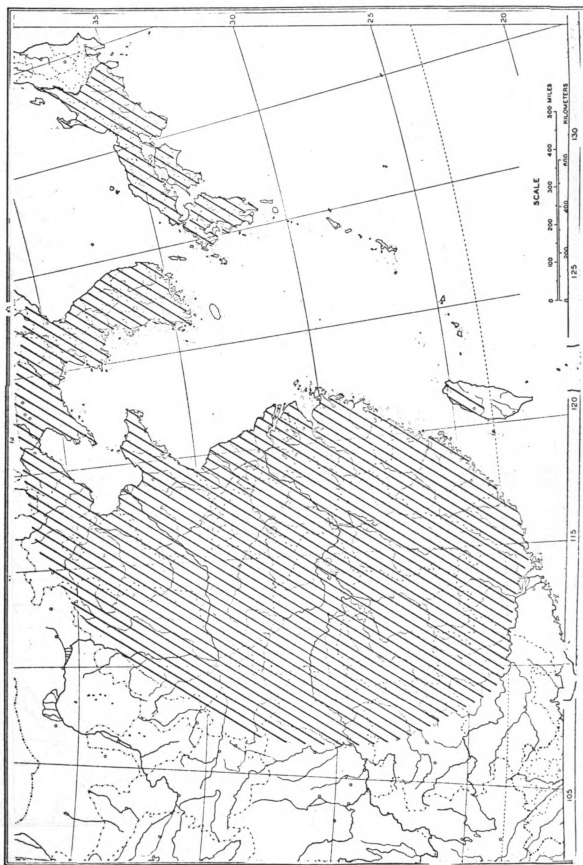
The range of *Mimus minor*



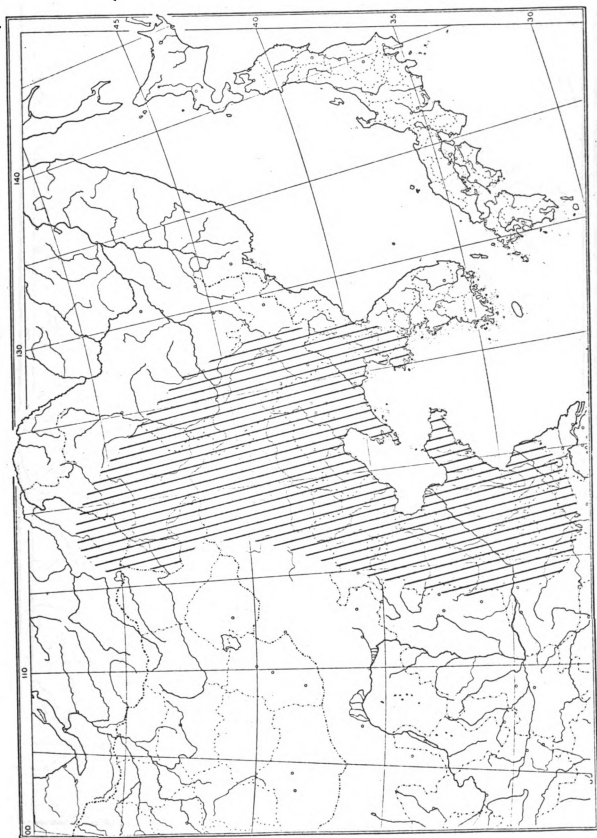
The range of *Ulmus canescens*



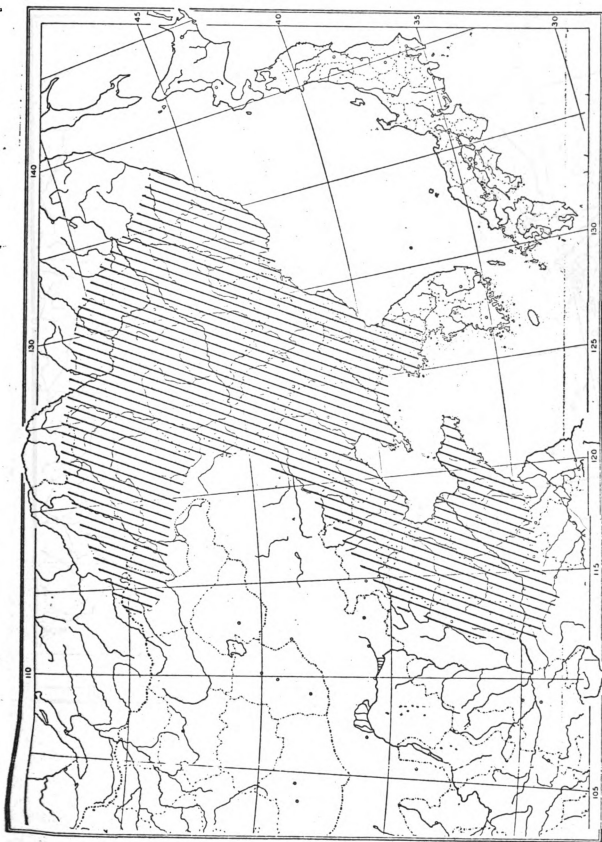
The range of Ulmus pumila



The range of Ulmus parvifolia



The range of *Ulmus davidiana*



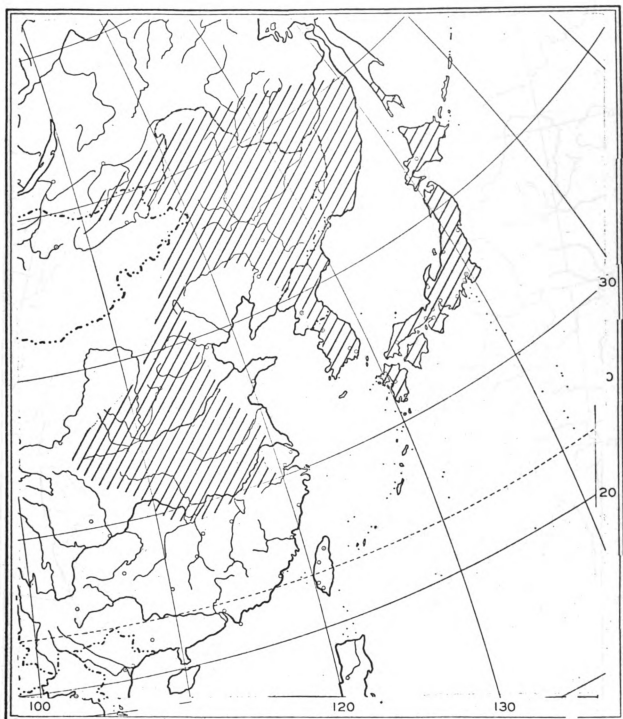
The range of *Ulmus macrocarpa*



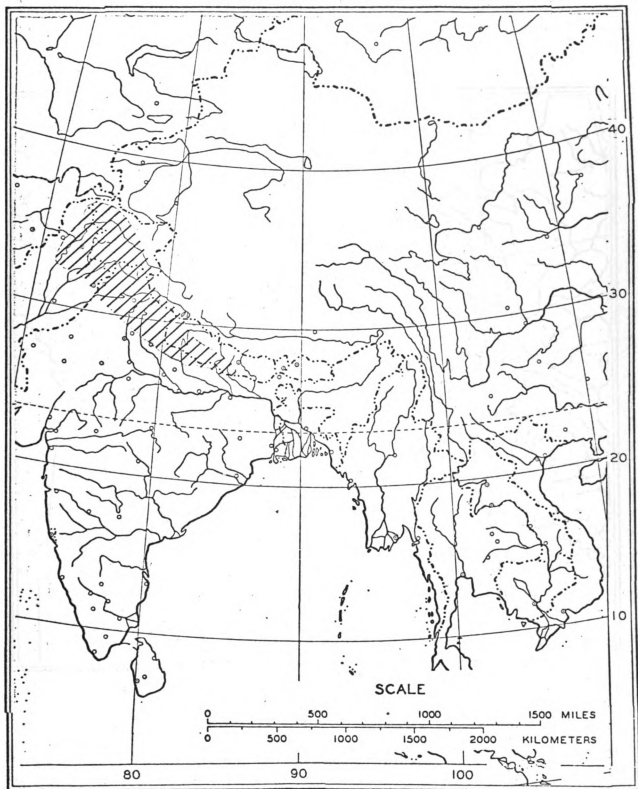
The range of *Ulmus wilsoniana*



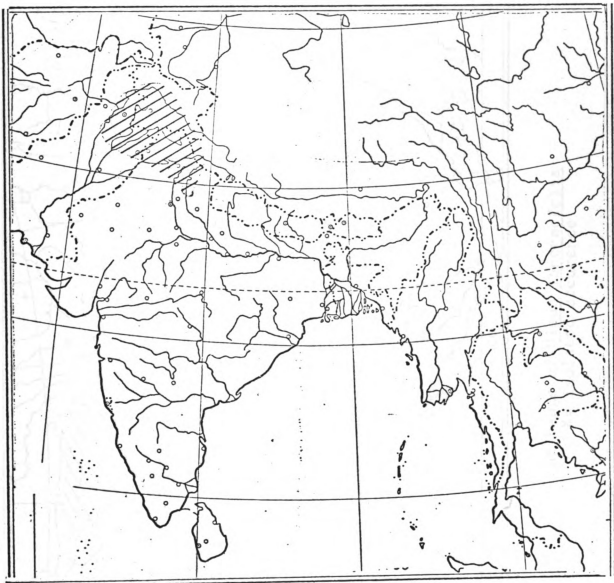
The range of *Ulmus bergmaniana*



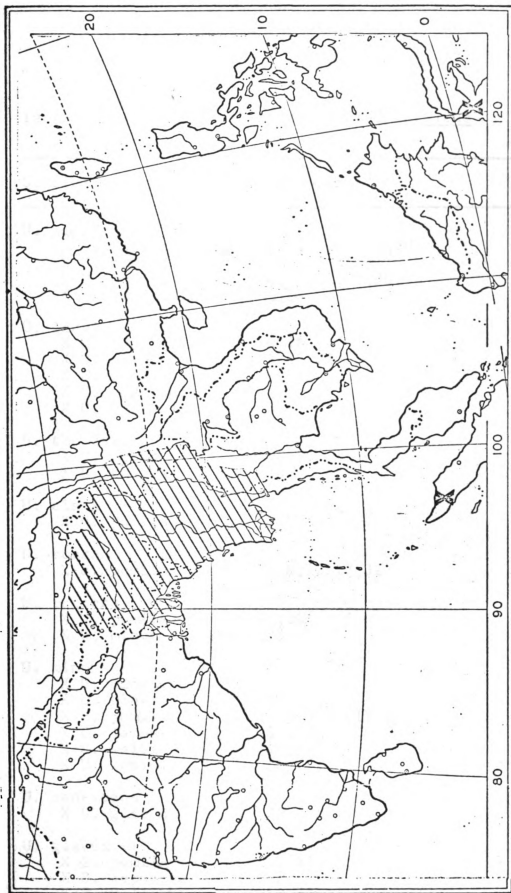
The range of *Ulmus japonica*



The range of *Ulmus wallichiana*



The range of *Ulmus villosa*



The range of *Ulmus lanceaeefolia*
X= isolated occurrence

Appendix B

Table B1 Species hybrids reported in Ulmus

Species	Authority ¹
U. americana	
X U. laevis	6,7,17,18,22,28
X U. rubra	18
X U. pumila	4,14,22,27,30
X U. bergmaniana	5,6
U. laevis	
X U. thomasi	6,18
X U. minor	2,17,22
X U. pumila	1,2,5
X U. bergmaniana	6
X U. wilsoniana	6
U. thomasi	
X U. rubra	9,15
X U. pumila	30
U. alata	
X U. pumila	6
U. rubra	
X U. pumila	3,6,12,17,31
U. procera	
X U. pumila	5,18
X U. minor	23
U. minor	
X U. canescens	20
X U. glabra	16,17,21,
X U. pumila	2,6,8,10,13,16,24
X U. japonica	16, 34
X U. wallichiana	16,34
X U. laciniata	16
U. canescens	
X U. glabra	20
U. glabra	
X U. pumila	11,17,21,22,
X U. japonica	29
X U. wallichiana	16,34
X U. laciniata	16

Table B1 (Con't.)

U. pumila	
X U. japonica	16,19,34
X U. wallichiana	16
X U. wilsoniana	5
U. japonica	
X U. wallichiana	7,16,22,33
X U. wilsoniana	12,29,32
U. wallichiana	
X U. chumila	16
XU. laciniata	34
U. parvifolia	
X U. crassifolia	26
U. crassifolia	
X U. lanceaefolia	16

1 authorities are listed by number below

-
- | | |
|---------------------------------|-------------------------------|
| 1. Albensky 1951 | 18. Johnson & Heimbürger 1946 |
| 2. Albensky 1969 | 19. Lester 1968 |
| 3. Anon. 1950 | 20. Melville 1957 |
| 4. Anon. 1954 | 21. Rehder 1940 |
| 5. Britwum 1961 | 22. Richens 1945 |
| 6. Collins 1967 | 23. Richens 1961a |
| 7. Doorenbos 1938 | 24. Rovskii 1951 |
| 8. Ehrenberg 1954 | 25. Rovskii et al. 1950 |
| 9. Fowells 1965 | 26. Santamour 1969 * |
| 10. Goidanisch & Azzerolli 1938 | 27. Santamour 1970 |
| 11. Goidanisch & Azzerolli 1939 | 28. Sax 1933 |
| 12. Graves 1948 | 29. Smith & Nicholas 1941 |
| 13. Grudzinskaja 1961 | 30. Smucker 1944 |
| 14. Heimbürger 1966 | 31. Swingle 1945 |
| 15. Hess & Dunn 1967 | 32. Weikoff 1941 |
| 16. Heybroek 1968 | 33. Went 1938 |
| 17. Johnson 1939 | 34. Went 1954 |

*Unpublished report to the N.C.R.32 committee on vascular wilt diseases Morgantown, West Virginia Oct. 27, 1969

Appendix C

Characters Studied

Table C1. Name and Description of the Eight Samara Size Characters Measured and the Ratios Computed.

Character Number	Character Name	Measured From
1.	Base length	Base of samara to base of seed
2.	Seed length	Base to tip of seed
3.	Seed-notch	Tip of seed to base of notch
4.	Notch length	Base of notch to furthest point on samara tip
5.	Samara width	Widest point on samara
6.	Widest point-base	Widest point on samara to base of samara
7.	Seed width	Widest point on seed
8.	Samara length	Base to tip of samara

Ratios Computed

9.	Base length/samara length
10.	Seed length/samara length
11.	Seed-notch/samara length
12.	Notch length/samara length
13.	Samara width/samara length
14.	Widest point-base/samara length
15.	Seed width/samara length
16.	Seed width/samara width

✓ All samara characters were measured to the nearest thirty-second of an inch and recorded as the total number of thirty seconds of an inch for four samaras.

Table C2. Name, Range and Limits of the Eight Samara
Shape and Color Characters.

Character Number	Character Name	Range	Lowest No. Assigned to	Highest No. Assigned to
17.	Tip Shape	1-5	pointed	2-cleft
18.	Base shape	1-5	straight	most outcarved
19.	Openness of notch	1-5	closed	openest
20.	Style length	1-5	shortest	longest
21.	Style shape	1-5	straight	most curved
22.	Wing color	1-5	lightest	darkest
23.	Seed color	1-5	lightest	darkest
24.	Greenness of samara	1-5	no green	greenest
25.	Persistent calyxes	0-4 ¹⁾	none persisting	all persisting
26.	Contrast between seed color and wing color	2)	same color	largest contrast

1) Persistent calyx was scored by counting the number still attached to the samara.

2) The contrast in color was computed by subtracting character 22 from 23. Seed color was always as dark or darker than wing color.

Table C3. Name and Description of the Leaf Characters and the Ratios Computed.

Character Number	Character Name	Description of Character
27.	Leaf length ^{1/}	Measured from the tip of the leaf to the lowest point on the base.
28.	Leaf width	Measured at the widest point
29.	Number of veins	Counted on the smallest half of the leaf.
30.	Number of major serrations	Counted on the smallest half of the leaf.
31.	Total number of serrations	Counted on the smallest half of the leaf.
32.	Widest point to tip	Measured from the widest point on the leaf to tip of leaf.
33.	Serration depth ^{2/}	Measured from the tip of serration to base of next higher serration
34.	Serration length ^{2/}	Measured from tip of serration to base of next lower serration
35.	Serration width ^{2/}	Measured across the base of serration from base of next lower to base of next higher.
36.	Major-minor serration	Measured from the tip of major serration to the tip of first lower serration.
37.	Major-major serration	Measured from the tip of major serration to the tip of the next major serration.
38.	Obversity	The difference between the distances from the tip of the leaf to the furthest point on the short side and the long side of the leaf

Table C3 . Leaf Characters (continued)

39.	Petiole length	Length of the petiole
40.	Pubescence of upper leaf surface	Scored on a scale of 1 (glabrous) to 5 (densely pubescent).
41.	Pubescence of lower leaf surface	Scored on a scale of 1 (glabrous) to 5 (densely pubescent).

Ratios Computed

42.	Number of veins/number of major serrations
43.	Number of major serrations/total number of serrations
44.	Leaf width/leaf length
45.	Number of veins/leaf length
46.	Number of major serrations/leaf length
47.	Total number of serrations/leaf length
48.	Widest point to tip/leaf length
49.	Serration depth/leaf length
50.	Serration length/leaf length
51.	Serration width/leaf length
52.	Major-minor serration/leaf length
53.	Major-major serration/leaf length
54.	Obversity/leaf length
55.	Petiole length/leaf length

1/ All size measurements were made to the nearest m.m. and scored as the total number of m.m. for five leaves.

2/ All serration measurements were made on the largest serration which is usually located just above the middle of the leaf.

Table C4 . Name and Description of the Seedling Characters Measured in the Nursery.

Char. No.	Character	Date Recorded	Range	Description
56.	Percent opposite leaves	Sept. 68 ^{1/}	0-100	Percentage of seedlings in each accession with opposite leaves.
57.	<u>Gnomium ulmi</u> ^{2/}	Oct. 68	0-4	Percent of trees in each accession showing symptoms of this leaf spot disease; to nearest 25%.
58.	Red fall color	Oct. 68	0-4	Percent of seedlings in each accession that have some red leaves; to nearest 25%.
59.	Frost injury	Nov. 68	0-10	Percent of leaves damaged by frost; to nearest 10%.
60.	<u>Gnomium ulmi</u> injury	Aug. 69 ^{3/}	0-5	Relative amount of injury in each plot from none to severe.
61.	Corky twigs	Sept. 69	0-10	No. of seedlings in each plot with corky outgrowths on twigs.
62.	Fall color	Oct. 69	0-4	Relative amount of fall color in each plot.
63.	Long shoot-short shoot	Oct. 69	0-10	Some seedlings had 2 types of leaves, large leaves on the main stem and small ones on branches, rated as the number of seedlings in each plot showing this character.
64.	Frost injury	Nov. 69	0-5	Relative amount of injury from slight to severe.

Table C4. Nursery Characters (continued)

65.	Green leaves	Dec.69	0-10	No. of seedlings in each plot that still retained green leaves on Dec 12.
66.	Stem color	Mar.70	0-10	Rated from the lightest to the darkest.
67.	Twig color	Mar.70	0-10	Rated on the same scale as char. 66.
68.	Number of branches	Mar.70	0-100	Estimates as the sq. root of the average no. of branches per seedling
69.	Secondary branching	Apr.70	0-10	No. of seedlings in each source that were branched more than once.
70.	Branch angle	Apr.70	1-4	Angle of the branches with the stem from 0-15 degrees to 45-90 degrees.
71.	Leafing out	Apr.70	0-5	Scored as the average progress of leafing in each plot from 0 (dormant) to 5 (leaves fully expanded).
72.	Average height	Sept.69		Measured to the nearest inch.
73.	Susceptibility to Dutch Elm Disease	Aug.70	0-100	Percentage of seedlings in each source showing symptoms 60 days after inoculation.
74.	Insect attack	Aug.70	0-100	Percentage of seedlings in each source attacked by an unidentified leaf eating insect.
75.	Contrast between stem and twig color			Computed by subtracting char.66 from char.67.

1/ All 68 measurements were made in original unreplicated nursery beds.

2/ Gnomium ulmi disease identified by Dr. John Hart ,
Dept. of Plant Pathology.

3/ All 69 and 70 measurements made in replicated transplant beds

Appendix D

Ulmus minorTable D1. Source of U. minor accessions

Locality no. and place	Lat. N.	Long. E.	MSFG No.
Austria			
10. Vienna	48°11'	16°23'	6351-54, 6357 6360-61
Czechoslovakia			
20. Brno	49°10'	16°35'	6381, 6385, 6387-89, 6512-15
25. Prague	50°10'	14°30'	6498, 6834, 6837, 6839, 6840, 6842
26. Stanvico	48°52'	19°03'	6580-82
England			
30. Kew	51°29'	0°02'	6408, 6481
Germany			
40. Freiburg	48°05'	7°35'	6433-38
41. Munich	48°10'	11°30'	6464
42. Hannover-Munden	51°24'	9°40'	6519-20, 6522
Greece			
50. Thessalonika	40°35'	23°02'	6341-6349
Hungray			
60. Asvanyaro	47°05'	18°00'	6395-6400
66. Szeged	46°15'	20°05'	6988-92
Italy			
70. Florence	43°40'	11°10'	6325-35 6533-36
72. Padova	45°24'	11°50'	6324
Poland			
115. Krakow	50°00'	20°00'	6418
116. Kornicke	52°17'	17°06'	6475
117. Wroclaw	51°10'	17°00'	6488, 6491

Table D1. (Con't.)

U.S.S.R.

130.	Baku	40°10'	48°30'	6556-61
134.	Krasnodar	45°00'	38°30'	6711-13
135.	Nikitiski	55°10'	37°15'	6562-71
138.	Tbilisi	42°00'	45°00'	6643-44
139.	Yerevan	40°00'	44°30'	6697-98, 6716-20
146.	Makhachkala	43°40'	56°10'	6795-6803

Yugoslavia

155.	Skopje	42°00'	21°30'	6336, 6338-40
157.	Zagreb	45°49'	15°58'	6632

Table D2. The percent of variance in samara traits of U. minor accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
1. Base length	10*	32**
2. Seed length	3	19*
3. Seed-notch	6	9
4. Notch length	11*	25**
5. Samara width	4	30**
6. Widest point-base	5	34**
7. Seed width	20**	20**
8. Samara length	11*	39**
9. Base length/samara length	3	19**
10. Seed length/samara length	14	0
11. Seed notch/samara length	7	9
12. Notch length/samara length	7	0
13. Samara width/samara length	13*	0
14. Widest point-base/ samara length	0	17*
15. Seed width/samara length	7	11
16. Seed width/samara width	13*	11
17. Tip shape	5	7
18. Base shape	0	27**
19. Openness of notch	0	30**
20. Style length	0	31**

Table D2.(Con't.)

21. Style shape	3	14
22. Wing color	2	25**
23. Seed color	2	27**
24. Greeness of samara	4	37**
25. Persistant calyxes	4	24**
26. Seed-wing color contrast	1	19*

*, ** significantly different at .05 and .01 level respectively.

TableD3. The percent of variance in leaf traits of U. minor accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
27. Leaf length	31**	29*
28. Leaf width	14	4
29. Number of veins	27**	22*
30. Number of major serrations	44**	0
31. Total number of serrations	17*	49**
32. Widest point to tip	48**	21
33. Serration depth	14	68**
34. Serration length	35**	2
35. Serration width	31**	19
36. Major-minor serration	43**	0
37. Major-major serration	35**	18
38. Obversity	9	40**
39. Petiole length	4	11
40. Pubescence of upper leaf surface	17*	20
41. Pubescence of lower leaf surface	0	22*
42. Number of veins/number of major serrations	1	3
43. Number of major serrations/total number of serrations	0	0

Table D3. (Con't.)

44. Leaf width/leaf length	23*	0
45. Number of veins/leaf length	0	0
46. Number of major serrations/ leaf length	29**	0
47. Total number of serrations/ leaf length	0	70**
48. Widest point to tip/ leaf length	0	6
49. Serration depth/leaf length	0	33**
50. Serration length/leaf length	8	0
51. Serration width/leaf length	2	17
52. Major-minor serration/ leaf length	0	11
53. Major-major serration/ leaf length	0	50**
54. Obversity/leaf length	3	33**
55. Petiole length/leaf length	0	11*

*, ** significantly different at .05 and .01 level respectively.

Table D4. The percent of variance in nursery traits of U. minor accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality error.

Character no and name	Percent of variance accounted for by	
	Region	Locality/region
56. Percent opposite leaves	24	36**
57. <u>Gnomium ulmi</u> , injury 1968	0	0
58. Red fall color	0	12
59. Frost injury, 1968	12	9
60. <u>Gnomium ulmi</u> injury, 1969	0	0
61. Corky twigs	0	9
62. Fall color	8	20*
63. Long shoot-short shoot	39**	0
64. Frost injury. 1969	0	17
65. Green leaves, 12/12/69	60**	2
66. Stem color	1	27
67. Twig color	11	4
68. Number of branches	20	0
69. Secondary branching	0	18
70. Branch angle	15	0
71. Leafing out	7	0
72. Average height	45**	10
73. Susceptability to Dutch elm disease	2	10
74. Insect attack	0	0
75. Contrast between stem and twig color	37**	5

*, ** significantly different at the .05 and .01 level respectively

Appendix E
Ulmus laevis

Table E1. Source of U. laevis accessions

Locality no. and place	Lat. N.	Long. E.	MSFG No.
Austria			
10. Vienna	48°11'	16°17'	6355, 6357-58
Czechoslovakia			
20. Brno	49°10'	16°35'	6377-80, 6386, 6391, 6509-11, 6516
25. Prague	50°10'	14°30'	6502, 6829-31, 6838-41
England			
30 Kew	51°29'	0°02'	6404-05
Germany			
40. Freiburg	48°05'	7°35'	6440-44
41. Munich	48°10'	11°30'	6468-69
Hungary			
60. Asvanyaro	47°05'	18°00'	6392-94, 6401-03, 6983-87
66. Szeged	46°15'	20°05'	6368-69
Netherlands			
100. Wageningen	51°55'	5°30'	6621-22
Poland			
115. Krakow	50°00'	20°00'	6413-16, 6420-21
116. Kornicke	52°17'	17°06'	6425-26
117. Wroclaw	51°10'	17°00'	6489-90, 6493-94
118. Rogow	51°00'	20°00'	6583-87
Romania			
122. Oradea	47°00'	22°00'	6763-64

Table E1 (Con't.)

U.S.S.R.			
132. Minsk	53°52'	27°32'	6722
133. Leningrad	59°58'	30°18'	6685, 6724-28
134. Krasnodar	45°00'	38°30'	6708, 6710
137. Riga	56°58'	24°04'	6683-84, 6686-90
139. Yerevan	40°08'	44°28'	6691-6695
140. Voronezh	51°42'	39°02'	6709, 6781
143. Alma Ata	43°14'	76°56'	6772-76, 6785-89
144. Kiev	50°24'	30°27'	6777
Yugoslavia			
155. Skopje	42°00'	21°28'	6337
157. Zagreb	45°49'	15°29'	6637-39

Table E2. The percent of variance in samara traits of U. laevis accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
1. Base length	28*	7
2. Seed length	17	14*
3. Seed-notch	5	15*
4. Notch length	44**	15*
5. Samara width	30*	0
6. Widest point-base	5	25**
7. Seed width	16	0
8. Samara length	24*	43**
9. Base length/samara length	0	10
10. Seed length/samara length	13	0
11. Seed notch/samara length	0	0
12. Notch length/samara length	41**	10
13. Samara width/samara length	0	13
14. Widest point-base/ samara length	0	9
15. Seed width/samara length	0	0
16. Seed width/samara width	25*	0
17. Tip shape	25*	13
18. Base shape	40**	17*
19. Openness of notch	30*	0
20. Style length	0	23*

Table G2. (Con't.)

21. Style shape	0	82**
22. Wing color	0	84**
23. Seed color	0	89**
24. Greeness of samara	0	88**
25. Persistant calyxes	55*	24
26. Seed-wing color contrast	3	25

*, ** significantly different at .05 and .01 level respectively.

Table E3. The percent of variance in leaf traits of U. laevis accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
27. Leaf length	18*	10
28. Leaf width	29**	10
29. Number of veins	19*	14*
30. Number of major serrations	7	13
31. Total number of serrations	17*	18*
32. Widest point to tip	25**	19*
33. Serration depth	4	7*
34. Serration length	25**	26*
35. Serration width	10	7
36. Major-minor serration	6	8
37. Major-major serration	9	8
38. Obversity	0	18*
39. Petiole length	19*	11
40. Pubescence of upper leaf surface	0	0
41. Pubescence of lower leaf surface	0	0
42. Number of veins/number of major serrations	0	9
43. Number of major serrations/ total number of serrations	23**	6

Table G3. (Con't.)

44. Leaf width/leaf length	15	41**
45. Number of veins/leaf length	0	25*
46. Number of major serrations/ leaf length	35*	0
47. Total number of serrations/ leaf length	0	33*
48. Widest point to tip/ leaf length	32*	4
49. Serration depth/leaf length	0	48**
50. Serration length/leaf length	50**	33*
51. Serration width/leaf length	0	3
52. Major-minor serration/ leaf length	0	49**
53. Major-major serration/ leaf length	0	7
54. Obversity/leaf length	44**	21
55. Petiole length/leaf length	0	63**

*, ** significantly different at .05 and .01 level respectively.

Table E4. The percent of variance in nursery traits of U. laevis accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
56. Percent opposite leaves	3	11
57. <u>Gnomium ulmi</u> injury, 1968	32*	18
58. Red fall color	0	0
59. Frost injury, 1968	17	21*
60. <u>Gnomium ulmi</u> injury, 1969	41**	25*
61. Corky twigs	0	0
62. Fall color	0	0
63. Long shoot-short shoot	0	0
64. Frost injury, 1969	13	33**
65. Green leaves, 12/12/69	0	32**
66. Stem color	61**	0
67. Twig color	12	25**
68. Number of branches	52**	15
69. Secondary branching	33*	13
70. Branch angle	13	13
71. Leafing out	0	29**
72. Average height	2	47**
73. Susceptibility to Dutch elm disease	13	43**
74. Insect attack	29*	2
75. Contrast between stem and twig color	64**	0

* ** significantly different at .05 and .01 level respectively

Appendix F

Ulmus glabraTable F1. Source of U. glabra accessions

Locality no. and place	Lat. N.	Long.	MSFG No.
Austria			
10. Vienna	48°11'	16°18' E.	6350, 6359
11. Innsbruck	47°14'	11°29' E.	6411-12, 6766
12. Judenburg	47°10'	14°40' E.	6458-63, 6592
Czechoslovakia			
20. Brno	49°10'	16°35' E.	6372-76, 6390 6517-18
25. Prague	50°10'	14°30' E.	6495-97, 6500-01, 6503, 6835-36
26. Stiavnica	49°00'	19°00' E.	6572-80
England			
30. Kew	51°29'	0°02' W.	6406-07
31. Oxford	51°50'	1°10' W.	6477-78, 6625-26
32. Banburg	52°10'	1°20' W.	6479, 6481
33. Towcester	52°10'	1°00' W.	6480
34. Warlingham	51°25'	0°00'	6623-24
35. Long Ashton	51°01'	2°40' W.	6659-64
36. Wrecclesham	51°05'	1°06' W.	6659-64
Germany			
40. Freiburg	47°56'	7°53' E.	6428-32
41. Munich	48°10'	11°30' E.	6465-67
42. Hannover-Munden	51°24'	9°40' E.	6521, 6523
43. Gottingen	51°00'	9°55' E.	6455-57
Hungary			
65. Sopron	47°41'	16°30' E.	6367, 6370
Italy			
71. Florence	43°40'	11°10' E.	6445-52, 6537-44

Table F1. (Con't.)

Poland			
115. Krakow	50°04'	19°58' E.	6417, 6419, 6423, 6427
116. Kornik	52°17'	17°06' E.	6476
117. Wroclaw	51°07'	17°07' E.	6492
118. Rogow	51°49'	19°55' E.	6588-91
Romania			
121. Bucurest	44°30'	26°50' E.	6453-54
122. Oradea	47°00'	22°00' E.	6761
123. Cluj	46°40'	23°40' E.	6832-33, 6894
U.S.S.R.			
132. Minsk	53°52'	27°32' E.	6721
133. Leningrad	59°58'	30°18' E.	6677-78, 6729-34, 6805
134. Krasnodar	45°00'	39°00' E.	6714
137. Riga	56°58'	24°04' E.	6679-80, 6843-47
138. Tbilisi	41°40'	44°57' E.	6641, 6715
Yugoslavia			
155. Skopje	42°00'	21°28' E.	6382-84
157. Zagreb	45°49'	15°59' E.	6633-36
Scotland			
160. Dingwall	57°32'	4°27' W.	6627-31

Table F2. The percent of variance in samara traits of U. glabra accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
1. Base length	1	35**
2. Seed length	4	24**
3. Seed-notch	2	47**
4. Notch length	5	0
5. Samara width	2	21*
6. Widest point-base	2	26**
7. Seed width	1	37**
8. Samara length	4	22*
9. Base length/samara length	2	29**
10. Seed length/samara length	6	33**
11. Seed notch/samara length	3	37**
12. Notch length/samara length	3	0
13. Samara width/samara length	6	3
14. Widest point-base/ samara length	0	7
15. Seed width/samara length	10*	17*
16. Seed width/samara width	0	5
17. Tip shape	4	0
18. Base shape	1	22*
19. Openness of notch	4	22*
20. Style length	0	36**

Table F2. (Con't.)

21. Style shape	6	22**
22. Wing color	0	47**
23. Seed color	1	43**
24. Greeness of samara	0	27**
25. Persistant calyxes	0	17**
26. Seed-wing color contrast	0	32**

*, ** significantly different at .05 and .01 level respectively.

Table F3. The percent of variance in leaf traits of U. glabra accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
27. Leaf length	12	6
28. Leaf width	15	7
29. Number of veins	0	31
30. Number of major serrations	32*	13
31. Total number of serrations	35*	0
32. Widest point to tip	15	5
33. Serration depth	9	36
34. Serration length	25	5
35. Serration width	16	5
36. Major-minor serration	21	26
37. Major-major serration	9	25
38. Obversity	10	0
39. Petiole length	0	0
40. Pubescence of upper leaf surface	1	33
41. Pubescence of lower leaf surface	0	75
42. Number of veins/number of major serrations	30*	25
43. Number of major serrations/total number of serrations	0	18

Table F3. (Con't.)

44. Leaf width/leaf length	0	23
45. Number of veins/leaf length	0	30
46. Number of major serrations/ leaf length	0	26
47. Total number of serrations/ leaf length	0	0
48. Widest point to tip/ leaf length	12	11
49. Serration depth/leaf length	5	0
50. Serration length/leaf length	0	7
51. Serration width/leaf length	4	21
52. Major-minor serration/ leaf length	21	0
53. Major-major serration/ leaf length	0	48
54. Obversity/leaf length	17	0
55. Petiole length/leaf length	0	0

*, ** significantly different at .05 and .01 level respectively.

Appendix G
Ulmus pumila

Table G1. Source of U. pumila accessions

Locality no. and place	Lat. N.	Long. E.	MSFG No.
Italy			
71. Florence	46°10'	13°15'	6545-55
Japan			
84. Nabeyashiki	39°30'	141°00'	6504-07
Korea			
90. Suwon	37°20'	127°00'	6656-57, 6742-43
Romania			
Cluj			6895
U.S.S.R.			
131. Khabarovsk	47°50'	135°10'	6675
133. Leningrad	59°58'	30°18'	6645
137. Riga	56°58'	24°04'	6676
139. Yerevan	40°00'	44°30'	6699-6703
140. Voronezh	51°42'	39°02'	6782
143. Alma Ata	43°14'	76°56'	6767-71, 6790-94
144. Kiev	50°24'	30°27'	6778-79
145. Askania Nova	33°58'	46°27'	6780
147. Krasno yarsk	52°10'	92°24'	6972
U.S.A.			
M.S.U. Campus			6967-69, 6971
Brookings, South Dakota			6892

Table G2. The percent of variance in samara traits of U. pumila accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
1. Base length	0	69**
2. Seed length	0	8
3. Seed-notch	0	8
4. Notch length	5	17
5. Samara width	14	6
6. Widest point-base	3	17
7. Seed width	0	32*
8. Samara length	0	14
9. Base length/samara length	0	0
10. Seed length/samara length	0	42*
11. Seed notch/samara length	0	0
12. Notch length/samara length	0	41*
13. Samara width/samara length	16	41*
14. Widest point-base/ samara length	44*	0
15. Seed width/samara length	0	26
16. Seed width/samara width	0	47*
17. Tip shape	0	0
18. Base shape	0	17
19. Openness of notch	0	83**
20. Style length	0	75**

Table G4. The percent of variance in nursery characters of U. pumila accounted for by differences among regions and localities within regions. The remaining variance not accounted for is due to parent within locality and error.

Character no. and name	Percent of variance accounted for by	
	Region	Locality/region
56. Percent opposite leaves	4	16
57. <u>Gnomium ulmi</u> injury, 1968	0	0
58. Red fall color	3	15
59. Frost injury, 1968	39*	20
60. <u>Gnomium ulmi</u> injury, 1969	0	0
61. Corky twigs	0	0
62. Fall color	0	0
63. Long shoot-short shoot	0	12
64. Frost injury, 1969	24	14
65. Green leaves, 12/12/69	4	6
66. Stem color	0	0
67. Twig color	0	17
68. Number of branches	17	19
69. Secondary branching	5	23*
70. Branch angle	0	0
71. Leafing out	15	19
72. Average height	32*	36*
73. Susceptibility to Dutch elm disease	18	31*
74. Insect attack	19	24*
75. Contrast between stem and twig color	0	12

*, ** significantly different at .05 and .01 level respectively.

Appendix H
Ulmus japonica

Table H1. Sources of U. japonica accessions

Locality no. and place	Lat. N.	Long. E.	MSFG No.
Japan			
80. Sapporo	43°00'	141°00'	6819-28, 6973-82
81. Ashoro Machi	43°18'	142°00'	6646-55
82. Ebetsu	43°04'	141°03'	6744-48
83. Kuriyama	43°00'	142°00'	6665-74
86. Chichibu	36°00'	139°10'	6819-28, 6973-82

Appendix I

Ulmus parvifoliaTable II. Sources of U. parvifolia accessions

Locality no. and place	Lat. N.	Long. E.	MSFG No.
Japan			
85. Fugi-Yoshido	35°30'	139°00'	6323
87. Nagasaki	32°50'	129°40'	6858
88. Nagoya	35°10'	136°55'	6859-66
Korea			
90. Suwon	37°20'	127°00'	6658
90. Suwon	37°20'	127°00'	6873-74
U.S.A.			
171. M.S.U. campus			6848-51, 6870-71

Appendix J

Ulmus laciniataTable J1. Sources of U. laciniata accessions

Locality no. and place	Lat. N.	Long. E.	MSFG No.
England			
30. Kew	51°29'	0°02'	6410
Netherlands			
100. Wageningen	51°55'	5°30'	6620
Japan			
84. Morioka	39°30'	141°00'	6508
86. Chichibu	36°00'	139°10'	6807
89. Yamabe	43°00'	142°30'	6749-54

Appendix K

Ulmus wallichianaTable K1. Sources of U. wallichiana accessions

Locality no. and place	Lat. N.	Long. E.	MSFG. No.
West Pakistan 180. Peshawar	34°10'	71°50'	7000
Netherlands 100. Wageningen	51°55'	5°30'	6614-19

Appendix L

Ulmus elliptica

Table L1. Sources of U. elliptica accessions

U.S.S.R.			
139. Yerevan	40°08'	44°28'	6696-97
138. Tbilisi	41°40'	44°57'	6642
133. Leningrad	59°58'	30°18'	6681-82
133. Leningrad	59°58'	30°18'	6741
