bedingungen vorherrschen. Der zeitigere Beginn der Ernte ermöglicht auch eine nicht unbedeutende Verringerung des Arbeitskräftebedarfes.

Summary

Title of the paper: Possibilities oj early cone harvest in *Scotch* pine seed orchards. —

The results of the investigations, carried out in the experimental clonal seed orchard Sárvár/Bajti may be summed up as follows:

(1) Cone and seed moisture content characterise well the process of ripening. The end of mitotic activity and storage coincide with a sudden decrease of cone and seed moisture content by the end of October.

(2) Early harvested cones may reach a desiccation state after a careful storage of one month.

(3) Full germinative capacity of seeds is reached by October. The process of ripening shows differences among the clones.

(4) If early harvested cones are extracted instantly, germination energy remains low. After appropriate storage germinative power reaches normal level. Based on this data the beginning of cone collection during the month of October seems to be permissible if an appropriate desiccation of at least one month is secured.

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Variation in Ornamental Traits and Disease Resistance among Crosses of Ulmus pumila, U. ruba, and Putative Natural Hybrids

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Elms, principally *Ulmus* americana L., have been a major component of municipal planting in the eastern United States. Majestic habit, adaptability to urban environments, and simplicity of establishment and management are outstanding features of the species. Contemporary use of U. americana in urban landscaping, however, has been virtually eliminated by spread of the lethal Dutch elm disease (Ceratocystis ulmi (Buisman) C. Moreau) from initial introduction about 40 years ago. Spray programs to control the insect vector are now largely unacceptable to an environmentally conscious public and systematic chemicals have been too toxic for general use. Municipal forestry budgets are now burdened with high removal expenses for large street trees and replanting efforts are concentrated on other genera.

From a genetic point of view, re-introduction of elms in municipal landscaping seems both desirable and feasible. Elms can broaden the genetic base of urban tree planting and thus reduce the potential for large scale losses to pathogens, air and soil pollution, or unusual weather. A genetic basis for disease resistance to the Dutch elm disease has been established among species of elms and among clones, especially in hybrid combinations between U. *carpinifolia* and U. glabra (Heybroek, 1969).

As a broad approach to identifying elms with low disease susceptibility, world-wide importations of elm seed were begun by E. B. Smalley in 1958. One-year-old seedlings are transplanted, maintained under clean cultivation, and artificially inoculated with fungus spores at ages three or four. These studies have identified individuals and progenies with low susceptibility and have confirmed the generally low susceptibility of U. pumila L. An open-pollinated progeny from one tree of U. pumila in the Botanic Garden of Hokkaido University, Sapporo, Japan showed low susceptibility in combination with crown form and leaf size which were much improved over the maternal parent. Location of the maternal parent, morphological and physiological traits of the progeny, and controlled hybridization experiments suggest that the pollen was from U. japonica (Rehd.) Sarg.

With U. pumila and U. pumila X japonica as sources of disease resistant germplasm, crosses were planned to see whether low susceptibility could be combined with ornamental characters to produce trees of acceptable habit. U. rubra Mühl. was chosen as the source of improved ornamental traits although disease susceptibility levels in U. rubra are believed to be moderate (Smalley and Kais, 1965). Several putative natural hybrids between U. rubra and U. pumila have been offered by the nursery trade (Green, 1962). These hybrids have some ornamentally acceptable features but disease susceptibility has not been reported.

The present work was designed to estimate inheritance of disease susceptibility and ornamental traits in combinations of U. rubra with U. pumila and the putative natural hybrid U. pumila X japonica.

Materials and Methods

Parental materials of U. pumila included three trees grown from commercial seed collections in Iowa and Michigan and one tree of the Dropmore variety, an introduction from Harbin, Manchuria (Green, 1962). The three U. rubra trees were from two native populations in southern Wisconsin. Putative natural hybrids of U. rubra X pumila were the Fremont elm and a tree in a native population of U. rubra. Two maternal parents from the putative U. pumila X japonica hybrid progeny were chosen on the basis of available flower buds and decurrent branching. Putative hybridity of parents was based on leaf, twig, bud, and bark characteristics.

Pollination was achieved by traditional tree breeding techniques using greenhouse-forced pollen and sausage-casing isolation bags on field-grown trees. Full-sib crosses using from 2 to 5 parents for each species or hybrid were made except where *U. pumila* × *japonica* was used as the male parent. This hybrid yields little pollen and a pollen mix from three trees excluding those used as maternal parents was necessary. Pollination of isolated flowers was accomplished by a glass syringe inserted through the sausage casing. Isolation bags remained on the trees until the stigmas withered and were then replaced by cheese cloth bags in which mature seed was collected. Seed was sown outdoors in vermiculite and three-week-old seedlings were transplanted in a randomized complete block design with four replicates. One-year-old dormant seedlings were field planted at 1.8 m × 1.8 m spacing in the same design, kept weed free during the first field season, and maintained in mown grass thereafter. Plot sizes varied from 4 to 14 seedlings. Hybrid verification in the seedbed and in field plantings was by morphological comparison of leaves and growth habit between *U. pumila* and each putative hybrid progeny.

Characters chosen for measurement were those with some apparent ornamental significance and with obvious progeny differences in the field. Average leaf size was estimated on a plot-mean basis after two growing seasons. Total height after two growing seasons was measured for the first six trees per plot. Flushing was scored at the start of the third growing season. A score of one represented plots in which no leaves were visible; in plots scored as five, individual leaves were visible in open buds on all trees. Stem dieback was estimated in tenths of feet on the main stem after leaf buds had opened in the third growing season.

The pathogen was prepared by culturing isolates from diseased wood collected in 14 Wisconsin localities. At the time of inoculation the isolates were combined to give an approximate spore density of 5×10^3/ml. Inoculation was achieved by drilling a 1.5 mm hole into the xylem of a 12 mm branch and filling the hole to over-flowing with spore suspension from a hypodermic syringe. Two inoculation times were chosen to lessen the possibility that different progenies might have markedly different patterns of seasonal susceptibility. The first inoculation on June 1, 1970 was at the estimated general peak susceptibility and the second inoculation time, two weeks later, was expected to come during a general decline in susceptibility. Response to the fungus was measured by foliar and stem symptoms evaluated at various times and from that data (discussed in detail in Lester and Smalley, 1972 a, b) symptom frequency and estimated crown damage at fifty-six weeks after inoculation were chosen as measures of response. Symptom frequency was expressed as the percentage of trees exhibiting disease in each plot. Crown damage was expressed as percent of crown wilted or dead.

Prior to analysis the angular transformation was applied to percentages. Crown damage scores were transformed to $\sqrt{X + 0.5}$ to normalize data including zeros. Analyses of variance for growth and phenological traits were calculated in a complete randomized block design with four replicates. Variance in disease response data was analyzed as a split-plot design with inoculation time as the main plot. The significance of differences among species combinations was estimated by the w-procedure (Steel and Torrey, 1960). Linear correlation coefficients were calculated to express associations among the variables.

Results and Discussion

Growth and phenological traits. — Means for species combinations differed at a probability of 99% for each trait. *Table 1* presents means arrayed with an increasing proportion of germplasm from *U. rubra*. Leaf length and total height generally increased as a function of increasing amounts of *U. rubra* germplasm until in the backcross pr × r, both traits approached *U. americana* in size. *U. japonica* genes in combination with *U. pumila* resulted in small increases in leaf size and in reduced height growth. In three-species combinations genes from *U. japonica* resulted in increased leaf length but had contradictory effects on height growth. Large leaf size is definitely a desirable trait for the common landscape uses of elms in the United States. Early rapid height growth is similarly desirable unless future landscape plans accept elms as useful in smaller forms.

Flushing was delayed as a function of the proportion of *U. rubra* genes. *U. japonica* genes had little effect in combination with *U. pumila* and had contradictory, but small

Table 1. — Sample sizes, means for six traits, and experimental error rate for elm species combinations. Offset columns distinguish crosses of p and r from crosses of p and j.

Cross[1]	Number of[2] Progenies	Leaf Size (cm.)	Total Height (meters)	Flushing (score)	Dieback (centimeters)	Frequency of Symptoms (%)	Damage Crown (%)
p × p	8	3.6	.85	4.6	4.3	3	4
p × pj	8	4.0	.73	4.8	2.4	7	10
pj × pj	2	4.8	.55	5.0	.3	4	4
pj × pr	5	5.6	.76	4.6	2.7	30	28
p × pr	11	4.6	.91	3.8	6.4	21	18
pj × r	7	8.0	1.04	3.4	3.7	71	48
p × r	16	6.8	.91	3.8	5.8	65	50
pr × pr	2	6.0	.73	2.0	8.5	59	34
r × pr	7	9.4	1.25	1.2	17.4	85	68
a × wind	2	10.8	1.10	2.8	11.0	97	72
Approximate w[3]	.05	1.0	0.12	0.6	3.0	15	18

[1] p = *U. pumila*, pj = putative *U. pumila* × *japonica*, pr = putative *U. pumila* × *rubra*, r = *U. rubra*, a = *U. americana*.

[2] Number of progenies includes three reciprocal crosses in p × pr, p × r, and r × pr, and one in pr × pr.

[3] In 95% of similar experiments, means differing by more than the indicated amount are not elements in a homogeneous set. Values for untransformed variables are approximate because precise significance testing must be accomplished on means of transformed data.

Table 2. — Ranges of variation among progenies within some highly variable elm species combinations.

Character	Cross	Range
Leaf Size (cm)	p × pr	3.8—6.4
Height (feet)	pj × r	2.7—4.3
Flushing (score)	p × r	2.5—5.0
Symptom Frequency (%)	p × r	35—95
Crown Damage (%)	p × r	16—64

effects in three-species combinations. The ornamental significance of early flushing is uncertain though we assume that early foliation is desirable unless spring frost damage occurs.

Stem dieback, presumably resulting from frost damage to late season stem elongation, increased with increasing representation of genes from *U. rubra*. Genes from *U. japonica*, by contrast, reduced dieback, although their effect was statistically significant only for one species combination. The ornamental consequences of stem dieback could not be estimated because response to subsequent fungal inoculation damaged most of the crowns exhibiting dieback. We assume that dieback, if common in successive years would be a significantly undesirable trait.

Although differences among species combinations was the major source of variance, additional variation was attributable to differences among progenies within species combinations. Variation within species combinations was statistically significant at 99% probability for leaf length, total height, and flushing, and at 95% probability for stem dieback. Certain species combinations were especially heterogeneous for certain traits *(Table 2)*. General combining ability was clearly indicated for some morphological traits within some species combinations. For example, when three *U. rubra* trees were crossed with two *U. pumila* trees, flushing score ranged from 2.8 to 3.6 in progenies from one maternal parent and from 4.5 to 5.0 in progenies from another.

Disease response: main-plot analysis. — Main-plot analyses for disease response included blocks and inoculation time as sources of variation. Differences in response to inoculation on June 1 or June 15 were marked though statistically significant only for symptom frequency (95% probability). Overall symptom frequency at 56 weeks was 50% for June 1 inoculations and 30% for June 15 inoculations. Experience over several years has shown that the duration of susceptibility varies widely among species (Smalley and Kais, 1966). The importance of inoculation time is further illustrated in the present study by separate analyses of progenies containing *U. japonica* genes. In crosses where p × j hybrids were used, inoculation time was a highly significant source of variation for several measures of inoculation response, particularly early response variables (Lester and Smalley, 1972 b).

Consideration of seasonal susceptibility patterns in preliminary screening studies probably would be inefficient unless inoculation at, or near, peak susceptibility cannot be assured. The determination of susceptibility, however, should be a part of final evaluation before progenies or clones are released for commercial use. Differences in the timing of peak susceptibility could give misleading indications of progeny value whereas identification of progenies with minimum duration of susceptibility could provide additional protection from infection.

Disease response: sub-plot analysis. — The sub-plot analysis included species combination, progeny within combination, and progeny-inoculation time interaction as sources of variation. Species combination and progeny within combination each contributed significantly to total variance (99% probability) for both disease traits. Interaction was non-significant.

The principal feature of the arrays for disease response by species combinations is the relationship of susceptibility to proportion of genes from *U. rubra (Table 1)*. As the proportion of *U. rubra* genes increased, susceptibility increased until in the backcrosses pr × r, disease response was comparable to that of *U. americana*. Perhaps the corresponding increase in leaf size and susceptibility is linked to anatomical changes in the xylem which allow more rapid distribution of fungal spores. Individual and group vessel diameters have been correlated with susceptibility (Elgersma, 1970; McNabb, *et al.*, 1970) and increased leaf size is perhaps associated with increased vessel diameter. Fortunately for elm breeders the correlation between vigor, as measured by leaf length, and response to inoculation is less than complete on both an individual-tree basis (Lester and Smalley, 1968) and a plot-mean basis *(Table 3)*.

Evidence on the effect of genes from *U. japonica* is limited, but encouraging, in terms of disease susceptibility. Disease response changed only slightly when *U. japonica* germplasm was combined in small amounts with *U. pumila*. In three-species combinations *U. japonica* genes raised susceptibility somewhat though not to a marked degree.

Wide variation in disease response among progenies within certain species combinations was recorded *(Table 2)*. This variation may be of great value in advanced stages of breeding for disease resistance, yet if the breeding objective is for seed propagation of disease resistant trees, testing and selection of specific parents probably should be delayed until certain species combinations are chosen for intensive exploitation. The least susceptible full-ship progeny of p × r, for example, was too susceptible for commercial use and was of higher susceptibility than the average p × pr progeny. Only one set of crosses clearly demonstrated general combining ability. In the exceptional case, crosses of three *U. rubra* maternal parents with four *U. pumila* trees resulted in consistently lower disease symptoms among individuals with one specific parent.

Table 3. — Linear correlation coefficients for ornamental and inoculation response characters for all progenies ($n = 270$, $r_{.01} = .16$).

	Height	Flushing	Dieback	Frequency of Symptoms	Crown Damage
Leaf Size	.57	—.52	.33	.72	.66
Height		—.41	.24	.50	.49
Flushing			—.49	—.50	—.45
Dieback				.26	.28
Frequency of Symptoms					.74

The absence of interaction between inoculation time and progeny supports earlier data on the similar timing of maximum susceptibility for different species (Smalley and Kais, 1966). Differences among progenies in duration of susceptibility can, however, result in a significant interaction. Analysis of crosses between *U. rubra* and *U. pumila* showed significant interaction (95% or 99% probability) for two disease response variables (Lester and Smalley, 1972 a). Both variables were measures of disease response relatively soon after inoculation.

These early results suggest that, in terms of landscape planting, the susceptibility of hybrids containing *U. rubra* germplasm precludes access to ornamental traits of *U. rubra* in seed-propagated materials without an extensive search for resistance genes in *U. rubra* or advanced generation crossing. Unless strong disease recovery mechanisms are common in the hybrids, susceptibility frequencies of more than 10% or crown damage of more than 20% are probably too high for general ornamental usage. Unlike forestry plantations where intermediate and final harvests may represent less than half the trees planted, each specimen and street tree is planted with the expectation that it will survive to be appreciated daily for many years. For seed propagation, further investigation of *U. pumila* × *japonica* hybrids is needed. Possibly the backcross to *U. japonica* will produce an adequate replacement for *U. americana*.

An alternative which may allow access to a broader array of genes is vegetative propagation. Within all progenies inoculated in this study some symptomless individuals were observed. Additional testing will be needed to substantiate the apparent resistance of these individuals but the general occurrence of at least some symptomless individuals in nearly all screening tests[1]) suggests that resistant individuals can be produced in most crosses. A commitment to vegetative propagation could allow the breeder a totally different orientation toward producing ornamental trees. Crossing could be designed to combine desirable ornamental traits of various species or individuals with little or no regard for disease susceptibility. Artificial selection for ornamental traits can be markedly less intense than for disease resistance so that the few resistant individuals in ornamentally desirable, but highly susceptible, progenies could be utilized commercially.

Character Correlations

Correlations among disease response and ornamental traits were calculated at two levels. First, correlations for the data as a whole were intended to illustrate the extent of general character associations in widely variable materials as a guide to which trait combinations might be expected in selection of species combinations for further breeding. Secondly, correlations within each species combination were calculated as a guide to character associations among progenies with a more restricted genetic base. All calculations were based on plot means thus would not necessarily have meaning in clonal selection.

The correlation coefficients in *Table 3* show generally non-random, low to moderate association between variables. Some associations are clearly desirable, others are undesirable but none appear to reflect linkages which would be exceptionally difficult to break in advanced generation breeding. Three associations seems worthy of comment. The negative relationship between flushing and other traits reflects transmission of genes responsible for early flushing, small leaf size, and low susceptibility in *U. pumila*. The association of leaf size and response to inoculation was noted in discussion of variation among species combinations. An association of similar magnitude ($r = 0.82$) was reported for individual-tree data on trees produced by wind pollination of our *U. pumila* × *japonica* hybrid progeny (Lester and Smalley, 1968). This undesirable relationship is perhaps the major obstacle to early commercial utilization of *U. rubra* germplasm and may plague breeding for large leaves in other species combinations. Finally, the moderate association of symptom frequency and a measure of symptom intensity adds confidence that the picture of disease response obtained in this study adequately represents the range of disease effects.

Trait associations between variables within species combinations were generally low and statistically non-significant except for the correlation of symptom frequency and crown damage. Measurement methods were probably too imprecise to adequately test associations in reduced ranges of variation.

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Summary

Crosses among *U. pumila*, *U. rubra*, and the putative natural hybrids *U. pumila* × *rubra* and *U. pumila* × *japonica* were analysed for four ornamental traits and two measures of response to artificial inoculation with *C. ulmi*. The importance of inoculation date in relation to patterns of seasonal susceptibility was illustrated and discussed.

In crosses between *U. pumila* and *U. rubra*, leaf size, height, lateness of flushing, stem dieback, and susceptibility to *C. ulmi* increased in proportion to the amount of germplasm present from *U. rubra*. These results suggest that for production of ornamentals by seed, the utilization of desirable genes from *U. rubra* would require either location of genes for resistance in *U. rubra* or advanced generation crossing to combine desirable *U. rubra* genes with resistance genes from *U. pumila*. For clonal propagation, the presence of symptomless individuals in all progenies suggests that highly ornamental clones of low susceptibility can be produced from first generation hybrids. With a clonal approach, progeny evaluation could emphasize ornamental qualities rather than response to the fungus.

Preliminary crossing indicated that *U. japonica* may be a source of genes with which to improve ornamental traits of *U. pumila* while introducing less susceptibility to *C. ulmi* than in crosses with *U. rubra*.

Variation among full-sib progenies within species combinations suggested that progress in breeding could be made through selection of parents. Parental selection, however, probably should be deferred until certain species combinations are chosen for intensive breeding.

Simple linear correlation coefficients for ornamental and disease response variables with pooled data from all crosses demonstrated that breeding progress may be impeded by a negative association between leaf size and susceptibility to *C. ulmi*. This association is fortunately variable so that the combination of resistance and ornamental value probably can be accomplished in advanced generation crossing.

Key words: Dutch elm disease, *Ceratocystis ulmi*, *Ulmus pumila*, *U. rubra*, *U. japonica*, ornamental traits, resistance, inoculation date, seasonal susceptibility, breeding.

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[1]) Smalley, E. B.: Unpublished data. 1958—1970.

Zusammenfassung

Kreuzungen zwischen den Ulmenarten *U. pumila* und *U. rubra* und vermutliche natürliche Bastarde *U. pumila* × *U. rubra* und *U. pumila* × *U. japonica* wurden auf 4 Ziergehölz-Merkmale hin untersucht und die Reaktion auf künstliche Beimpfung mit *Ceratocystis ulmi* (Erreger des Ulmensterbens) in 2 Fällen gemessen. Die Beziehungen zwischen dem Datum der Beimpfung und der jahreszeitlichen Anfälligkeit werden dargestellt und diskutiert.

Bei den Kreuzungen zwischen *U. pumila* und *U. rubra* nimmt die Blattgröße, die Höhe, die Austriebsverzögerung, der Umfang des Absterbens und die Anfälligkeit für *C. ulmi* gleichsinnig mit dem Umfang des enthaltenen Veranlagungsanteiles von *U. rubra* zu. Diese Ergebnisse besagen, daß bei der Produktion der Zierbäume aus Samen die Nutzung der erwünschten Gene von *U. rubra* eine Prüfung auf vorhandene Resistenzgene erfordert, oder daß man in systematischen Kreuzungen erwünschte *U. rubra*-Gene mit Resistenzgenen von *U. pumila* kombiniert. Das Vorhandensein von Individuen ohne Symptome in allen Nachkommenschaften deutet darauf hin, daß wertvolle Zierklone mit geringer Anfälligkeit durch Klon-Vermehrung aus der ersten Bastardgeneration angezogen werden können. Bei einer vorhandenen Verklonungsmöglichkeit könnte die Entwicklung von Nachkommenschaften mehr Gewicht auf die Zierqualitäten legen als auf die Pilzbefallsreaktion.

Probekreuzungen mit *U. japonica* zeigen, daß man dadurch Ziermerkmale von *U. pumila* verbessern kann bei weniger Anfälligkeit für *C. ulmi* als bei Kreuzungen mit *U. rubra*.

Die Variation unter Vollgeschwister-Nachkommenschaften innerhalb von Artenkombinationen weist darauf hin, daß durch Selektion der Eltern ein Züchtungsfortschritt erreicht werden könnte. Doch sollte eine Eltern-Selektion wahrscheinlich so lange hinausgeschoben werden, bis sichere Artenkombinationen für eine intensive Züchtung ausgewählt worden sind.

Einfache lineare Korrelationskoeffizienten für Variable von Ziermerkmalen und Krankheitsreaktion bei gepoolten Daten von allen Kreuzungen zeigen, daß ein Züchtungsfortschritt durch eine negative Abhängigkeit von Blattgröße und Anfälligkeit für *C. ulmi* verhindert werden kann. Diese Abhängigkeit ist aber glücklicherweise variabel, so daß Kombinationen von Resistenz und Zierwert wahrscheinlich bei fortschreitenden Generations-Kreuzungen angereichert werden können.

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