

Not all organizations can or should have complete breeding populations. The larger organizations and the government must be responsible for establishment and maintenance of genetic base populations. Free exchange of material is mandatory. Organizations, both large and small, will be dependent upon these breeding populations for continued gains; in fact, for a healthy eucalypt forest industry in Brazil. Too often activities concentrate on short-term gain for operational planting but the really important job for the long term welfare of Brazilian forestry is to have good gene conservation measures combined with the development, maintenance and testing of genetic base populations of eucalypts.

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Compatibility and Crossability Studies in *Ulmus*

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Summary

Eleven *Ulmus* species at the Arnold Arboretum were tested for compatibility and crossability. All these species, *Ulmus americana*, *carpinifolia*, *glabra*, *japonica*, *laciniata*, *laevis*, *procera*, *pumila*, *rubra*, *thomasi* and *wilsoniana*, are self-fertile. The successful intersectional crosses and the unsuccessful intrasectional crosses demonstrated, suggest that the current infregeneric classification of *Ulmus* is artificial. The form of dichogamy (protandry or protogyny) seems to be correlated with the compatibility between different species. The condition of dichogamy deserves consideration in sectional delimitations of the genus.

Key words: *Ulmus* species, self-compatible, interspecific crossings, protandry, protogyny.

Zusammenfassung

Im Arnold Arboretum wurden elf Ulmenarten auf Verträglichkeit und Kreuzbarkeit untersucht. Alle Arten, *Ulmus americana*, *carpinifolia*, *glabra*, *japonica*, *laciniata*, *laevis*, *procera*, *pumila*, *rubra*, *thomasi* und *wilsoniana*, waren selbstfertil. Die erfolgreichen inter- und die erfolglosen intrasektionalen Kreuzungen zeigten, daß die derzeitige systematische Einordnung der Gattungen von *Ulmus* künstlich ist.

Die Form der Dichogamie (Protandrie oder Protogynie) scheint mit der Kompatibilität zwischen verschiedenen Ar-

ten korreliert zu sein. Bei der Einteilung der Gattung in Sektionen verdient die Dichogamie besondere Beachtung.

Introduction

The elms are ornamental and timber trees. The principal and practical objective of controlled pollinations in the past has been to combine resistance to Dutch elm disease with desirable ornamental and growth traits. As a consequence of prevailing dichogamy in this anemophilous genus, previous workers (BRITWUM, 1960; COLLINS, 1967; HEYBROEK, 1968; SANTAMOUR, 1972) assumed elms to be self-sterile in the controlled hybridization experiments and no emasculation attempts were made. Successful crosses between species belonging to different sections of the genus *Ulmus* L. were reported. Considerable variation and taxonomic complexity exists, presumably as a result of natural hybridization among species (MELVILLE, 1975, 1978; RICHENS and JEFFERS, 1975, 1978; RICHENS, 1980).

The American elm has been the subject of research on floral biology and breeding systems. LESTER (1968) indicated that protogyny in this species does not make it fully self-sterile (see also JOHNSON, 1946). To avoid any confusion in the results, LESTER (1971) made use of previously known self-sterile and self-fertile individuals in the self-compatibility studies of American elm.

To test whether or not other species of *Ulmus* are self-fertile and interbreeding, studies were conducted at the Arnold Arboretum of Harvard University during the spring of 1980. This paper deals with the compatibility and crossability patterns of eleven species of *Ulmus*.

Materials and Methods

Intra- and interspecific crosses involving eleven species (*Ulmus americana* L., *U. carpinifolia* GLED., *U. glabra* HUDSON, *U. japonica* (REHDER) SARG., *U. laciniata* (TRAUTV.) MAYR, *U. laevis* PALLAS, *U. procera* SALISB., *U. pumila* L., *U.*

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rubra MUHL., *U. thomasi* SARG. and *U. wilsoniana* SCHNEIDER were conducted in the green house and on the grounds of the Arnold Arboretum during the spring of 1980. The brief and almost simultaneous period of blooming of elms was staggered to some extent (1) by forcing inflorescences in the green house (55° F) about two weeks before bud opening in the field, and (2) by refrigerating the inflorescences (buds) at 35—40° F and forcing them later. The flowering branches which were forced in the green house were covered with bags to prevent contamination. Transparent polyethylene bags were used as pollination bags outside because these could withstand rain and wind. The laborious procedure of emasculation was conducted just before anthesis or stigma receptivity. In some protogynous species acting as female in interspecific crosses, the flowers were fixed in 1:3 acetic alcohol 24 hours after the crosses were made. Growth of the pollen tube on the stigma was examined following MARTIN'S (1958) UV fluorescent microscope technique. The samaras (fruits) were observed against the light to test for development of seed and distinguish between empty and filled samaras.

Results and Discussion

Intraspecific crosses

All the investigated species of *Ulmus* showed 50 to 85 per cent self-fertility as revealed by fruit set after selfing (see Table 1). The crosses between two individuals of the same species were 40 to 65 percent successful. The lower percentage of fruit set in crosses than in selfs may be due to some inadvertent damage to the delicate inflorescences during emasculation. In both selfs and crosses a small percentage of fruits had the tendency to abscise prematurely, probably due to some physiological disorders; and these were omitted in the analysis.

To confirm self-fertility as revealed by green house experiments, bagging was done on some species in the field. The pollen was dispersed inside the bag apparently with bag movement by wind. Fruit set was 80 to 100 percent within the bags as well as with the open controls. Again,

a number of fruits tended to fall prematurely in both cases. The fruits inside the bags developed faster than did those of the open controls. The pollination bags that remained on flowering branches for 10 to 14 days presumably acted as miniature green houses and accelerated the development of fruits. In addition to the species noted above, the following cultivars showed self-fertility: *Ulmus americana* 'Littlefordii' and 'Princeton', *U. carpinifolia pendula*, *U. glabra* 'nana', *U. laciniata* 'nikkoensis', *U. pumila arborea* and 'Hamburg', and *U. × hollandica* 'belgica' and 'major'. These cultivars may also, of course, be cross pollinating.

The periods of anthesis and stigma receptivity in elms do overlap in the same inflorescence, rendering dichogamy less effective and the trees vulnerable to self pollination.

Interspecific crosses

Of the many interspecific crosses attempted, several were between species that belong to different sections of the genus.

Section *Blepharocarpus* DUMORT.: *Ulmus americana* and *U. laevis*.

Section *Chaetoptelea* (LIEBM.) SCHNEIDER: *U. thomasi*.

Section *Ulmus* (Madocarpus Dumort.): *U. carpinifolia*, *U. glabra*, *U. japonica*, *U. laciniata*, *U. procera*, *U. pumila*, *U. rubra* and *U. wilsoniana*.

The self-compatibility studies revealed the necessity of the hard task of emasculation. Where emasculation could not be performed, the examination of pollen tube growth on the stigma was conducted to determine the success or failure of the cross. If the pollen grains did not germinate, the cross was considered incompatible.

The results (Table 2) showed no barrier to some inter-sectional crosses. For instance, *Ulmus laevis* (Section *Blepharocarpus*) crossed successfully with *U. thomasi* (Section *Chaetoptelea*) and *U. pumila* (Section *Ulmus*). However, the failure of *U. americana* (belonging to the same section as *U. laevis*) to cross with *U. pumila* is due to the fact that *U. americana* is tetraploid with $2n = 56$ (SANTAMOUR 1969, and more references in A. A. FEDOROV, Ed. 1969).

Table 1. — Results after selfing and intraspecific crossings of various species of *Ulmus*.

1: Two trees of each species were used except in *Ulmus laevis* where a single tree was chosen.

<i>Ulmus</i> species ¹	Fruit set (per 20 flowers)		Seed set (per 20 flowers)	
	Self	Cross	Self	Cross
<i>U. americana</i> L.	16	10	16	9
<i>U. carpinifolia</i> Gled.	11	10	10	8
<i>U. glabra</i> Hudson	15	12	13	12
<i>U. japonica</i> (Rehder) Sarg.	15	11	14	10
<i>U. laciniata</i> (Trautv.) Mayr	15	13	15	10
<i>U. laevis</i> Pallas	12	-	9	-
<i>U. procera</i> Salisb.	16	10	11	8
<i>U. pumila</i> L.	17	12	17	8
<i>U. rubra</i> Muhl.	17	13	17	11
<i>U. thomasi</i> Sarg.	12	12	12	10
<i>U. wilsoniana</i> Schneider	10	8	8	8

Table 2. — Crossability pattern in some species of *Ulmus* arranged under sections
C = Compatible, IC = Incompatible, SC = Self Compatible.

Ulmus species acting as female	male	BLEPHAROCARPUS		CHAETOPTOLEA	ULMUS									
		<u>americana</u>	<u>laevis</u>			<u>thomasi</u>	<u>carpinifolia</u>	<u>glabra</u>	<u>japonica</u>	<u>laciniata</u>	<u>procera</u>	<u>pumila</u>	<u>rubra</u>	<u>wilsoniana</u>
<u>americana</u>		SC								IC				
<u>laevis</u>			SC	C						IC	C	IC		
<u>thomasi</u>				SC		IC	C		IC					
<u>carpinifolia</u>				IC	SC	C	IC							
<u>glabra</u>			IC			SC	IC			IC	C			
<u>japonica</u>							SC	IC						C
<u>laciniata</u>				IC		C		SC	C	IC				
<u>procera</u>						C	IC		SC	IC	C			
<u>pumila</u>		IC		C				C		SC	IC	C		
<u>rubra</u>				IC		C					SC			
<u>wilsoniana</u>								C	IC					SC

All other species of *Ulmus*, inclusive of *U. pumila* are diploid.

On the other hand, about half the number of crosses within the largest section (*Ulmus*) were not compatible: *carpinifolia* × *japonica*, *glabra* × *japonica*, *procera* × *pumila*, *laciniata* × *pumila*, *pumila* × *rubra* to cite a few.

The picture regarding sectional delimitations seems to be blurred due to some compatible intersectional crosses and incompatible intrasectional crosses. Obviously, taxonomy based on morphological characters alone is not enough.

The results, however, reveal a subtle trend between the successful and unsuccessful crosses. Among the dichogamous *Ulmus* species, some are protogynous and others are protandrous (Table 3, Figure 1). The compatible crosses are either between protogynous species or protandrous ones, while incompatible crosses turn out to be between protogynous and protandrous species. The compatibility between species is therefore greatly influenced by the type of dichogamy. This criterion should be given much importance in sectional classification of the genus and should

be the primary delimiting factor. The natural hybrids reported by MELVILLE (1975) happen to be between protogynous species. RICHENS (1980) reports that no crossing between *Ulmus laevis* (protandrous) and other European members of Section *Ulmus* occurs; this might be due to differences in dichogamy. It is difficult to accept the early reports (for references, see SANTAMOUR, 1972) of crosses between Dutch elm disease — resistant *U. pumila* and DED susceptible *U. americana*. The two species belong to different sections of the genus *Ulmus*, are at different ploidy levels, and have different operational dichogamy.

Table 3. — List of protogynous and protandrous species of *Ulmus*.

Section	Species showing	
	Protogyny	Protandry
Blepharocarpus Dumort.	<u>U.americana</u>	<u>U.laevis</u>
Chaetoptelea (Liebm.) Schneider		<u>U.thomasi</u>
Ulmus (Madocarpus Dumort.)	<u>U.carpinifolia</u>	<u>U.japonica</u>
	<u>U.glabra</u>	<u>U.pumila</u>
	<u>U.laciniata</u>	<u>U.wilsoniana</u>
	<u>U.procera</u>	
	<u>U.rubra</u>	

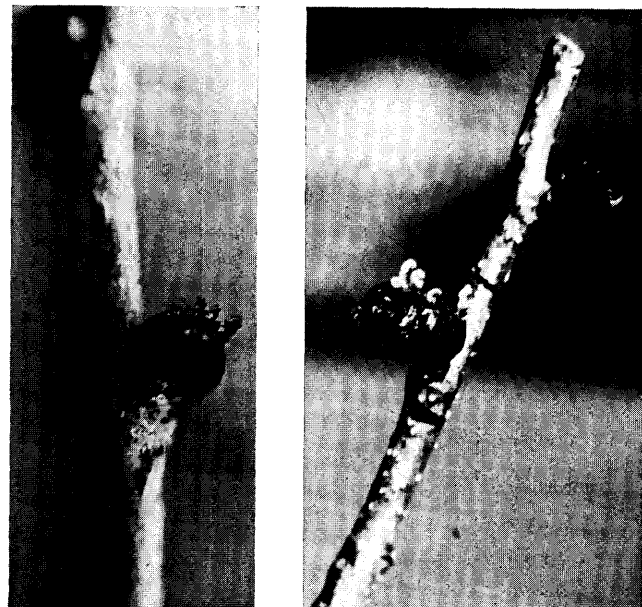


Figure 1. — Protandry in *Ulmus japonica* (left) and protogyny in *U. laciniata* (right), both × 2. Note the extruding stamens and stigmata from the flowers still enclosed by bud scales.

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Nachweis und physiologische Aspekte von Glucose-6-Phosphat-Dehydrogenase-Inhibitor(en) in keimendem Fichtensaatgut (*Picea abies* (L.) Karst.)

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Zusammenfassung

Durch enzymatische Messungen wird nachgewiesen, daß in der Quellungsphase der Keimung von Fichtensaatgut G6P-DH-Inhibitor/en ausgeschieden wird/werden.

Die vorliegenden Ergebnisse deuten darauf hin, daß der/die nachgewiesene(n) Inhibitor(en) die Aktivität endogener G6P-DH und damit die Keimfähigkeit des Saatgutes beeinflussen kann/können.

Schlagworte: Glucose-6-Phosphat-Dehydrogenase, Inhibitor, keimendes Fichtensaatgut, Nachweis, physiologische Aspekte, *Picea abies*.

Summary

It is demonstrated by enzyme measurements that during soaking stage of seed material from Norway spruce substance/s inhibitory to G6P-DH is/are secreted.

The inhibitor/s proved is/are supposed to influence the activity of endogenous G6P-DH, i.e. the germination rate of seed material.

Key words: Glucose-6-Phosphate-Dehydrogenase, inhibitor, germinating seed, Norway spruce (*Picea abies*), proof, physiological aspects.

Abstract

Proof and Physiological Aspects of Glucose-6-Phosphate-Dehydrogenase-Inhibitor(s) in Seed Material from Norway

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Spruce (*Picea abies* (L.) KARST.) during Germination. By means of enzyme measurements germinating seed material (*P. abies*) of different vitality is shown to secrete substance(s) inhibitory to vital Glucose-6-Phosphate-Dehydrogenase. Physiological aspects of the results (kinetic data) are discussed.

1. Einleitung

Die Keimfähigkeit von Saatgut ist durch das Zusammenwirken exo- und endogener Faktoren festgelegt. Umweltbedingte Einflüsse wie Feuchtigkeit, Temperatur, Substratzusammensetzung u. a. sind exogene Faktoren, während die genetische Anlage und damit physiologisch-biochemische und morphologische Merkmale des Saatgutes zu den endogenen Faktoren zählen. Diese Faktoren können die Keimung fördern oder hemmen. So sind bei der Saatgutlagerung reversibel keimhemmende, im Keimstadium hingegen optimal keimfördernde Faktoren zu beachten (SCHÖNBORN VON, 1964).

Bei Fichte konnte bereits früher zwischen Keimfähigkeit und Ionenausscheidung durch keimendes Saatgut eine enge Korrelation nachgewiesen werden (SCHINDLBECK, 1981). Dieser Befund und die Tatsache, daß viele lebensnotwendige Enzyme (endogene Faktoren) durch Ionen gehemmt bzw. aktiviert werden (BERGMAYER, 1970), waren Anlaß zur vorliegenden Arbeit.

Am Beispiel der Glucose-6-Phosphat-Dehydrogenase (G6P-DH), einem Enzym von zentraler Bedeutung für die Keimfähigkeit, sollte untersucht werden, ob und unter welchen Bedingungen die endogenen, teilweise ionischen