ever, other evidence in hoop pine (Queensland Forest Service, unpublished results) indicates that although maternal effects accounted for 11% of the variation in height shortly after planting, this declines to around 3% by age eight years. Also at eight years, maternal effects accounted for only 1% of the variation in diameter and 4% of the variation in straightness. Even assuming comparable figures at age 15 years for spiral grain and compression wood, the effect is not large enough to cause a negative estimate of dominance variance. Considering these results and those of comparable analyses in other species (Queensland Forest Service, unpublished results), the value of this method as a means of estimating non-additive variance is questionable.

Offspring-parent regression

The estimated heritability of basic density derived from the offspring-parent regression was 0.99 (±se 0.25), and of mean spiral grain was 0.64 (± 0.26). These estimates do not differ significantly from those derived using sib-analysis in the same experiment (progeny trial II), shown in *table 4*.

The theoretical expectation of heritabilities estimated from offspring-parent regression differs in several respects to those estimated by sib-analysis. Firstly, bias can arise using the latter technique either through the algebraic properties of the estimation procedure (ROBERTSON, 1977; PONZONI and JAMES, 1978) or through gametic disequilibrium due to selection (BULMER, 1971). Offspring-parent regression, on the other hand, provides estimates unaffected by selection (HILL and THOMPSON, 1977). For the families reported here, no selection pressure was exerted on wood characteristics when the parents were selected, except via the correlations with vigour and form (*Table 6*). According to PONZONI and JAMES (1978), both these effects should be relatively small.

Secondly, a potential disparity arises between the two methods of estimation in that the parents are not growing together under trial conditions, and they range in age at sampling. Environmental effects, if appreciable, would therefore tend to increase the variance of the traits measured in the parents. This in turn could be expected to decrease the offspring-parent regression. Estimates derived using this technique would therefore be appropriate to individual trees of various ages and in various environments, as opposed to trees growing in similar environments and of the same age such as in a replicated progeny trial. As reported above, the variances for basic density and mean spiral grain were not significantly different in the parents and progeny, so this source of disparity is also likely to be negligible.

These results give a strong indication that age and site effects do not appreciably affect basic density or spiral grain. The relatively small effect of block effects on wood quality traits (*Tables 3* and 7) adds support to this argument. This implies that for the purposes of providing a genetic ranking for basic density and spiral grain, it may be satisfactory to directly compare plus trees of different ages and growing in different environments. Should this be the case, considerable time and effort could be saved by screening plus trees on the basis of their phenotype for basic density and spiral grain, regardless of whether or not they are grown in replicated progeny trials. However, more data are needed from a wider range of environments and ages to fully test the generality of this hypothesis. Studies currently underway should provide the data necessary to better test this hypothesis.

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Hybridization Studies in the Eurasian Species of Elm (Ulmus spp.)

By L. MITTEMPERGHER[1]) and N. LA PORTA[2])

[1]) Forest genetics, Centro di Studio per la Patologia delle Specie Legnose Montane del CNR, Florence, Italy

[2]) Research worker, Istituto di Miglioramento genetico delle Piante Forestali del CNR, Florence, Italy

Summary

This paper presents data on crossability, and rate of selfing derived from crossing trials carried out for four years among 11 species of elm. Crossability barriers among

species were found to be weak, with success of several combinations dependent on male-female interaction and the parental individual. Hybrid seed production was generally related to the taxonomic affinity of the parental species. *U. villosa* Brandis did not produce seed in our environment but was a successful male parent in several hybrid combinations. A unique crossability barrier was found to exist among *U. laevis* Pall. and the other species. A particular case of delayed sterility was observed between *U. laevis* and *U. villosa* where hybrid seedlings died during the first vegetative season. Four of the species under study showed selfcompatibility with production of more than 1% full seeds. Selfing was particularly pronounced in *U. parvifolia* Jacq. and *U. japonica* (R.) Sarg. Variation in selfing ability among individuals was high and the environment appeared to also play a role. Attention was payed to pollen preservation and viability evaluation.

Key words: Ulmus hybridization, crossability among species, delayed hybrid sterility, self-compatibility, pollen preservation, pollen viability testing.

Introduction

Breeding of resistant elms seems to be one of the most successful ways of reducing the impact of Dutch elm disease (DED) on the native elms of Europe and North America. This activity has been carried out at more than seven laboratories in the Northern Hemisphere. It started in the Netherlands more than 60 years ago (Heybroek, 1957, 1966), a few years after the discovery of the causal agent, the fungus *Ophiostoma ulmi* (Buisman) Nannfeldt. Several Laboratories in the U.S.A. undertook elm breeding projects in order to find a substitute to the very susceptible American elm (*Ulmus americana* L.) which has a distinctive vase-shaped crown (Lester and Smalley, 1972a; Santamour, 1972; Sinclair et al., 1974; Lester, 1978). Another reason for starting new elm breeding projects is that the Dutch selections are not suitable for North America (Lester, 1978; Townsend, 1975) as well as for the hot and dry areas of the Mediterranean basin (personal observations). That is why more than 10 years ago we also undertook a breeding program aimed at releasing resistant elms more adapted to our environment and more desirable for the ornamental traits and growth. Resistant elms can be obtained by introducing resistance from some Asiatic species into the susceptible European and American species (Lester and Smalley, 1972a; Santamour, 1972; Townsend and Schreiber, 1976; Townsend, 1979; Heybroek, 1983) or by crossing Asiatic species among themselves (Smalley and Lester, 1973; Santamour, 1974; Lester, 1975). The most important elm species in the plains of central and southern Europe is *U. carpinifolia* Gled., which has been widely used in our crosses and is the standard for our selection products. Related to this species is the renowned English elm (*U. procera* Salisb.) which is considered a 'small species' belonging to the 'carpinifolia group' (Richens, 1983; Heybroek, 1968). The Asiatic species of elm which have been commonly used as resistant parents in the breeding programs are: *U. pumila* L., *U. japonica* (R.) Sarg., *U. parvifolia* Jacq. and *U. wallichiana* Planch. (Lester and Smalley, 1974; Santamour, 1974; Heybroek, 1976, 1979, 1981). Much information has been accumulated in the last years on floral and seed biology and on crossability patterns among elm species (Johnson, 1939, 1946; Smith and Nichols, 1941; Barton, 1953; Rowley and Rowley, 1953; Went, 1954; Britwum, 1960; Collins, 1967; Heybroek, 1968; Long, 1971; Lester and Smalley, 1972b; Santamour, 1972;

Townsend, 1975; Hans, 1981; Ager and Guries, 1982; Bob et al., 1986). Nevertheless, new oriental elm species have become available for breeding work, as for example *U. villosa* Brandis and *U. chenmoui* Cheng, which could turn out to be useful in broadening the genetic diversity of resistant clones. No data on crossability of these species are available. In addition, conflicting results are found in the literature on self-fertility and crossing success, and some of the putative hybrids were never authenticated. On account of this it may be useful to add further data to the existing knowledge in this field. While carrying out our program aimed at breeding hybrid progenies of elm resistant to DED we collected data on: a) the crossability potential among species; and b) the rate of selfing.

Materials and Methods

During 1985 to 1988, crossing trials were carried out using as male and female parents 2 to 3 individuals of the following species: *Ulmus carpinifolia* (*U. ca*), *U. japonica* (*U. ja*), *U. chenmoui* (*U. che*), *U. wilsoniana* Schn. (*U. wi*) (one specimen), *U. glabra* Huds. (*U. gla*), *U. x hollandica*, *U. elliptica* Koch. (*U. el*) (one specimen), and *U. pumila* (*U. pu*) belonging to the section *Ulmus*; *U. parvifolia* (*U. pa*) belonging to the section *Microptelea*; *U. laevis* Pall. (*U. lae*) belonging to the section *Blepharocarpus*, and *U. villosa* (*U. vi*). of uncertain classification (Heybroek, 1979). Three-four branchlets, each containing at least 300 to 400 flowers, were isolated for every cross combination before flower opening by means of polyester pollination bags (P.B.S. International, Scarborough, North Yorkshire, U. K. YO11 3UZ). Several cross combinations were repeated the following year. Care was taken to ensure flower isolation well ahead of flowering because of the general protogyny of elm species. Only *U. wi* and, partially, *U.pu* from the species under study turned out to be protandrous whereas the other 9 species were more or less protogynous. Because of the small dimensions of the flowers we did not carry out emasculation, but relied on reported self-incompatibility (Johnson, 1946; Heybroek, 1957; Britwum, 1960; Townsend, 1975) which is common practice in elm breeding.

Pollen was obtained from cut branchlets held in vases with water. Each species was placed separately in small rooms kept at 20 °C and illuminated by 500 watt lamps. In this way we succeeded in accelerating flowering of *U. lae* by up to 30 days. Pollen was collected from sheets of polished packing-paper with a vacuum pump, subsequently filtered, and stored at 3 °C to 4 °C in a desiccator. Long-term preservation of pollen for up to one year was achieved at 3 °C to 4 °C and 10% relative humidity (R.H.) or at —20 °C and about 6% R. H. following Snyder and Clausen (1974). Pollen viability was estimated through the fluorochromatic (FCR) test procedure (Heslop-Harrison and Heslop-Harrison, 1970; Shivanna and Heslop-Harrison, 1981; Heslop-Harrison et al., 1984. Peterson and Taber, 1987). Dehydrated pollen was rehydrated in a humid chamber before being subjected to the FCR test. Flower pollination was carried out by injecting pollen into the bags with forced air. In fall pollinations on *U. pa*, terylene bags were substituted after seed set with net bags in order not to impair the functioning of the leaves inside. In spring pollinations pollination bags were kept in place until fruit ripening. Samaras were counted and separated into full and empty, and the data analyzed by ANOVA and LSD tests after transforming percentages into angular

values. Seed from *U. pa* was stratified for 30 days before sowing, while that from other species was sown immediately after counting. Sowing was done in open air nursery beds. Seed from each pollination bag was sown in a plot randomly located in the beds and its germination was monitored several times. Seedlings obtained from hybridization were checked morphologically during the first and second growing seasons in order to ascertain their hybrid nature. The characters used to distinguish among the species were: colour and hairiness of leaves and twigs; size, form, and margin of the leaves and their position on the twig; corky wings on twigs. In several cases it was possible to make use of these morphological traits to prove the hybridity of the progeny by comparing it with self seedlings and/or with wind pollinated seedlings. Such discriminating traits were the reddening of leaves and twigs of *U. vi*; the intensive hairiness of *U. che* leaves; the corkiness of twigs of *U. wi*, *U. ja* and *U. ca*; the distinctive form and margin of U. lae leaves (obovate, with biserrate margin curving upwards and acuminate apex); and the small and thick leaf with obtuse teeth of *U. pa*.

Results and Discussion

Crossability

Figure 1 shows that the flowering period of the species under study took more than 2 months and another species, *U. pa*, flowered at the end of August. Therefore, pollen must be preserved up to one year for all possible diallelic crosses to be completed. The percentage of viable grains in fresh pollen evaluated with the FCR method is different among the species (four species tested) and the procedures for collecting and conditioning it are determining factors for pollen viability (*Fig. 2*). The FCR procedure showed that storage at —20 °C versus + 4 °C
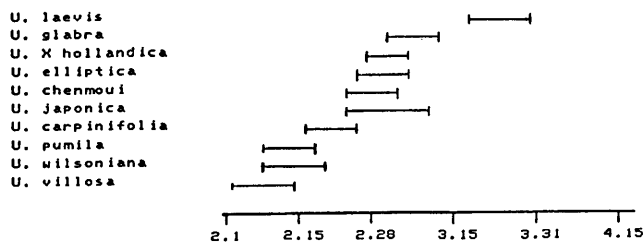

Figure 1. — Flowering dates (2.1 is February 1) in Florence of the spring-flowering elms species studied.
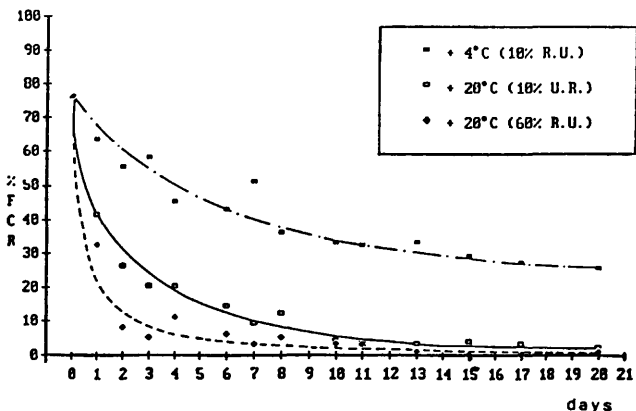

Figure 2. — Decline of pollen viability of *U. carpinifolia* evaluated by FCR method in the first 3 weeks after collection with or without control of temperature and relative humidity.
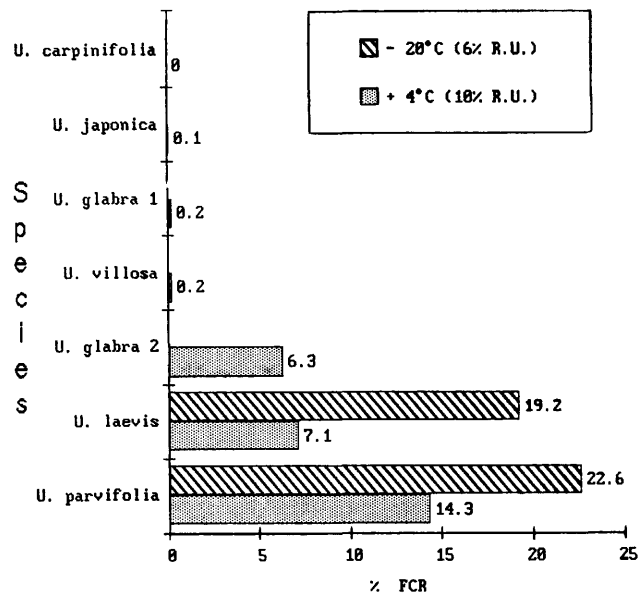
Figure 3. — Viability, expressed as a percentage of fluorescent grains with the FCR method, for pollen of 6 species. Pollen preserved for 1 year at +4 °C temperature, and at about 10% relative humidity. Pollen of *U. parvifolia* and *U. laevis* was also preserved at —20 °CT and 6% R.U.

Table 1. — Data of hybridizations carried out on *U. pumila* (a) and *U. parvifolia* (b), respectively in spring and summer 1987, by using fresh (*U. carpinifolia* 1987) or preserved pollen for 6 months (*U. carpinifolia* 1987 +4 °C; *U. leavis* 1987 + 4 °C, *U. leavis* 1987 —20 °C) or for 1 year or more at +4 °C or —20 °C. Data followed by different letters are significantly different by LSD procedure (P=0.05).

A.   U. pumila 7.3P ♀

δ	n° flowers	% seeds/fls	% seedlings/fls
self	1269	0.0 a	0.0 A
U. carpinifolia 1986 +4°C	917	0.0 a	0.0 A
U. carpinifolia 1986 -20°C	1694	16.3 b	10.7 8
U. carpinifolia 1987	2582	47.2 c	24.9 C

B.   U. parvifolia PA1-2 ♀

δ	n° flowers	% seeds/fls	% seedlings/fls
self	2238	8.1 a	2.8 A
U. laevis 1987 +4°C	2133	9.9 a	2.1 A
U. carpinifolia 1987 +4°C	2528	14.9 ab	5.7 AB
U. laevis 1987 -20°C	1877	20.7 bc	4.9 AB
U. carpinifolia 1986 -20°C	2940	20.9 c	10.7 8
wind	2951	74.4 d	55.2 C

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U. carpinifolia ♀

- LA — 2.2 a
- ✶ CH — 13.6 b
- ✶ VI — 13.7 b
- ✶ WI — 19.3 b
- EL — 25.3
- ✶ PA — 26.2 b
- ✶ PU — 31.3 bc
- ✶ GL — 43.5 c
- Se — 3.4 a

0 10 20 30 40 50

U. glabra ♀

- PU — 1.2 a
- ✶ LA — 2.6 a
- ✶ VI — 4.1 ab
- ✶ PA — 5.7 ab
- EL — 18.1 bc
- ✶ CH — 27.1 cd
- WI — 39.8 cd
- ✶ JA — 46.3 d
- Se — 1.2 a

0 10 20 30 40 50

U. hollandica ♀

- PU — 0.0 a
- PA — 0.2 a
- VI — 0.3 a
- EL — 0.4 a
- LA — 0.5 a
- GL — 28.7 b
- ✶ CH — 42.9 bc
- ✶ JA — 61.4 c
- Se — 0.6 a

0 10 20 30 40 50 60 70

U. pumila ♀

- LA — 0.1 a
- ✶ PA — 10.2 b
- ✶ VI — 15.9 b
- ✶ WI — 38.0 c
- ✶ CA — 47.2 c
- ✶ GL — 73.7 d
- Se — 0.2 a

0 10 20 30 40 50 60 70 80

U. laevis ♀

- JA — 0.3 a
- EL — 0.5 a
- CA — 0.5 a
- PU — 0.8 a
- CH — 0.8 a
- GL — 0.9 a
- WI — 1.1 a
- PA — 1.1 a
- ✶ VI — 22.6 b
- Se — 0.7 a

0 5 10 15 20 25

U. elliptica ♀

- PA — 13.8 b
- ✶ VI — 19.5
- GL — 60.8 c
- ✶ JA — 62.2 c
- ✶ CH — 64.6 c
- WI — 69.6 c
- HO — 77 c
- Se — 0.7 a

0 20 40 60 80 100

U. wilsoniana ♀

- ✶ VI — 1.1 a
- ✶ PA — 1.4 a
- ✶ PU — 1.6 a
- GL — 7.6 b
- EL — 12.1 b
- Se — 0.3 a

0 2 4 6 8 10 12 14

U. chenmoui ♀

- PA — 0.0 a
- PU — 0.1 a
- VI — 0.3 a
- GL — 0.8 a
- ✶ WI — 19 b
- Se — 0.0 a

0 5 10 15 20

U. japonica ♀

- ✶ PA — 11.5 a
- ✶ GL — 28.2 b
- ✶ PU — 29.7 b
- LA — 51.8 c
- ✶ VI — 65.5 cd
- ✶ CH — 71.5 de
- CA — 75.1 de
- HO — 77.4 e
- Se — 10.7 a

0 20 40 60 80 100

U. parvifolia ♀

- HO — 3.9 a
- EL — 4.8 a
- ✶ CH — 7.1 ab
- ✶ WI — 7.8 b
- ✶ VI — 9.9 bc
- ✶ LA — 12.1 bc
- ✶ CA — 14.6 bc
- ✶ GL — 16.4 c
- ✶ JA — 16.5 c
- ✶ PU — 18 c
- Se — 4.2 a

0 5 10 15 20

% FULL SEEDS

U. villosa ♂

- HO — 0.3
- CH — 0.3
- WI — 1.1
- GL — 4.1
- PA — 9.9
- CA — 13.7
- PU — 15.9
- EL — 19.5
- LA — 22.6
- JA — 65.5

0 10 20 30 40 50 60 70

% FULL SEEDS

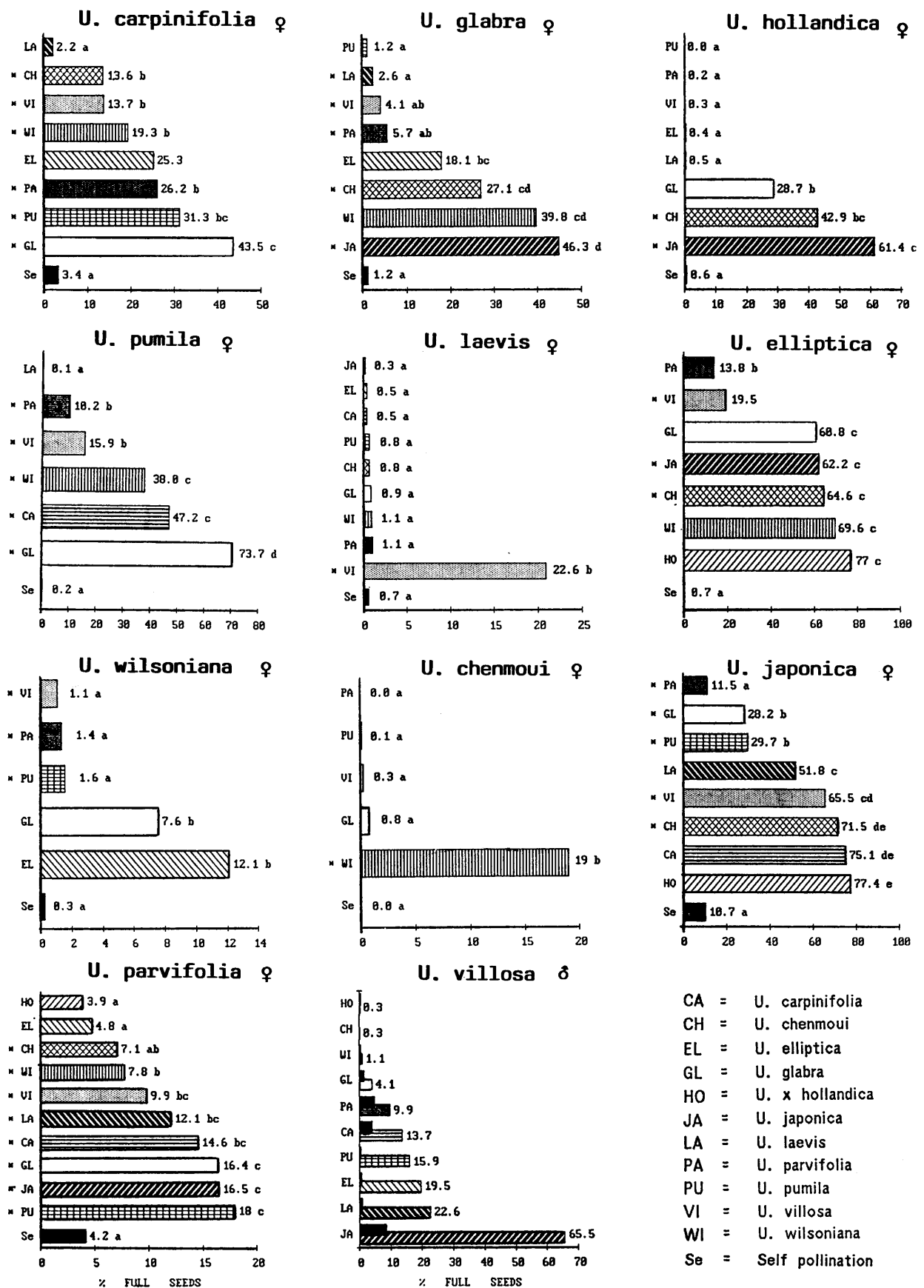|		
CA	=	U. carpinifolia
CH	=	U. chenmoui
EL	=	U. elliptica
GL	=	U. glabra
HO	=	U. x hollandica
JA	=	U. japonica
LA	=	U. laevis
PA	=	U. parvifolia
PU	=	U. pumila
VI	=	U. villosa
WI	=	U. wilsoniana
Se	=	Self pollination

Figure 4. — Results of hybridization experiments. Data refer to percentage of full seeds on pollinated flowers; in black are mean values of selfing. Data followed by different letters are significantly differented by LSD procedure (P = 0.05). An asterisk ✶ denotes presence of characters of the male parent on some of the seedlings of the hybrid progeny.

Table 2. — Summary of the results of 4 year hybridizations carried out on a minimum of 1000 flowers and maximum of 1500 for each combination. All the positive results correspond to the production of certified hybrid seedlings. As for the negative datum of the combination *U. laevis* X *U. villosa* see the text. A result of incompatibility along the diagonal of selfing means that less than 1% of full seeds are produced.

CROSSABILITY AMONG <u>ULMUS</u> SPECIES

	ca	ja	wi	ch	ho	gl	pu	el	la	pa	vi
U. carpinifolia	sc		+	+		+	+	+	-	+	+
U. japonica	+	sc		+	+	+	+	+	+	+	+
U. wilsoniana			ic			+	+	+		+	+
U. chenmoui			+	ic		-	-		-	-	-
U. hollandica		+		+	ic	+	-	-	-	-	-
U. glabra		+	+	+		sc	-	+	+	+	+
U. pumila	+		+			+	ic		-	+	+
U. elliptica		+	+	+	+	+		ic		+	+
U. laevis	-	-	-	-		-	-	-	ic	-	-
U. parvifolia	+	+	+	+	-	+	+	-	+	sc	+
U. villosa											

sc: selfcompatible
ic: selfincompatible
+: positive
—: negative

was significantly better in preserving (1 year) pollen viability (*Fig. 3*) and prevented the risk of using unviable pollen. Crosses carried out with pollen preserved at + 4 ⁰C and —20 ⁰C (*Tab. 1*), confirmed the FCR test and reinforce the need to check pollen viability.

Not all the possible crosses among the species were accomplished. A particular case is that of *U. vi* which did not produce seed in any cross, probably because of the unfavourable climatic conditions during the flowering period. As shown in *figure 1* *U. vi* is the first species to flower when frost is still common. We have obtained full seeds and a few seedlings from self-pollination of *U. vi* only once prior to the experiments reported here. The results of crossing work over four years is summarised in *figure 4* and *table 2*. Hybrids were certified by the presence of paternal traits on the seedlings and/or by the significance of the difference of seedling numbers obtained relative to the self-pollinated controls. Data are reported as full seed production instead of seedling production since the latter can sometimes be affected by insect and animal damage ,or by microclimatic variables in the nursery. Out of 76 hybrid combinations attempted 24 failed, with 13 of these involving *U. lae*. Unilateral crossing barriers were observed for many species combinations. The following combinations succeeded only when the first species was the female parent: *U. ja* x *U. lae*, *U. gla* x *U. lae*, *U. pa* x *U. lae*, *U. pa* x *U. che*, *U. el* x *U. pa*, *U. gla* x *U. che*, *U. pu* x *U. gla*. Townsend (1975) reported that the crosses *U. gla* x *U. ja*, *U. wi* x *U. pa* and *U. pa* x *U.rubra* Muhl. succeeded only undirectionally. As Santamour (1972) successfully completed the reciprocal cross *U. rubra* x *U. pa*, and we succeeded with *U. ja* x *U. gla* and *U. pa* x *U. wi*, it appears that genotype effects determine the success of the cross (Heyroek, 1968).

Overall, our data indicate that, except for species of the section *Blepharocarpus*, there are weak or nonexistent crossing barriers within the genus *Ulmus*. Of course, the rate of success varies among the different hybrid combinations, and is generally related to the taxonomic distance between the parental species. For example, U. gla furnishes more full seed when crossed to *U. el*, *U. che*, *U. wi* and *U. ja* which belong to the same section, than with *U. vi*, *U. pa* and *U. lae* which belong to other sections (*Fig. 4*).

An interesting result was obtained with the cross *U. lae* x *U. vi*. *U. lae* does not hybridize with any other species with the exception of *U. vi*, a species so far of uncertain classification. This cross produces seeds with smaller embryos that germinate regularly. The seedlings have traits characteristic of *U. vi*, and some seedlings even show hybrid vigour. However, after about 3 months of growth, when seedlings are 10 cm to 15 cm high and bear about 6 pairs of fully expanded and normal leaves, they begin to wilt and dry up and none survives the following year. We attempted this cross in three successive years using 3 different female parents and obtained the same result: only one hybrid seedling out of 1650 germinants survived the second year of trials. In 1989, we repeated the cross on a very high number of flowers in order to further examine the phenomenon. Growing seeds from this cross *in vitro* did not alter the situation; after 2 to 3 months, hybrid seedlings started dying while the open-pollinated seedlings developed normally. This excludes susceptibility to pathogens as the cause of this mortality. A similar case was reportet by Sholz (1957) with the combination *U. thomasii* Sarg. x *U. pu*. It appears that postzygotic breakdown operates here preventing hybridization. As male parent, *U. lae* gave hybrids in only 3 cases out of 7 attempted, confirming the negative results of Townsend (1975) and the statements of Heybroek (1968) and Richens (1980). However, Hans (1981) reports having crossed successfully *U. lae* with *U. thomasii*, an American species not studied by us, and with *U. pu*. The latter cross gave negative results in our trials. It should be observed that Hans, by working on a few tens of flowers, carried out flower emasculation and used trans-

parent polyethylene bags for isolation; thus his techniques and environment were different from those commonly used. Furthermore, his criterion for success was the number of filled seed rather than authenticated hybrid seedlings. Full seeds and seedlings can be obtained from a cross combination in many ways, but seedlings must be proved to be hybrid in order to show that the two species are crossable (see HEYBROEK, 1968, for a comment). We believe that the hybridization results and the inferences on the taxonomy of the genus *Ulmus* by HANS (1981) need re-examination.

Another species that often failed in crosses when used as female is *U. che*. However, the trees reached the flowering stage only two years before these experiments were initiated and it is possible that fertility could be influenced by the young age of the female parent, as we have seen with *U. pa*. *U. che*, (which has previously not been reported) appears to be highly fertile when used as a male parent. Fertility of *U. wi* and *U. pa* as female parents in hybrid combinations was generally low, which is the same result obtained by L. R. SCHREIBER (personal communication) for the first species and by SANTAMOUR (1972) for the latter.

Self-compatibility

Self-incompatibility is a common phenomenon in *Ulmus* (JOHNSON, 1946; HEYBROEK, 1957; BRITWUM, 1960; COLLINS, 1967) which makes breeding possible without requiring emasculation. Considerable intraspecific variation in self-incompatibility has been reported (WENT, l.c.; LESTER, 1971; AGER and GURIES, l.c.). AGER and GURIES (l.c.) documented that self-incompatibility in *U. americana* results from incompatibility barriers that operate on the stigma surface. HANS (l.c.) found 11 species to be self-compatible with better seed production in self versus outcross combinations. Our experiments showed four of the 11 species tested to be self-compatible, the others effectively self-incompatible. One of those seven, *U. vi*, which had produced a few self seedlings prior to the reported experiments, never formed full seed during the 4 years of trials. Our definition of effectively self-incompatible refers to species that produced less than 1% full seed from selfing. The probability of finding self seedlings in the progeny of these species would be very low. Of the 4 species scored as self-compatible, *U. gla* produced slightly more than 1% full seed, *U. ca* and *U. pa* about 4% and *U. ja* even more than 10%. For *U. pa* SANTAMOUR (1972) had found a value of 6.6% to 10.3% self-compatibility, rated as full seeds, which is very close to our finding. However, variability among individuals for this trait was pronounced. We observed a specimen of *U. pa* (PA1-VB) growing in an urban garden producing abundant crops of full seed even though the closest pollen source was 6 km away (all the other species of elm found in the country flower in spring). Isolating flowers of this specimen by pollination bags showed it to be highly self-compatible, producing more than 30% full seeds (*Tab. 3*). However, in seedling terms, this tree produced 6% to 7% self compared to 25% to 30% seedlings from the intraspecific cross. Another specimen of *U. pa* selected by SANTAMOUR (1984, 'Dynasty', NA36533), a well differentiated Korean provenance, produced less than 1% full seed by selfing. Other specimens of *U. pa* produced intermediate amounts of selfed seed. The selfing of 5 individuals of *U. pa* in two consecutive years (*Tab. 3*) showed significant variation among clones in seed set and significant clone x year interaction. This

Table 3. — Data on self-fertility of 5 genotypes of *U. partifolia* collected in 1986 and 1987 and expressed as percentage of full seeds on flowers. Data followed by different letters are significantly different by LSD procedure (P = 0.05)

Self fertility in U. parvifolia

clones	1986 % seeds/fls.	1987 % seeds/fls.	difference 1987 - 1986
NA36533	3.1 a	0.1 b	- 3.0
PA1-5	3.4 b	5.2 bc	+ 1.8
PA1-1	4.4 bc	7.0 c	+ 2.6
PA1-2	12.6 d	8.1 cd	- 4.6
PA1-VB	30.5 e	35.8 e	+ 5.3

ANOVA

Source of variation	d.f.	Mean squares	F
Years	1	17.00167	2.919
Clones	4	944.21000	162.119**
Clones X Years	4	50.96722	8.751*
Error	16	5.82417	

* significant at $P < 0.05$
** significant at $P < 0.01$

means that the environment can act selectively on individuals and change their selfing rate.

Conclusion

In our study, crossability barriers among tested species were weak or not present, but the success of several combinations depended on favorable male-female interactions. This result may well explain the variable results reported in previous studies. In fact, choosing the individual parent appears to be decisive for the success of many interspecific crosses. The overall lack of interspecific incompatibility observed here is in contrast with hybridization studies in *U. americana*, where strong interspecific barriers have been observed (AGER and GURIES, l.c.; BOB et al., 1986). A unique barrier was found in crosses with *U. lae*: when using this species as female parent only the combination with *U. vi* was successful, but the many apparently normal seedlings obtained died after about 3 months as a consequence of physiological disorders. This documents a case of post-germination barrier operative in species of the *Blepharocarpus* section which is known to be genetically isolated from the other sections of the genus (HEYBROEK, 1968; TOWNSEND, 1975). For this reason treatments that could be applied to overcome the stigmatic barriers identified in one of the two species belonging to this section (AGER and GURIES, l.c.) may well be insufficient to obtain hybrid elms.

Half of the species under study showed self-compatibility, which was particularly pronounced in *U. pa* and *U. ja*. Variation in selfing ability was high among individuals and the environment also played a role. It may be interesting to add that in some elm species selfing was

enhanced when they were co-pollinated with dead pollen of another elm species (Alan A. AGER, personal communication, and unpublished data from our experiments on 'mentor pollen'). Thus, in some crosse that are actually incongrous, seed set may be enhanced over self controls, which makes it appear that the hybridization worked. It is therefore essential to monitor selfing and to authenticate the hybrids (in the breeding work as is commonly done in elm) especially when trying the effectiveness of 'mentor pollen'. In some cases morphological characters are suitable, but biochemical markers may be more reliable. For this purpose the quantitative determination of elm leaf flavonoid glycosides by HPTLC followed by discriminant analysis looks promising in identifying hybrid progeny of controlled and natural cross-combinations (HEIMLER et al., 1990a, 1990b, and another work in preparation).

Acknowledgements

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Variation of Pollen Contamination in a Scots Pine Seed Orchard

By R. YAZDANI[1]) and D. LINDGREN[2])

[1]) Department of Forest Genetics, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

[2]) Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

Summary

A grafted Scots pine seed orchard at latitude 62 °N at the Baltic coast was studied for the occurrence of pollination from nonorchard origin (contamination). Altogether 2318 seeds were analyzed by means of isozyme embryo