Review. Reproductive ecology of riparian elms

J. C. López-Almansa*

Departamento de Ingeniería Agroforestal y Cartográfica. Universidad Católica de Ávila. 05005 Ávila. Spain

Abstract

This paper review our current knowledge of the reproductive ecology in the genus *Ulmus*, for which few investigations has been conducted and relatively little information is available. In the genus *Ulmus*, as in other riparian or sub-riparian genera, trees reproduce either vegetatively (by sprouting) or sexually. These mechanisms work differently. Sprouting permits colonization of open areas close to the trees, being especially frequent from large trees following death of their stem. Sprouting from the surviving roots of trees affected with Dutch Elm Disease is abundant in Spanish *Ulmus minor*. Sexual reproduction is infrequent, and requires some special conditions to be successful. It probably occurs coincidently with massive river floods that remove riparian vegetation and deposit a fertile muddy bed suitable for seed germination. Many *Ulmus minor* genotypes do not produce seed owing to seed abortion and other mechanisms. As a result, two gender-classes, male and cosexual, are presumably present in Spain, although this requires confirmation. A hypothesis trying to explain female sterility as the result of a trade-off between sexual and vegetative reproduction has been recently proposed, but it requires to be confirmed. Further research is also necessary for a better knowledge of flooding effect on elm regeneration and for evaluating other aspects of its reproductive ecology.

Key words: female sterility, flood, riparian ecology, seed, sexual reproduction, sexual dimorphism.

Resumen

Ecología reproductiva de los olmos de ribera

Este artículo revisa el actual conocimiento de la ecología reproductiva en el género *Ulmus*, del que hay poca información disponible. Las especies del género *Ulmus* se reproducen, al igual que ocurre en otras especies riparias o sub-riparias, tanto sexual como vegetativamente (a través de renuevos). Estos mecanismos son efectivos en situaciones distintas. Así, los renuevos permiten la colonización de zonas abiertas próximas a los árboles, y son especialmente frecuentes tras la muerte del tronco principal de grandes árboles, como se ha observado en España, donde el rebrote a partir de raíces supervivientes de ejemplares de *Ulmus minor* afectados por la grafiosis es muy abundante. La reproducción sexual, por otra parte, es infrecuente, y requiere ciertas condiciones especiales para ser exitosa, teniendo lugar, probablemente, cuando se producen grandes inundaciones que eliminan la vegetación riparia y depositan una fértil capa de barro adecuada para que las semillas germinen. Gran número de genotipos de *Ulmus minor* no producen semilla debido a distintos mecanismos, entre los que destaca el aborto de la semilla. Como consecuencia, en España se encuentran presumiblemente dos géneros distintos de árboles en relación con sus características sexuales, masculino y cosexual, aunque esto requiere confirmación. Recientemente se ha propuesto una hipótesis que trata de explicar la presencia de esterilidad femenina como resultado de un equilibrio entre la reproducción sexual y vegetativa, pero esto requiere igualmente confirmación. También es necesario realizar nuevos estudios para conocer mejor el efecto de las inundaciones en la regeneración del olmo y para evaluar otros aspectos poco conocidos de su ecología reproductiva.

Palabras clave: esterilidad femenina, inundación, vegetación riparia, semilla, reproducción sexual, dimorfismo sexual.

Introduction

Knowledge of reproductive ecology is a key element for the understanding of ecological dynamics of a tree species, and particularly for the study of succession and temporal relationships with other plant species. It also has importance in forestry with respect to forest regeneration. However, the study of reproductive ecology in trees presents some major difficulties that discourage this kind of works, especially when these species lack great economical interest.

The genus *Ulmus* has a wide distribution in the Northern hemisphere, with about 40 species (Buchel, 2000). The centre of distribution is Eastern Asia, especially China and the neighbour countries, where about 30 species are present. In South-eastern Asia, species of elms extended to Sumatra and Sulawesi. In Europe and the Mediterranean basin four or fives species are present ranging from Scotland and Scandinavia to Algeria and Near East. In America, about 10 species of this genus are distributed from eastern North America southward into Mexico, Central America and Colombia (Richens, 1983; Buchel, 2000).

Within this wide range of distribution, interspecific differences exist in ecological behaviour, from tropical moist mountain forest, e. g. *Ulmus mexicana* in Mexico (Todzia and Panero, 1998; Pérez-Cálix and Carranza González, 1999), to temperate forests, e. g. *U. glabra* in Europe (García-Nieto *et al.*, 2002; Romo Díez, 1988). However, most show a clear preference for water-rich soils, and elms of many species are distributed near rivers, streams or on floodplains (e.g., *U. minor* and *U. laevis* in Europe, *U. americana* and *U. rubra* in North America, and *U. davidiana* and *U. parvifolia* in Asia).

Intrinsic features of riparian habitat restrict the ecological behaviour of the inhabiting plant species. Vegetation in riparian habitats responds to gradients in fluvial dynamics, soil moisture and floods (Malanson, 1993). These gradients determine the characteristics of plant communities and their succession mechanisms.

Presence of aperiodic floods, which causes both plant death and new reproductive opportunities, is the main disturbance in riparian habitats, and constitutes a key factor in riparian ecology. The intermittent recurrence of large floods is a major determinant of the age structure in woody riparian plants (Stromberger *et al.*, 1991; Johnson, 1994; Cordes *et al.*, 1997; Cooper *et al.*, 2003). The disturbance regime in a particular forest usually consists of a complex mixture of infrequent, large-scale events and more frequent, small-scale events (Perry, 1994). According to Brinson (1990), power and frequency of inundation are inversely proportional and exist in a continuum from infrequent high-power floods that affect the whole floodplain to more frequent low-power floods that influence only the area adjacent to the riparian channel. Seed germination and seedling survival respond positively on the flooding regime, and so the frequency of reproductive opportunities decreases with increasing distances from the river or stream (Barsoum, 1998). As a consequence, the distribution of vegetation on floodplains is strongly influenced by spatial and temporal patterns of flood inundation (Niiyama, 1990; Duncan, 1993; Towsend, 2001).

As a response to the environmental uncertainties, riparian woody species frequently present a number of characteristics allowing them to optimise reproductive effort. Most significant are trade-offs between sexual and asexual reproduction, timing of seed dispersal, mechanisms of seed dispersal, and dormancy (Naiman and Décamps, 1997).

Little research has been specifically made for understanding the reproductive ecology and regeneration in riparian elms, although it is an important matter for the natural persistence of elm stands, for the establishment of elm stands using elms from breeding programmes in natural or semi-natural habitats, and for riparian restoration. In this work, reproductive characteristics of riparian elms are revised.

Reproduction in riparian elms

Similarly to other riparian species, elms present a double reproductive strategy, sexual and asexual, to avoid the risk and to take advantage of the opportunities when the floods appear.

Vegetative regeneration is accomplished, in natural conditions, mainly through sprouting and root suckering, although in cultural conditions much experience has also been acquired using cuttings (Dorand and Mackenzie, 1949; Bretz and Swingle, 1950; Schreiber, 1963; Tchernoff, 1963; Mittempergher *et al.*, 1991). Sprouting is especially frequent at short distances, near the trunk, and at least *U. minor*, *U. americana*, *U. rubra*, *U. serotina* and *U. thomasii* have been reported as showing such a habit naturally or as a response to stem or root injuries (Ley, 1910; Richens, 1983; Burns and Honkala, 1990). Asexual regeneration is continuous, with sprouts arising yearly from the roots. Survival is high for suckers, especially in drought and under flooding conditions, due to their connection to the roots of the parent tree. They also respond to increased light in canopy gaps.

Another remarkable characteristic of elm sprouting is their great development as a response to trunk mortality due to Dutch Elm Disease (DED), at least in *U. minor* in Spain. Thus, numerous sprouts and suckers can frequently develop into new elm trees from the surviving roots, though susceptibility of these new trees to DED remains high.

Sexual reproduction is effective mainly at middle and long distances, due to the high capability of seed dispersal. Successful seedling establishment is aperiodical, because it requires the presence of a flooding just in the moment of seed dispersion. Most elm species flower in late winter or spring, dispersing their seed in the spring or early summer (Burns and Honkala, 1990; Mittempergher and La Porta, 1991), but in two American species (*U. serotina* and *U. crassifolia*) seed dissemination is known to occur in the Fall (Sargent, 1949; Burns and Honkala, 1990), and during mild winters in South-eastern North America for *U. americana*.

Elm easily colonize new habitats as indicated by their light, well-dispersed fruit, and the histochemistry of seed. Elm samara posses a great dispersal capacity as indicated by Streng *el al*. (1989), who found, in a floodplain forest in Texas, that *U. americana* was, with *Platanus occidentalis*, the best dispersed species. Elm samaras can be fall *in situ* or be carried by wind and water, due to their buoyancy (Burns and Honkala, 1990), although zoochory has also been suggested in *U. alata* (Snow, 1990). The distance of seed dispersal by gravity and wind from the parent tree is about 91 m for *U. americana* and 40-45 m in *U. thomasii*, although some samara in *U. americana* may be carried 400 m or more from their source (Burns and Honkala, 1990). Hanson *et al*. (1990) studied wind-dispersal function of some species seed, including *U. americana*, according to theoretical models (Fig. 1).

Hydrochory, a frequent mode of seed or fruit dispersal in riparian plants by flowing water, plays a important role in plant community development (Nilsson *et al*., 1991). It has been reported as a means of samara dispersal in *U. americana*, *U. alata*, *U. rubra* and *U. thomasii* (Schneider and Sharitz, 1988; Burns and Honkala, 1990; Malanson, 1993), and is probably responsible for the great post-glacial spread of *U. minor* (Thébaud and Debussche, 1991). In *U. thomasii*, hidrochory is responsible for seed concentration along the banks of streams and lakes (Crow, 1990). As a consequence of hidrochory, the greater a flooding is, the greater the
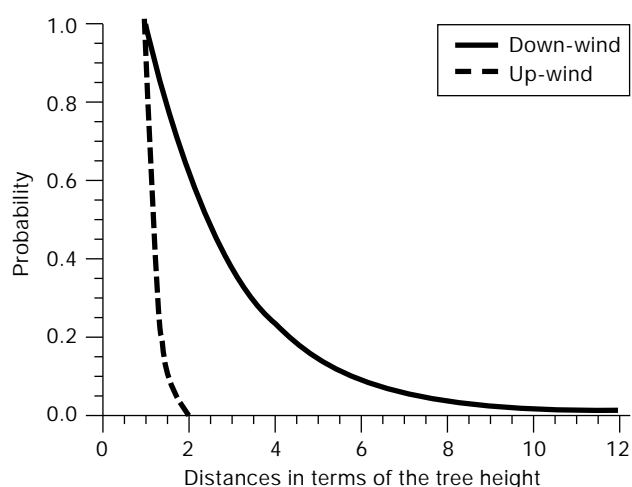

Figure 1. Dispersal functions for *Ulmus americana* seed based on anemochory rules (redrawn with data from Hanson *et al.,* 1990).

distances that can be reached by the seeds are, allowing elms to exploit reproductive opportunities. Consequently, when seed production coincides with a great flood, elm samaras can be transported downstream for many kilometres, and germinate upon the return of floodwater to their channels. In this situation, when wet mud has been deposited and competition removed, the opportunities for seed germination and seedling establishment are optimal.

The chemical components of elm seed also favour their colonizing potential. The seed reserves are mainly proteins, whereas the mature embryo lacks starch (López-Almansa *et al*., 2004). According to Bonner (1971, 1974), *U. alata*, *U. americana* and *U. serotina* have low carbohydrate contents, lipids and proteins being the predominant reserves (Table 1). Due to this shortage of carbohydrates, the onset of photosynthetic reaction early after germination is necessary for the young seedling to survive and to undergo rapid growth, thanks also to their protein content. In *U. minor*, seedlings are frequently more than 1 m tall after the first growing season, at least in nursery conditions. For taking advantage of these favourable growth conditions, high luminosity levels are required, e.g. for *U. alata*, con-

Table 1. Chemical contents of the seed of three North American elms species expressed as percentage of dry weight (after Bonner 1971, 1974). Proteins were obtained by multiplying total nitrogen by 6.25

Species	Lipids	Proteins	Carbohydrates	Starch
Ulmus alata	15.3	27.4	8.9	NO
Ulmus americana	7.9	14.8	11.0	NO
Ulmus serotina	19.0	24.1	7.4	NO

sidered a light demanding species and an invader of forest openings, old fields and rangelands, and for *U. americana* (Burns and Honkala, 1990).

Apparently, water transport could improve seed germination in elms. Hosner (1957) found that seeds of *U. americana* soaked for periods from 4 to 32 days consistently germinated at a higher rate after being removed from water than did unsoaked seeds. DuBarry (1963) found that *U. americana* seeds increased their germination potential to 76% while immersed in water for a 30-days period, as compared to 44% in the controls. Bey (1990) indicates that American elm seeds can remain on flooded ground for as long as one month with little adverse effect on germination, except possibly where siltation occurs in flooded bottoms.

Flood frequency, duration and magnitude directly influence litter distribution through transportation, concentration, physical destruction and sediment deposition (Bell and Sipp, 1975). Litter influences physical and chemical environment, affecting particularly to germination and seedling establishment (Facelli and Pickett, 1991) because it impedes or retard the plant to reach the mineral soil (Grime, 1979; Pearsson *et al.*, 1987; Facelli and Pickett, 1991). This effect can be specially important in colonizing species with little carbohydrates storage, such as the elm. The amount of organic detritus at the soil level is especially high in streamside forests, being in the upper range of values reported for deciduous forests (Bell and Sipp, 1975). This organic detritus can interfere with seed germination and seedling recruitment (Van der Valk, 1986; Langlade and Décamps, 1994). Litter removal in riparian habitat was found to enable seed germination (Walker *et al.*, 1986). In this respect, Hosner and Minckler (1963) noted that flooding washed down the soil to its mineral layer, forming good seed beds as needed by some riparian species. Day *et al.* (1988) found that litter removal by flowing water paves the way for the establishment of tall species («gap colonizers»). Floods also removes herbaceous and woody vegetation, thus lowering competition, increasing luminosity, and allowing a greater photosynthetic rate (Naiman and Décamps, 1997). Another significant effect of floods is the deposition of a wet mud by providing the moisture essential for seed germination (Kramer and Kozlowsky, 1979; Bonner, 2003) and seedling establishment, as in the case for most riparian species (Bradley and Smith, 1986; Hughes 1990). In opposition, floods constitute also a risk for the young seedlings because they might be killed by unexpected floodings (Streng

et al., 1989; Malanson, 1993). And so, floods in riparian habitats are an opportunity both for life or death, depending on the season of occurrence, the topography and the physiological condition and size of the plant.

In Hokkaido forest in Japan, Seiwa (1997) found that the presence of litter inhibits germination and seedling emergence in *U. davidiana* var. *japonica*, suggesting that Japanese elm regeneration should be confined to sites undergoing large disturbances at both canopy and soil level. The strong inhibition of seedling emergence by litter can be due to either mechanical barriers or dark-induced dormancy (Seiwa, 1997), which is maintained in *U. davidiana* var. *japonica* seeds kept indefinitely in darkness, as also probably in *U. americana* and *U. rubra* (Rudolf, 1937; Dirr and Heuser, 1987). Seeds that are dispersed in a dark understorey remain dormant until they are exposed to light. As a consequence, seed germination and seedling emergence are controlled by spatiotemporally-changing environmental conditions such as litter accumulation and variation in the presence of canopy leaves, provoking two periods of seed germination in the seeds. At the forest edge, which is exposed to high luminosities, the seeds germinate in the summer immediately after their dissemination, while in the poorly lit understorey germination is inhibited until the following spring, before the vegetative budburst.

Jones *et al.* (1994) found that in the Savannah River floodplain, South Carolina, *Ulmus americana*, a typical riparian elm, exhibited a basal area of 0.88 m²/ha in a large flooded site, versus 0.07 m²/ha in a large unflooded site. However, *Ulmus alata*, a less typically riparian species which prefers mesic forests that are somewhat elevated above nearby flood plains, presented a greater basal area in the large unflooded site (1.76 m²/ha) than in the large flooded site (0.41 m²/ha). The data regarding seedlings are still of a greater significance. Thus, the density of *Ulmus* spp. seedlings (smaller than < 1 m) was 0.08 seedlings/m² in the large unflooded site versus 2.20 seedlings/m² in the large flooded site (Jones *et al.*, 1994). In a study made at a forest in Neches river floodplain, Texas, seedlings of *Ulmus americana* grew at lower elevations (Streng *et al.*, 1989), in microsites consequently more frequently flooded. These authors also found that seedlings of this species tended to emerge earlier in frequently flooded microhabitats.

Streng *et al.* (1989) found a significant correlation between numbers of seed and of newly germinated seedlings in *U. americana*, but none with established se-

edlings by the first and second autumns after seed germination, due to the great mortality of the young seedlings. Seedling mortality in *U. americana* decreased significantly (p < 0.0001) with seedling age (Streng *et al*., 1989). The degree of seedling survival increased with increasing distances from an adult American elm. The cause of this effect is not well known, but it was apparently partially related to grazing, as shown by the fact that the age at which a seedling was first grazed declined with increasing distance from elm trees (Streng *et al*., 1989).

Another important cause of mortality in elms seedlings was floods. Depending of the time of flooding, the deleterious effect varied according the various species present in this Texas floodplain forest (Streng *et al*., 1989). Late floodings (May-June) killed most of the newly germinated seedlings of American elm, whereas early floodings (February-March), prior to elm seed spread and germination, removed the established, competitive plants of other species. According to Newsome *et al*. (1982), soil flooding induced in young *Ulmus americana* seedlings several physiological, morphological and growth changes, including stomatal closure, accelerated ethylene production, stem swelling, formation of hypertrophied lenticels and inhibition of growth of leaves, stems, and roots.

Some riparian elms have peculiar problems related to sexual reproduction, notably regarding female sterility and the abundance of empty samara, that have been long well known. The earliest references to the absence or scarcity of seed in elm are those from Roman authors such as Columella and Pliny the Elder in the I century (Columella, *De re rustica*; Plinius Se-

cundus, *Historia Naturalis*). Columella says that Tremellius Scrofa was mistaken saying that Atinia elm (probably *U. minor* var. *vulgaris*) did not produce samaras, though he recognized that Atinia elm generally displayed just a few samaras generally concealed by the leaves. Pliny the Elder indicates that Atinia elm produced no seed. Both authors agreed that this fact caused the use of cuttings for elms propagation. Stokes (1812), describing *U. surculosa* (considered within *U. minor* var. *vulgaris* according to Richens, 1983) indicated that its seeds rarely if ever ripen. This datum was lately confirmed by Ley (1910). Laguna (1883) reported that *U. minor* in Spain produced a large percentage of empty samaras.

In *Ulmus* x*hollandica* var. *belgica*, Leliveld (1935) attributed the presence of empty samaras to the absence of cross pollination. Development of fruits without ovule fertilization has also been found in *U. minor* (López-Almansa and Gil, 2003). A substantial proportion of the empty samaras, however, has its origin in seed abortion (López-Almansa *et al*., 2003, 2004). In some individuals, seed abortion is general for all the seeds. As a consequence, *U. minor* could behave, at least in some Spanish populations, as a functionally sub-androdioecious species, that is, in the same population coexist two gender-classes: cosexual trees, with both pollen and seed production, and female-sterile trees, that are functionally male, and produce no seed (López-Almansa *et al*., 2003).

Phenotypic femaleness at the elm clonal bank at Puerta de Hierro, close to Madrid, in 2001 and 2002 and at the natural elm-stand at Rivas-Vaciamadrid, in 2002, is shown in figure 2. Phenotypic femaleness es-
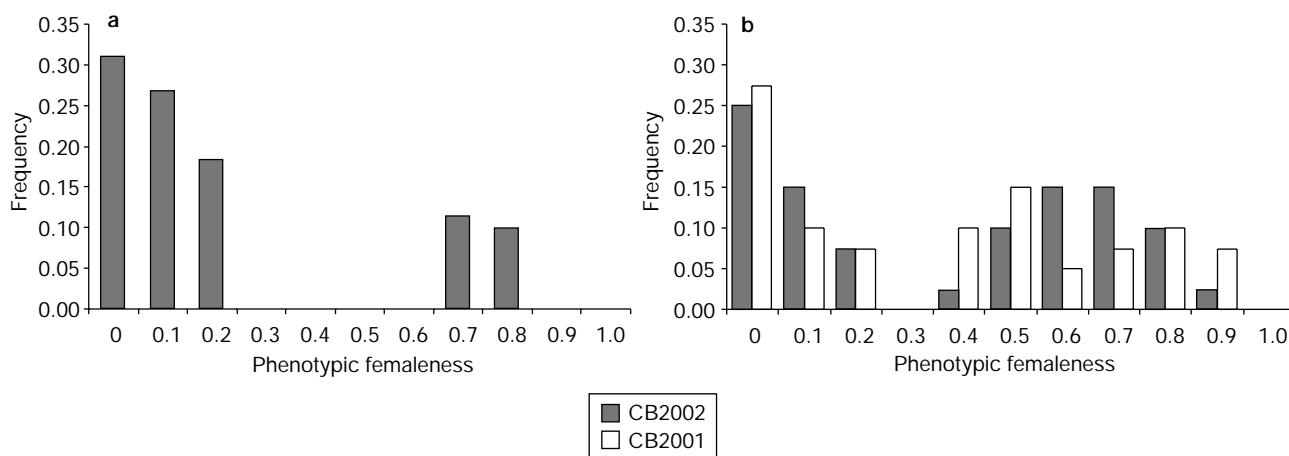

Figure 2. Distribution of phenotypic femaleness in *Ulmus minor* at (a) a semi-natural population at Rivas in 2002, and (b) the clonal bank at Puerta de Hierro in 2001 and 2002 (after López-Almansa *et al.,* 2003)

timates the proportional contribution to male and female function in every individual (Lloyd, 1980; Lloyd and Bawa, 1984). In both sites it was observed that a number of individuals produced very little or no seed at all. Other individuals, however, reproduce both through the male and female functions.

Evolutionary models for androdioecy consider that it is necessary that pollen production be at least twice as high for female-sterile individuals than for cosexual ones for the male to be maintained in the population (Pannell, 2002). However, it seems unlikely that female-sterile elms produce twice the pollen that hermaphrodites ones do. For explaining this apparent contradiction, the hypothesis that female-sterile individuals could maintain as a result of a trade-off between sexual and asexual reproduction has been proposed (López-Almansa *et al.*, 2003). According to this hypothesis, sexual reproduction is successful only in rare occasions, due to the necessity of seed dissemination being coincidental with a large flood. In such a situation, the absence of seed production could produce a greater reserve storage in female-sterile trees, allowing them to use these savings for a greater growth, survival or vegetative regeneration. As a consequence, the female-sterile genotypes, greater in size or developing a greater number of stems, could have a greater pollen production than the cosexual trees in those occasional episodes of sexual reproduction, and so maintain in the population. Alternatively, a greater survivorship in female sterile elms could allow them to stay for a greater span and, consequently, to reproduce effectively for a longer time.

The great effort required by elms for producing seed is indicated by Ley (1910). According to this author, in England in 1909, many individuals of *Ulmus scabra* Mill., and to a less extent *U. vegeta* and *U. glabra* Mill., non Huds., were rendered leafless, and almost if not quite killed, by the effort required to ripen a very unusual crop of seeds, while *U. surculosa* Stokes (an abortive elm) did not suffer at all. These data indicate that savings in abortive elms might be considerable.

In Rivas-Vaciamadrid elm stand, a different spatial distribution exists with respect to the trees gender (Fig. 3). In this stand, cosexual elms grow at the periphery and female-sterile trees generally are in the central area. That juxtaposition is also consistent with the hypothesis explained above. In the forest edge and at middle distances, the trees probably grew from seeds, and consequently they could have inherited their ef-

Figure 3. Distribution of cosexual and female-sterile elms in the Rivas-Vaciamadrid elm stand. Black dots indicate trees that were not studied (modified from López-Almansa, 2002).

fective seed production maternally. The stand centre, however, could be occupied by female-sterile elms derived from sprouts.

Finally, also isozyme studies suggest that sprouting is probably greater in female-sterile trees in the Rivas-Vaciamadrid elm stand (Maria del Carmen Dacasa, unpublished results), which is consistent with the statement by Ley (1910) that those elms with a poorest sexual reproduction exhibited the greatest suckering.

Could *U. minor* be effectively considered an androdioecious species? Here arises a problem regarding the taxonomical classification of elms and the historical use and transport given to them by humans. As seen above, *U. surculosa* Stokes, included by Richens (1983) in *U. minor* Mill. var. *vulgaris* (synonym *U. procera* Salisb.), is known for having abortive seeds and profuse suckerings (Ley, 1910). Also other authors indicate the lack of seed production in this taxon, which is frequently cited under different names (e.g. *U. campestris* aut., non L., in Henry, 1910). The taxonomical status and natural distribution of *U. minor* var. *vulgaris* assumes great importance for explaining the ecological sig-

nificance of female sterility in *U. minor*. If *U. minor* var. *vulgaris* is the only female-sterile elm, and simply a clone or a small number of closely related abortive, well-suckering clones that were widely distributed by humans by way of asexual regeneration, as proposed by Heybroek (2003), then the presence of mixed stands comprised by native cosexual elms and foreign female-sterile elms would lack ecological significance. Certainly, such a stand would currently work as an androdioecious population due to the intercrossability between most elm species (Johnson, 1946; Collins, 1967; Hans, 1981; Mittempergher and La Porta, 1991), but it would have no evolutionary significance. However, if seed abortion is not restricted to a clear taxonomical monophyletic category, or if female-sterile elms would naturally coexist with cosexual elms, then their evolutionary significance would persist.

Two main hypothesis regarding natural distribution of *U. minor* var. *vulgaris* exist. According to Richens (1983), both *U. minor* var. *minor* and *U. minor* var. *vulgaris* are native to Spain. In Britain, however, *U. minor* var. *vulgaris* (the English elm) would be exotic, and likely introduced from Spain or France in prehistoric times. Heybroek (2003), however, considers that *U. minor* var. *vulgaris* is not indigenous to the western Mediterranean basin but only in the eastern Mediterranean. According to this hypothesis, it could have arrived in Italy and Iberia from Greece as a complement for the vine culture, due to the extensive use by Romans of elms as a support for the vine.

Knowledge of the taxonomical status of female-sterile elms is so essential for elucidating this question. According to our current data, a great number of the female-sterile elms in Spain, including probably those at the Rivas-Vaciamadrid elm stand, could be effectively considered *U. minor* var. *vulgaris* on morphological grounds. However, in the elm clonal bank at Puerta de Hierro in Madrid, female sterility has been also found in some elms that are morphologically classified as *U. minor* s.l. and *U. minor* var. *minor*.

A finer analysis could be made using both molecular and sexual characteristics of the same trees. This study has been conducted on 18 elms from the clonal bank at Puerta de Hierro in Madrid that were molecularly characterised with RAPDs and I-SSRs by W. Goodall-Copestake, M. L. Hollingsworth, P. M. Hollingsworth, G. I. Jenkins and E. Collin (unpublished data) and with sexual characteristics studied for at least two years by López-Almansa *et al.* (2003). Figure 4 shows the results of combining both sets of data.
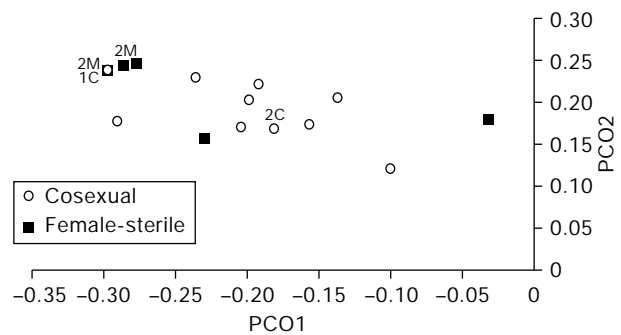

Figure 4. Principal Co-ordinated Analysis of 18 Spanish *Ulmus minor sensu latissimo* based on RAPD and I-SSR analysis (after W. Goodall-Copestake, M. L. Hollingsworth, P. M. Hollingsworth, G. I. Jenkins and E. Collin, unpublished data) related to their gender characteristics (after López-Almansa *et al.,* 2003). A number followed by a letter indicates the presence of various cosexual (C) or female-sterile (M) elms in the same position. PCO Analysis was realized over 535 European elms from three species *(Ulmus minor* Mill. *sensu latissimo, U. glabra* Huds. and *U. laevis* Pall.).

According to these data, five out of seven female-sterile elms concentrate in the *U. procera* cluster, in the left upper square of figure 4, with the two other female-sterile trees (UPM 044 and UPM 045), both collected at the same locality, occupying distant points. It is also remarkable that two female-sterile (UPM 030 and UPM 201) and one cosexual (UPM 159) elms in the *U. procera* cluster, collected at distant localities, present the same molecular characterization and could not be segregated according to the Principal Co-ordinated Analysis. Though these data might indicate that female-sterile and cosexual elms are widely distributed through all the molecular spectrum of *U. minor* in Spain, they are however not conclusive, and a further research is necessary. Particularly it would be necessary to test over a longer period the reproductive characteristics of the two female-sterile trees outside the *U. procera* cluster, especially through controlled crosses. It would be also necessary to increase the number of characterised elms.

The problem of judging the biological significance of reproductive characteristics in *U. minor* lies in the complex taxonomical nature of European elms (Richens, 1983; Armstrong and Sell, 1996). The most generalised treatment, at least in continental Europe, considers the presence of only three species in this continent, *Ulmus laevis* Pall., *Ulmus glabra* Huds. and *Ulmus minor* Mill. *sensu latissimo*, the latter represented by a number of varieties, and some hybrids (Richens, 1983). Other authors, mainly in the United Kingdom, recognize however a notably larger number

of species (Ley, 1910; Melville, 1939; Armstrong, 1992). One of these micro-species, *Ulmus plotii* Druce has been recently found to be probably a single, vegetatively propagated clone (Coleman *et al.*, 2000). A most accurate molecular analysis is necessary for knowing the actual nature of European elms. Before such an analysis could be evaluated, it would be critical to answer the question of androdioecy in *U. minor*.

The origin of female-sterility in *U. minor* is multiple (López-Almansa *et al.*, 2003). The primary cause is seed abortion in a great number of individuals. Essentially, the origin of embryo abortion is a miss-co-ordination between endosperm and embryo development that provokes a delay in the embryo development and, finally, the seed shrinkage and the embryo death when the seed dries later in the season (López-Almansa *et al.*, 2004). The second cause of female sterility is the presence of gynoecial necrosis, preventing fertilization and fruit formation. The last cause is the presence of empty, unicarpelled gynoecia (López-Almansa and Gil, 2002). Depending on the genotype, the proportional importance of each cause is different (Fig. 5). Frequently none of these causes of female sterility is absolute, and sometimes a small number of viable seed is present in the female-sterile trees.

An open question requiring a further research is how much the female sterility is affected by environmental, and particularly climatic, conditions. Slight differences in the degree of seed abortion in different years has been found on some female-sterile individuals

(López-Almansa *et al.*, 2003, 2004). A possible explanation could be related to the mechanism of seed abortion. For instance, it is possible that in wetter springs, with high humidity, the seed drying process could be delayed, permitting, in late-aborting individuals (López-Almansa *et al.*, 2004), a few seeds to overcome the abortive mechanism and complete maturation. Simultaneously, in those wetter springs, floods could be more frequent, and best condition for seed germination and seedling establishment present. The final consequence, then, would be that generally female-sterile elms could exceptionally produce some seeds in years that are favourable for sexual reproduction. But currently this is only a hypothesis requiring experimental demonstration.

Conclusions

Reproductive ecology in elms has been a briefly treated issue in the scientific literature. The origin of this situation is multiple. First, the study of sexual reproduction in trees is made difficult by their great size and the extended length of time before they reach sexual maturity. Second, elms receive little economical interest, and consequently sufficient funds have not been available. And finally, and perhaps more important, the conversion if riparian habitat to agriculture, coupled with the spread of Dutch Elm Disease, has provoked the disappearance of most natural elm-stands.
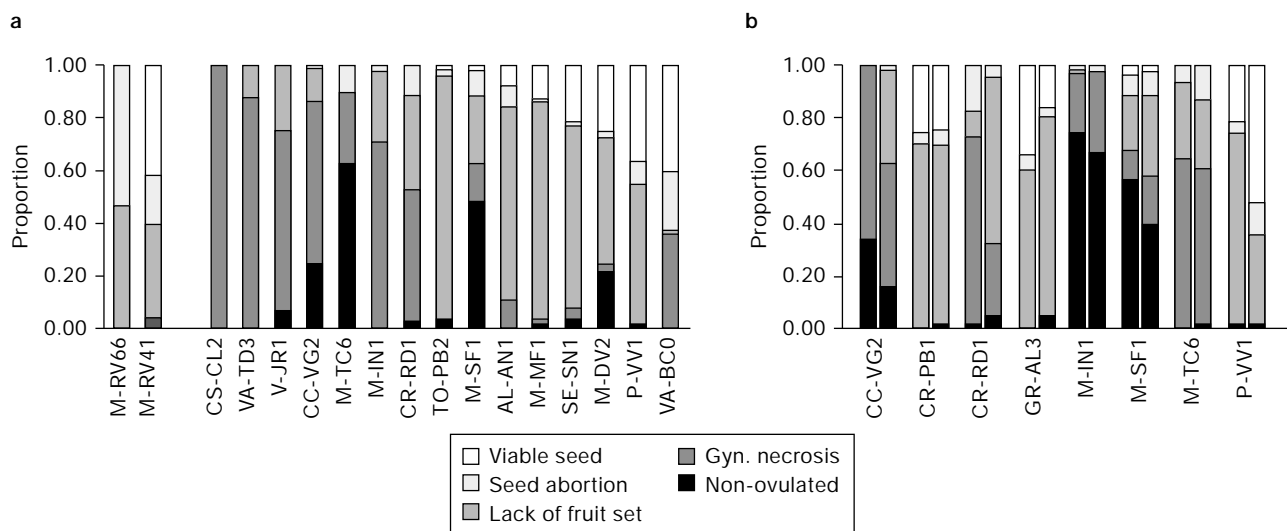

Figure 5. Contribution of factors affecting during 2002 the loss of phenotypic femaleness in Ulmus minor in (a) two individuals (M-RV66 and M-RV41) at Rivas-Vaciamadrid and 15 individuals at Puerta de Hierro, Madrid, and (b) in the lower and upper limbs in eight individuals at Puerta de Hierro, Madrid (left and right columns, respectively) (after López-Almansa *et al.,* 2003).

Knowledge of the dynamics of elm stands is scanty. Little is know on sprouting and asexual regeneration in natural conditions. Seed dispersion mechanisms, and particularly hydrochory, requires more accurate studies for a better understanding of elm colonization in new areas. Environmental conditions (light, soil moisture, competition) for seed germination and seedling establishment in natural conditions are well known only in *Ulmus davidiana* var. *japonica* (Seiwa, 1997). Importance of dormancy and seed survival has been little studied. Effects of floodings on seedlings dynamics are also poorly determined, and only Streng *et al*. (1989) have studied them. Such studies have a great interest not only for theoretical but also for practical purposes. Dam and canal constructions have greatly affected floods regime, and a better knowledge of the floods ecology is necessary for the floodplains conservation.

It is also important to verify the actual importance of female sterility on the reproductive structure of the elms. Currently this female sterility has been found only in *Ulmus minor* s.l., but it would be interesting to determine if it is present in other species of the genus. A priority objective would be to study the taxonomic and molecular nature and the geographical distribution (historical and present) of female-sterile elms to obtain definitive conclusions regarding androdioecy. It would also be interesting to test the hypothesis that female sterility is maintained as a consequence of trade-offs between sexual and asexual reproduction.

Another interesting question open to research would be the possible relationship between DED and current gender characteristics of *Ulmus minor*. If the economy of energy made through seed abortion confers greater resistance and survival, or more copious suckering, to female-sterile elms, then appearance of DED could have biased the gender relationship toward a predominance of aborting trees. This would be consistent with the occurrences in Spain of many small stands of elm, arising from sprouts after DED, comprised exclusively by female-sterile trees. However, to test this hypothesis would be most difficult and would require a long-term research.

Knowledge of reproductive ecology in elms is critical for the future establishment of elm stands by afforestation, and also for breeding programmes. We need to study the few surviving elm stands to determine reproductive and genetic structure. And we also need to find better DNA markers to identify the stocks that are used in research. Due to the current spread of Dutch Elm Disease, this work is difficult, and only a world wide research, covering different species, populations and countries, could help us to a better understanding of the reproductive ecology of riparian elms, and so to contribute to the restoration of elm forests.

Acknowledgments

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