

Empty Samara and Parthenocarpy in *Ulmus minor* s.l. in Spain

By J. C. LÓPEZ-ALMANSA¹ and L. GIL

Unidad de Anatomía, Fisiología y Genética Forestal, ETSI Montes, Universidad Politécnica de Madrid, Ciudad Universitaria, E-28040 Madrid (SPAIN)

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Summary

The relationship between empty samara production and parthenocarpy in *Ulmus minor* in Spain is analysed. The average percentage of empty samaras in the field between 1990–2001 was 78.9%, calculated over a sample of 321 trees, whereas it was 41.2% in a clonal bank of elm sited in Puerta de Hierro (Madrid, Central Spain). Differences were statistically significant ($p < 0.001$). There was also significant differences in seed yield between 25 elms in the field and their clonal copies in the clonal bank ($p < 0.001$). Presence of empty samaras was frequent on branches where cross pollination was prevented by setting paper bags. It is deduced from this that at least a part of the empty samaras produced in the field is caused by the parthenocarpic development of fruit in populations where genetic variability is low.

Key words: Elm, empty fruit, parthenocarpy, pollen, pollination, genetic variability.

Introduction

Production of empty fruit or seed is a very frequent fact in a great number of plant species, both gymnosperms and angiosperms. There are many causes of the formation of empty fruit or inviable seed. The most relevant are seed abortion (STEPHENSON, 1981; WIENS *et al.*, 1987) and parthenocarpy, that is, development of fruit without a previous ovule fertilization and, consequently, seed formation (SCHWABE and MILLS, 1981).

The function of parthenocarpy is unknown, though there are a number of hypothesis to explain it. One of them suggests that parthenocarpy is a mechanism of defence against predators (ZANGERL *et al.*, 1991; TRAVESET, 1993; FUENTES and SCHUPP, 1998). According to this hypothesis, the presence of fruits lacking the seed increases the probability of protecting seeded fruits from predation. A different explanation suggests that parthenocarpy could be a way of attracting animals participating in fruit or seed dispersion due to a greater attractiveness of those plants with a greater fruit production (JORDANO, 1989; FUENTES, 1995).

European field elm (*Ulmus minor* Mill., s.l.) produces a high percentage of empty fruits (samaras) in Spain, varying between 65% and 80% (LAGUNA, 1883; CATALÁN, 1985). Also in England empty fruit is frequent in some varieties of *Ulmus minor* (STOKES, 1812; LEY, 1910). A substantial proportion of these empty samaras has its origin in seed abortion (LÓPEZ-ALMANSA *et al.*, 2003a, b). However, LELIVELD (1935) indicated that empty samaras are produced in *Ulmus x hollandica* var. *belgica* as the result of the development of fruit in the absence of crossed pollination. As far as we know, this has not been invoked for *Ulmus minor*. The objective of the current research is to study the possible presence of parthenocarpy in *Ulmus minor* in Spain and its relationship with the frequent empty samara reported in this species.

Material and Methods

Samaras of *Ulmus minor* were collected in the field in Spain during different collections between 1990 and 2001. Fruit was collected in 321 individual trees. Percentage of empty and full samaras were estimated on the basis of at least 100 samaras per tree.

Some of the trees in the field where seed had been collected were vegetatively reproduced between 1990 and 1995 using cuttings and grafts. These ramets were located in a clonal bank at Centro de Mejora Genética Forestal de Puerta de Hierro in Madrid. Currently in this clonal bank there are more than 400 elms collected in field from 239 elms. The proportion of empty and full samaras was estimated between 1999–2002 in the clonal bank, using 100 samaras per tree in a number of individuals (see *Table 1*). In particular, empty samara production was estimated between 2000–2002 over 25 individuals at the clonal bank with known seed production in the ortet in the field.

In February 2001, floral branches in 26 individuals at the clonal bank (20 *Ulmus minor* and 6 *U. minor x pumila*) were isolated within paper bags in order to estimate samara production in the absence of alien pollen. This treatment was repeated in 2002 with 52 *U. minor* trees. On 20 of those that were taller than 3 m, bagging was done in the upper and lower parts of the crown in order to detect possible differences.

In 2002, the number of bagged floral buds was counted. It was also estimated the average number of flowers per floral bud. The number of isolated flowers within every bag was calculated as the product of the bagged floral buds and the average number of flowers per floral bud. A parthenocarpy index was calculated as $P = E_s / (F - F_s)$, where E_s is the number of empty samaras within the bag, F the number of flowers within the bag and F_s the number of full samaras within the bag.

Results

Samaras in field

Production of empty samaras in the field was high, varying between 61.9 to 94.4% in different collections (*Table 1*), with an average of 78.9%. There were remarkable differences between trees: in three trees the percentage of empty samara was less than 10%, though in half the trees it was greater than 90% (*Figure 1*).

Samaras in clonal bank

Production of empty samaras in the clonal bank has been quite uniform, varying between 34.1 and 48.1% (*Table 1*). There were no significant differences in empty seed production between years (Wilcoxon signed rank test, $p > 0.10$; Kruskal-Wallis test, $p > 0.10$). Average percentage of empty samaras in the clonal bank was 47.7% in *U. minor* and 32.6% in *U. minor x pumila* during the period 1999–2002. These differences, however, were not statistically significant (Kolmogorov-Smirnov test, $p = 0.454$).

¹ Present address: Departamento de Ingeniería Agroforestal, Universidad Católica de Ávila, C/ Canteros s/n, 05005 Ávila (Spain). Tfn: 913367113, Fax: 913366386, e-mail: jcarlos.lopez@ucavila.es.

Table 1. – Average value and standard deviation of the percentage of empty samara collected in the field (f) between 1990 and 2001, and in the clonal bank at Puerta de Hierro (cb) between 1999 to 2002. N = sampling number.

	f90	f91	f92	f93	f94	f95	f96	f99	f00	f01	cb99	cb00	cb01	cb02
N	23	26	36	27	40	19	45	49	51	22	20	28	51	48
Average	77.4	77.0	65.0	61.9	77.7	70.8	94.4	73.1	90.6	85.3	34.1	40.1	36.4	48.1
St. dev.	18.67	19.81	25.87	28.88	26.54	24.81	10.95	26.87	15.04	20.63	20.85	28.02	30.75	35.72

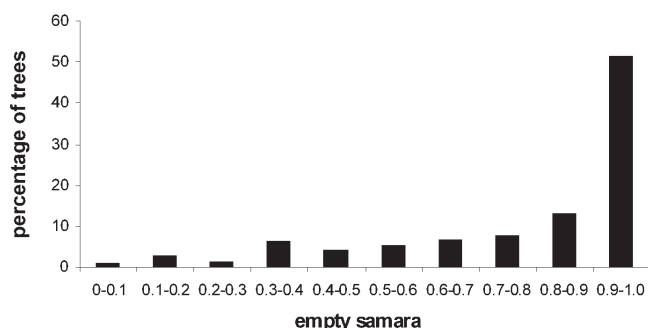


Figure 1. – Frequency of empty samara in 321 elms in the field between 1990 and 2001.

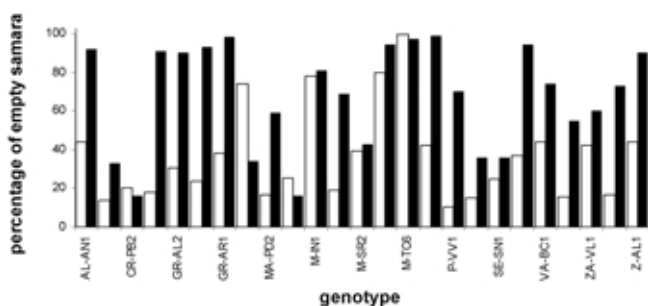


Figure 2. – Percentage in the average empty samara in the clonal bank (white) and in the field (black) in 25 individuals of elm.

Samaras in the field and clonal bank

There were significant differences in the percentage of empty samaras in the clonal bank and in the field, both comparing general production (41.20 ± 29.16 in clonal bank, 78.91 ± 24.43 in the field; Kolmogorov-Smirnov test, $p < 0.001$) and production in the 25 individuals with clonal copies in both clonal bank and the field (36.56 ± 23.70 in the clonal bank, 67.72 ± 26.20 in the field; Wilcoxon signed rank test, $p < 0.001$). Most of these 25 individuals had lower percentages of empty samaras in the clonal bank than in the field (Figure 2). The most remarkable exception was J-CA2, which presented a percentage of empty samara twice as high in the clonal bank than in the field (Figure 2).

Parthenocarpy

In 2001, 17 of 26 trees (65.4%) with isolated branches produced samara in the absence of crossed pollen. 95.7% of these samaras were empty, without signs of the seed. Parthenocarpy was more frequent in hybrid *U. minor* x *pumila* (83.3%) than in *U. minor* (60.0%). Under open pollination at clonal bank, these 17 trees had 38.7 empty seed. Differences between empty samara in self and open pollination were statistically significant (Wilcoxon signed rank test, $p < 0.001$). In 2002, production of empty samara in isolated branches was lower, affecting only 17 out of 52 studied *U. minor* genotypes (32.7%), though some of the individuals presented a parthenocarpy index greater

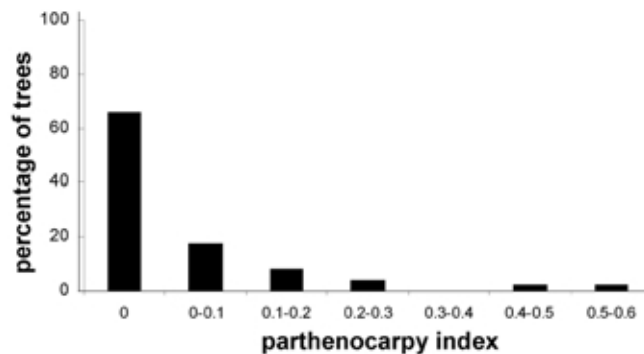


Figure 3. – Parthenocarpy index in 52 individuals of *Ulmus minor* in the clonal bank at Centro de Mejora Genética Forestal de Puerta de Hierro at Madrid in 2002. Parthenocarpy index measures the number of parthenocarpic samara per flower.

than 0.5 (Figure 3). However, there was a good correlation in the parthenocarpy index between 2001 and 2002 (Pearson $r = 0.84$, $p < 0.001$, $n = 15$). Eighteen of 25 elms with data both in the field ortet and in the clonal trees in the clonal bank produced samara by self-pollination in 2001 or 2002. Generally, parthenocarpy occurred only on the lower branches of the trees, appearing in the upper branches only in one individual (M-DV2).

Besides parthenocarpy, some samaras in isolated branches were due to self-fertilization. In 2001, 7 of 26 studied individuals presented a low quantity of seed in isolated branches, and in 2 of them the percentage of flowers that developed seed by self-fertilization was greater than 5%. In 2002, 13 of 52 studied individuals presented self-pollinated seed, 2 of which had a percentage of seed by self-pollination greater than 15%.

Discussion

Ulmus minor produces a great percentage of empty samaras in the field, thus limiting the possibilities of sexual reproduction. Empty samara production was remarkably lower in the clonal bank, where genetic variability is ensured. Particularly, percentage of empty samaras was significantly greater in the ortets in the field than in their clonal individuals in the clonal bank. This fact, added to the existence of fruit development without crossed pollination in the species, suggests that at least a part of the empty seed could have its origin in fruit development when there is a shortage of pollen from different genotypes, as was indicated by LELIVELD (1935) for *Ulmus* x *hollandica* var *belgica* in the Netherlands. It is improbable that differences between results at clonal bank and field could be a consequence of different conditions in site and year, because there were no important differences in empty seed production in a four-year-long period at clonal bank.

Results indicate that only a part of the elms in the clonal bank show parthenocarpy, contrasting with the high percentage of empty samara in the field. Some of this empty samara can have its origin in seed abortion (LÓPEZ-ALMANSA *et al.*,

2003a, b). However, this fact does not invalidate the hypothesis that a great part of the empty seed found in the field could originate by the parthenocarpic development of fruit. This is because the field data are probably biased toward genotypes possessing parthenocarpy, due to the fact that isolated elms lacking parthenocarpy were not recorded during the annual collections, because notes were taken only on those trees where samara was collected.

Currently, due to the disappearance in the decades of 1980 and 1990 of the great elm-woods that were sited in riversides, as a consequence of Dutch Elm Disease, seed is generally collected in more or less isolated trees or small stands. Considering that elm propagates extraordinarily well by sprouting, it is not surprising that most of the elm stands could have little genetic variability. COGOLLUDO AGUSTÍN (1999) indicates the presence in Madridejos (Province of Toledo) of an elm stand where the fifteen studied trees using isozymes belong to only one genotype. However, the average number of genotypes at this site was three per elm stand.

Parthenocarpic development of fruit could be related to self pollen deposition on the stigmatic surface. Pollen is a rich source of hormones, and constitutes a stimulus for the ovary growth (CRANE, 1964; NITSCH, 1970; BIALE, 1978). Unfortunately, it was not possible to emasculate flowers, due to flower and inflorescence morphology, and so it has not been possible to test if parthenocarpic fruit develops without self-pollination. In fact, we are not sure that the development of fruit was parthenocarpic, strictly as it was not studied if fertilization took place. However, seed abortion takes place early even in the case that self-fertilization actually occurs, as seed development was not observed except in rare self-pollinated samaras that finished the seed development. This behaviour is clearly different from seed abortion previously reported in *Ulmus minor*, where the embryo develops within the seed prior to seed abortion later in the season, and where some necrotic tissues of the seed remain (LÓPEZ-ALMANSA *et al.*, 2003b). So the final effect is similar to actual parthenocarpy. Also seed abortion contributes notably to the empty samara found in the field, and can affect most of the elms sited in some elm stands (LÓPEZ-ALMANSA *et al.*, 2003a).

Self-incompatibility is frequent in the genus *Ulmus*, though it varies between species and individuals (JOHNSON, 1946; HEYBROEK, 1957; COLLINS, 1967; MITTEMPHERGER and LA PORTA, 1991). In Puerta de Hierro, approximately a quarter of *Ulmus minor* trees showed self-fertilization, and the average selfing rate was 1% in 2002. Those data are similar to these of MITTEMPHERGER and LA PORTA (1991), which indicate that *U. carpiniifolia* (*U. minor*) produced about 4% full seed due to self-pollination. In fact, in Puerta de Hierro two *U. minor* individuals presented even 16.5 and 18.6% of full seed, respectively.

None of the proposed hypotheses for explaining the existence of parthenocarpy seems to be appropriate to elm. First, seed dispersion is anemocorous, without animal participation on it, and so parthenocarpic fruit has no role as animal attractor. Second, parthenocarpy seems not to be a defence mechanism against predators, at least against birds, because they discriminate perfectly between empty and seeded samaras, consuming only seeded fruits (LÓPEZ-ALMANSA, personal observation). Moreover, the only known insect that feeds on elm fruit is the larva of *Cirrhia gilvago*, a lepidopteran that, although widely distributed in Europe, is quite infrequent (RICHENS, 1983).

According to WILLSON and BURLEY (1983), development of parthenocarpic fruits could occur when there is no resource limitation. Water is one of these limiting resources, specially in

Mediterranean ecosystems. JORDANO (1988) found that parthenocarpy in *Pistacia lentiscus* was greater in a wet year than in a dry year. In the same species, however, VERDÚ and GARCÍA-FAYOS (1998) found that artificially irrigated individuals produced no parthenocarpic fruit, in contrast with non-irrigated ones. In any case, water seems not to be a limiting factor in the riparian sites generally occupied by *Ulmus minor*, especially in March and April, when fruit production takes place. Moreover, the fact that samaras photosynthesize mean that probably fruit production was not carbon-limited, and so fruit production may cost little in this species. Therefore, parthenocarpy could be maintained without an adaptive value.

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