

Reproductive biology of *Corema album* (L.) D. Don (*Empetraceae*) in the northwest Iberian Peninsula

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Summary. - We report a study of the reproductive biology of the dioecious shrub *Corema album* in Galicia (N-W Spain). Male flowers were larger and heavier than female flowers, though the overall investment in sexual reproduction by females was higher. Population pollen-to-ovule ratio was very high (about 173 000:1). Flowering phenology was synchronous between males and females. The relative spatial distribution of the sexes appears to be random. Fruit set was not significantly dependent on either distance to the nearest male or sum of distances to the nearest five males. However, our results suggest that fruit set is higher in population nuclei with high population densities. Furthermore, mean single-fruit weight was higher in the population nucleus with highest fruit set than in the other nuclei studied.

Résumé. - Nous présentons une étude de la biologie reproductive de *Corema album*, arbuste dioïque présent en Galice (N.-O. de l'Espagne). Les fleurs mâles sont plus grandes et plus lourdes que les fleurs femelles. Le rapport pollen / ovule dans la population est très élevé (environ 173 000:1). La phénologie de la floraison est synchrone entre les plantes mâles et femelles. La distribution spatiale relative des sexes semble se faire au hasard. Le niveau de fructification ne semble dépendre ni de la distance à la plante mâle la plus proche, ni de la somme des distances des cinq plantes mâles les plus proches. Cependant nos résultats suggèrent un niveau de fructification plus élevé dans des noyaux de population ayant des densités de population plus élevées. En outre le poids moyen d'un fruit est supérieur dans le noyau de population ayant le niveau de fructification le plus élevé.

Key-words : reproductive biology - *Corema* - dioecious - spatial distribution - fruit set.

I. INTRODUCTION

Understanding the reproductive biology of organisms which display sexual dimorphism is of interest in view of the light such understanding may shed on the evolution of sexual systems. In dioecious plants, sexual dimorphism may be apparent both in vegetative characters (Wilson, 1991) and in reproductive characters (Lloyd et Webb, 1977; Bawa, 1980; Flanagan et Moser, 1985; Ågren, 1987; Flanagan et Bain, 1988; Armstrong et Irvine, 1989a, b; Wilson et Ågren, 1989; Kevan, 1990; Niesenbaum, 1992; Gehring et Linhart, 1993; P. Guitián, 1995; J. Guitián, 1995). In some dioecious plants, the sexes differ not only in vegetative and reproductive characters, but also in microhabitat requirements and even survival rates; this may lead to spatial segregation of the sexes within populations (Shea *et al.*, 1993, for a review). Spatial segregation of the sexes may have effects on fruit set (Barrett et Thomson, 1982).

Dioecious plants are often wind-pollinated, and Shea *et al.* (1993) have suggested that spatial segregation of the sexes is more frequent among wind-pollinated dioecious species than among dioecious species pollinated in other ways. Other workers have attempted to identify other morphological and ecological correlates of dioecy, both at the regional scale (see for example Steiner, 1988) and the global scale (Renner et Ricklefs, 1995). The types of correlate detected tend to vary among systematic groups. Characters which have been reported to be particularly frequent in dioecious plants (in addition to wind pollination) include woody stems, fleshy fruits, frugivore-aided seed dispersal, and small inconspicuous flowers. However, none of these characters is as consistently present as wind pollination (Renner et Ricklefs, 1995).

In the present study we investigated various aspects of the reproductive biology of the wind-pollinated dioecious shrub *Corema album* in Galicia (northwest Spain). Particular attention was paid to the characterization of sexual dimorphisms, and to investigation of the possible effects of location with respect to males on an individual female's fruit set.

II. THE PLANT AND THE STUDY AREA

A. The plant

The genus *Corema* (L.) D. Don (*Empetraceae*) comprises two species, one on each side of the Atlantic: *C. album* (L.) D. Don occurs on the west coast of the Iberian Peninsula (*C. album* subsp. *album*) and in the Azores (*C. album* subsp. *azoricum* Pinto da Silva), while *C. conradii* Torr. occurs on the eastern coast of north America. *C. album* is a wind-pollinated dioecious shrub of up to one meter in height, with numerous flowers grouped in closely packed racemose inflorescences. The number of flowers per inflorescence varies considerably, both among male and among female plants, but never exceeds 20. The fruit is a more or less spherical berry (diameter 5 - 8 mm), white or pinkish white when ripe. Throughout its area of distribution, *C. album* is limited to coastal habitats, namely sand-dunes and rocky-coast sites (subsp. *album*) or volcanic lava and ash fields (subsp. *azoricum*).

B. Study area

The study area is located in the district (municipio) of Camariñas (A Coruña Province), on the coast of northwest Spain. Three population nuclei were studied, located i) in a coas-

tal gorse scrubland community on Balea beach, ii) on the side of a large dune on Trece beach, and iii) on a flat sandy site just landward of the dunes on Trece beach.

III. METHODS

Floral characters

Flowers (14 male flowers, 10 female flowers, from 24 plants) were measured in the laboratory with the aid of a stereomicroscope. Dry weight was determined (precision 1 μ g) for 10 male flowers and 10 female flowers (each from a different plant) after drying in an oven for 48 h at 50°C. Number of pollen grains per stamen was estimated by counting tetrads in a Neubauer chamber, by Dafni's (1992) method; counts were made of 16 stamens, each from a flower of a different plant.

Inflorescence and flower densities

Possible between-sex differences in inflorescence density were investigated by counting inflorescences on terminal stems (distal 20 cm) on 20 plants of each sex in each population nucleus. Mean number of flowers per inflorescence was estimated for each sex on the basis of examination of 360 male inflorescences and 80 female inflorescences (in both cases, plants from all three population nuclei).

Flowering and fruiting phenology

On 9th february 1995 (i.e. before the start of the flowering season), we selected ten individuals of each sex in each population nucleus (except in nucleus 2, in which only nine female plants were studied). On each plant, we marked one branch with a plastic tag. Phenology was then monitored every 6 - 12 days (flowering period) or every 7 - 28 days (fruiting period). On each day of monitoring during flowering, we recorded number of open flowers on each inflorescence. Male flowers were classed as 'open' until pollen was no longer visible on the anthers. On each day of monitoring during fruiting, we recorded number of initiated fruits and number of mature fruits on each inflorescence. The degree of synchrony between male and female flowering was investigated by calculating (for each sex, and each day, considering the three population nuclei together) number of open flowers as a percentage of peak number of open flowers; Spearman correlation coefficients (between male and female percentages, with data for all days of monitoring) were then determined.

Reproductive system and fruit set

It proved impossible to accurately count the number of flowers per inflorescence without removing the inflorescence. Inflorescence fruit sets were thus estimated on the basis of mean number of flowers per inflorescence (see above). To rule out the possibility of apomixis, we monitored four branches (each of a different plant) bagged with cellophane. To confirm that pollination is anemophilous, we monitored three branches (each of a different plant) bagged with mosquito netting.

Following Goldwing (1992), both initial and final fruit set were determined, where initial fruit set is the proportion of flowers which initiate a fruit after anthesis, and final fruit set is the proportion of flowers which produce a full-sized (though not necessarily ripe) fruit. Fruit sets were compared among the three population nuclei by analysis of variance.

Sex ratio, spatial distribution of sexes and effects on fruit set

Population sex ratio was investigated by determining the sex of plants along three transects, one in each population nucleus ($n = 181$ plants in total); a χ^2 goodness-of-fit test was then used to determine whether sex ratio differed significantly from one-to-one. To investigate whether the spatial distribution of the sexes in each population nucleus was random, sex-of-nearest-neighbour was determined for the plants along a transect in nucleus 1 ($n = 18$), along a transect in nucleus 2 ($n = 42$), and along two transects in nucleus 3 ($n = 31$, and $n = 36$). For each sample, a contingency table of sex versus sex-of-nearest-neighbour was then drawn up and analysed by a χ^2 test for association. To investigate the possible effects of distance from nearest male plants on fruit set, we measured (for each of the ten female plants whose fruit set was monitored in each population nucleus) distance to each of the five nearest males. For both initial and final fruit sets, Spearman correlation coefficients were then calculated between i) fruit set and distance to the nearest male plant, and ii) fruit set and sum of distances to the five nearest male plants.

Fruit characteristics

Ten mature fruits (each from a different plant) were collected from each population nucleus, and weighed both fresh and after oven-drying for 48 h at 50°C. Mean fruit weights were compared among population nuclei by analysis of variance and subsequent Tukey tests.

IV. RESULTS

A. Floral characteristics and pollen-to-ovule ratios

The data on floral morphometrics and flower weight are summarized in Table 1. The perianths of male flowers were longer than those of female flowers (mean 3,2 mm versus 2,3 mm; $t = 7,17$, $p < 0,0001$). The mean dry weight of male flowers was greater than that of female flowers (1 207 μg versus 499 μg ; $t = 5,57$, $p < 0,0001$). All male flowers had three stamens, and all female flowers had three ovules. The mean number of pollen tetrads per stamen was $21\,680 \pm 10\,836$ ($n = 16$); mean number of pollen grains per flower was thus 26 0155. Of the 181 plants on the transects in the three population nuclei, 97 were male and 84 female (ratio 1,15:1). Mean number of inflorescences per branch was 54,03 for male plants ($n = 60$ branches, 20 per population nucleus) and 36,28 for female plants ($n = 60$) (ratio 1,49:1). Mean number of flowers per inflorescence was $9,13 \pm 2,94$ (s.d.) for males ($n = 360$ inflorescences) and $7,84 \pm 2,11$ for females ($n = 80$) (ratio 1,16:1). Population pollen-to-ovule ratio (calculated from the pooled data for the three population nuclei) is thus 173 041:1 (Table 2).

	mean \pm s.d. (n)
Perianth length:	
- male flowers	3,24 \pm 0,33 (14)
- female flowers	2,26 \pm 0,33 (10)
Stamen length	5,05 \pm 0,49 (14)
Pistil length	3,71 \pm 0,43 (10)
Dry weight:	
- male flowers	1 206,6 \pm 388,99 (10)
- female flowers	499,3 \pm 99,04 (10)

Table 1.- Mean lengths of floral structures (mm), and mean dry weights (μg) of male and female flowers, in the study population of *Corema album*.

Tableau 1.- Longueurs moyennes des structures florales (mm) et poids sec moyen (μg) des fleurs mâles et femelles dans la population étudiée de *Corema album*.

B. Flowering and fruiting phenology

Flowering of both male and female plants began on february 21, and the flowering peak for both sexes was on april 7 (Fig. 1). From april 25 onwards pollen was not observed on the stamens of any male flowers. From may 10 onwards, all remaining female flowers had initiated fruit production.

Number of pollen grains per stamen ^(A)	86 718,25
Number of stamens per flower ^(B)	3
Number of pollen grains per flower ^{(C) = (A) x (B)}	260 154,72
Number of flowers per male inflorescence ^(D)	9,13
Number of pollen grains per male inflorescence ^{(E) = (C) x (D)}	2 375 212,6
Number of ovules per flower ^(F)	3
Number of flowers per female inflorescence ^(G)	7,84
Number of ovules per inflorescence ^{(H) = (F) x (G)}	23,52
Ratio of male to female inflorescence density ^(I)	1,49
Ratio of male to female plants ^(J)	1,15
Pollen-to-ovule ratio ^{(E x I x J) / H}	173 041,11

Table 2.- Steps in the calculation of pollen-to-ovule ratio for the study population of *Corema album*.

Tableau 2.- Calcul du rapport pollen/ovule pour *Corema album* dans le territoire étudié.

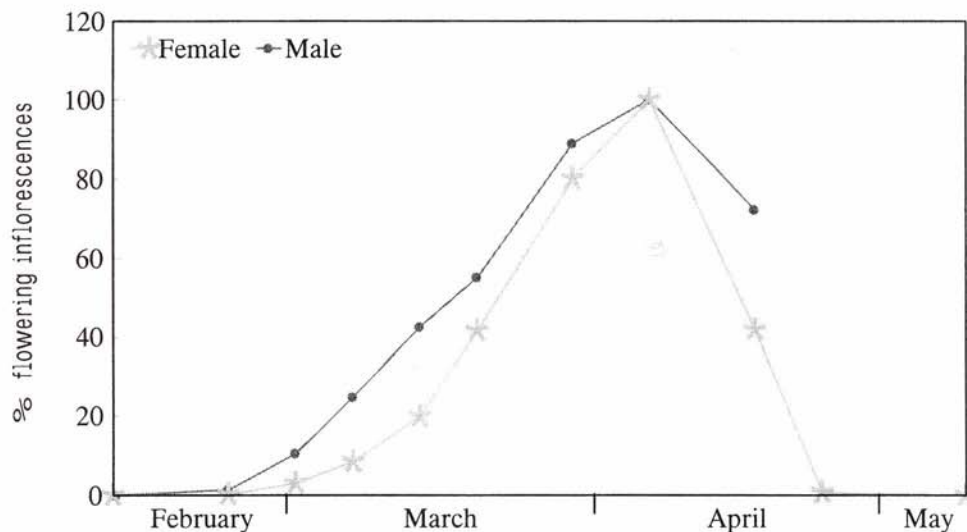


Fig. 1.- Time-course of male and female flowering at the study population of *Corema album*. The vertical axis shows percentages of inflorescences with at least one flower open.

Fig. 1.- Période de floraison des plantes mâles et femelles de la population de *Corema album* étudiée. L'axe vertical indique les pourcentages d'inflorescences ayant au moins une fleur ouverte.

	Flowers	Initiated fruits	Full-size fruits	Initial fruit set	Final fruit set
Nucleus 1	1 254	155	60	14,07	4,80
Nucleus 2	995	208	97	21,75	10,39
Nucleus 3	1 176	307	176	27,58	16,82

Table 3.- Fruit set data for the three *Corema album* population nuclei studied. In each nucleus, the flowers monitored were those on a single branch (distal 20 cm) of ten plants (nuclei 1 and 3) or nine plants (nucleus 2).

Tableau 3.- Degrés de fructification des trois noyaux de population de *Corema album* étudiés. Dans chaque noyau les fleurs ont été étudiées sur une seule branche (vingt derniers centimètres); il s'agissait de dix plantes pour les noyaux 1 et 3 et de neuf plantes pour le noyau 2.

	Fresh weight	Dry weight
Nucleus 1	0,2576 (\pm 0,04184) ^a	0,0541 (\pm 0,00813) ^c
Nucleus 2	0,2813 (\pm 0,03933) ^a	0,0516 (\pm 0,00782) ^c
Nucleus 3	0,3517 (\pm 0,07955) ^b	0,0601 (\pm 0,01028) ^c

Table 4.- Mean fresh weights and dry weights (g) of single fruits from each of the three *Corema album* population nuclei studied ($n = 10$ fruits per nucleus). Standard deviations are shown in brackets. Means followed by different letters differ significantly at the 5 % level.

Tableau 4.- Poids frais et secs moyens (g) d'un fruit de chacun des trois noyaux de population de *Corema album* étudié ($n = 10$ fruits par noyau). Les déviations standard sont indiquées entre parenthèses. Les valeurs suivies par des lettres distinctes diffèrent au niveau de 5 %.

C. Reproductive system and fruit set

None of the flowers on the cellophane-bagged branches produced fruit. Mean fruit set on the mosquito-netting-bagged branches was $6,86 \pm 5,37$ % (initial) and $4,93 \pm 4,56$ % (final). Mean initial fruit set of non-manipulated branches was 14 % (nucleus 1), 22 % (nucleus 2) and 28 % (nucleus 3) (Table 3); these values do not vary significantly among the three nuclei ($F_{(2,26)} = 2,87$, $p = 0,0748$). Mean final fruit set of non-manipulated branches was 5 % (nucleus 1), 10 % (nucleus 2) and 17% (nucleus 3); these values vary significantly (Tukey's tests indicate that there is a significant difference [$p < 0,01$] between the means for nuclei 1 and 3, but no significant difference [$p > 0,05$] between nuclei 1 and 2 or nuclei 2 and 3).

D. Sex ratio, spatial distribution of sexes and effects on fruit set

As noted above, the sample sex ratio (pooled data for the three nuclei) was 1,15:1, which for a sample of this size does not differ significantly from 1:1 ($\chi^2 = 0,93$; $p = 0,3339$). In population nuclei 1 and 2, the sex of an individual's nearest neighbour was independent of that individual's own sex ($\chi^2 = 0,03$, $p = 0,638$ for nucleus 1; $\chi^2 = 0,004$, $p > 0,999$ for nucleus 2). The same was true of one of the samples from nucleus 3 ($\chi^2 = 0,001$, $p = 0,7486$), but not of the other sample from this population, which showed evidence of a regular distribution of the sexes (i.e. an individual's nearest neighbour was more likely to be of the opposite sex than of the same sex) ($\chi^2 = 9,40$, $p = 0,001$).

	Females mean \pm s. d. (n)	Males mean \pm s. d. (n)
Number of flowers per inflorescence ^(A)	7,84 \pm 2,11 (360)	9,13 \pm 2,94 (80)
Number of inflorescences per branch ^(B)	36,28 \pm 25,49 (60)	54,03 \pm 33,59 (60)
Number of flowers per branch ^{(C) = (A) x (B)}	284,44	493,29
Dry weight of single flower (μg) ^(D)	499,3 \pm 99,04 (10)	1 206,6 \pm 388,99 (10)
Dry weight of flowers per branch (μg) ^{(E) = (C) x (D)}	142 018,5	595 203,71
Mean final fruit set (%) ^(F)	10,68 \pm 8,49 (29)	-
Mean number of fruits per branch ^{(G) = (C) x (F)}	30,35	-
Dry weight of single fruit (μg) ^(H)	55 266,66 \pm 9 243,58 (30)	-
Dry weight of fruits per branch (μg) ^{(I) = (G) x (H)}	1 677 526,75	-
Total investment (dry weight) in reproductive structures ^{(J) = (E) + (I)}	1 819 545,25 ^(JF)	595 203,71 ^(JM)
Ratio female: male investment ^{(JF) / (JM)}	3,06	

Table 5.- Steps in the calculation of the ratio of investment in sexual reproduction by females to investment in sexual reproduction by males. Calculations are based on comparison of estimated investment per branch (distal 20 cm). Fruit set is taken to be mean final fruit set in the study population.

Tableau 5.- Calcul du rapport entre l'inversion dans la reproduction sexuelle féminine et l'inversion dans la reproduction sexuelle masculine. Les calculs sont basés sur la comparaison des inversions estimées par branche (derniers vingt centimètres). On a utilisé le niveau de fructification moyen final dans la population étudiée.

Neither initial nor final fruit set showed signs of dependence on the proximity of male plants. There was a weak but significant negative correlation between initial fruit set and distance to the nearest male ($r = -0,39$, $p = 0,034$): however, there were no significant correlations at the 5 % level between either i) initial fruit set and sum of distances to the nearest five males, ii) final fruit set and distance to the nearest male, or iii) final fruit set and sum of distances to the nearest five males.

E. Fruit characteristics

Mean fresh weight of single fruits varied significantly among the three population nuclei ($F_{(2,27)} = 7,466$, $p = 0,0026$; Table 4). Tukey tests indicated that the mean weight of single fruits from nucleus 3 ($0,35 \pm 0,07$ g) differed significantly from that of fruits from both nucleus 1 ($0,25 \pm 0,04$ g) and nucleus 2 ($0,28 \pm 0,03$ g), but that there was no significant difference between nuclei 1 and 2.

F. Investment in reproduction by males and females

Considering the data for the distal 20 cm of branches, and pooling the data for the three population nuclei, the mean total dry weight of flowers produced per branch was 595,20 mg for males and 142,02 mg for females. However, overall investment by females is about three times that by males (see Table 5).

V. DISCUSSION

In the populations of *Corema album* studied, sex ratio did not differ significantly from 1:1. However, branches of male plants produced more inflorescences than branches of female plants, and male inflorescences contained more flowers than female inflorescences. One-to-one population sex ratios are often stated to be typical of dioecious plants (Bullock et Bawa, 1981; Flanagan et Moser, 1985; Armstrong et Drummond, 1986; Niesenbaum, 1992; Aronne *et al.*, 1993; J. Guitián, 1995; P. Guitián, 1995), though sometimes males may outnumber females (Richards, 1988; García et Antor, 1995; Feil, 1992; Allen et Antos, 1993; Thomas et La Frankie, 1993) or females may outnumber males (Feil, 1992). Furthermore, recent studies have shown that sex ratio within a species or a population may vary in response to environmental factors (Freeman *et al.*, 1976; Allen et Antos, 1993) or as a function of plant age (Alliende et Harper, 1989; Escarré et Houssard, 1991; Houssard *et al.*, 1994; García et Antor, 1995). It is thus probably unwise to generalize about the sex ratio of dioecious plants.

By contrast, the production of more flowers by male plants than by female plants appears to be a near-universal pattern (Gross et Soule, 1981; Flanagan et Moser, 1985; Armstrong et Irvine, 1989a; Thomas et La Frankie, 1993; Aronne *et al.*, 1993; Antos et Allen, 1994; J. Guitián, 1995; García et Antor, 1995). This is despite the fact that total investment in sexual reproduction by female plants is generally higher (Armstrong et Irvine, 1989a; Antos et Allen, 1994; García et Antor, 1995; J. Guitián, 1995); note, though, that Delph *et al.* (1993) found that male plants of *Carex picta* invest a similar amount to female plants, while other studies (Bell, 1985) have indicated that male investment may be high in species in which (unlike *Corema album* and *Carex picta*) males must produce elaborate perianth structures. In their study of *Carex picta*, Delph *et al.* (1993) consider that the heavy investment in flower production by males is a reflection of this species' wind-pollinated character. It seems likely that, in absolute terms, males of *Corema album* like-

wise invest heavily in flower production, but that the investment relative to females is low because the latter produce fleshy fruits.

In some dioecious plants the male flowering period starts earlier than the female flowering period (Bawa, 1983; Stephenson et Bertin, 1983; Armstrong et Irvine, 1989a), whereas in others the two periods are closely synchronic (Ågren, 1988; J. Guitián, 1995). *Corema album* conformed to the latter pattern, ruling out the possibility that the low fruit sets observed were due to asynchronicity of male and female flowering (and consequent pollen scarcity).

The estimated population pollen-to-ovule ratio is extremely high, as expected for a non-selfing wind-pollinated species.

All the above characteristics can be expected to influence fruit set. An additional local factor which may affect fruit set is the spatial distribution of the sexes. However, we found that fruit set by a given female branch was independent of the distance to the nearest male plant, and of the sum of distances to the nearest five male plants. Similar results have been obtained for other dioecious species (J. Guitián, 1995). Barrett et Thomson (1982) suggested that "presumably at some spatial scale the distribution and density of sexual morphs influence fecundity".

Our results suggest that fruit set was higher in population nuclei in which individuals (regardless of sex) are close to each other. Mean sum of distances to the five nearest plants was highest (19,4 m) in nucleus 1, which had the lowest fruit set (14 % initial, 4 % final). Likewise, the mean sum of distances was lowest (14,0 m) in nucleus 3, which had the highest fruit set (28 % initial, 17 % final); in nucleus 2, both the mean sum of distances (15,7 m) and fruit set (22 % initial, 9 % final) were intermediate. Furthermore, mean single fruit weight was highest in nucleus 3, despite the higher fruit set. This may reflect the higher availability of nonself pollen, and thus more intense gametophyte competition, in the nucleus with highest population density (Lee, 1984, 1988).

One of the two samples from nucleus 3 indicated a nonrandom spatial distribution of the sexes; specifically, an individual's nearest neighbour was more likely to be of the opposite sex. However, the fact that only one sample gave a significantly nonrandom result urges caution: quite possibly, the result is simply a sampling artefact. Furthermore, even if the result is a true reflection of population structure, the implications for population reproductive biology are unclear.

Future studies of *Corema album*, ideally based on monitoring of a larger number of populations, should aim to confirm the influence of population density on reproductive success and to clarify the possibility that males and females are nonrandomly distributed, particularly in view of Barrett et Thomson's (1982) suggestion that reproductive success in dioecious species is influenced by the spatial distribution of the sexes.

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