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Breeding system and temporal variation in fecundity of *Pancratium maritimum* L. (Amaryllidaceae)

Reproductive ecology of *Pancratium maritimum*

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Summary

Flowering phenology, breeding system and temporal variation in reproductive success were studied over two consecutive years in a population of *Pancratium maritimum* L. (Amaryllidaceae) on coastal sand-dunes in northwest Spain. The population flowering period was late June to early September, with the flowering peak in mid-July. Fruit set did not vary significantly between years. However, plants which flowered in July and August had higher fruit set than plants which flowered in June, though no such differences were observed in mean number of seeds per fruit or mean seed-to-ovule ratio. Pollen transfer experiments indicated that the plants of the study population are self-compatible and capable of spontaneous selfing: the value of the Schoen and Lloyd self-compatibility index was 0.91, indicating that the fertilization capacity of self pollen ist almost as high as that of nonself pollen. This contrasts with the results of a study of populations of *P. maritimum* in Israel, where plants were found to be self-incompatible; it thus seems possible that the breeding system of this species varies among populations.

Key words: *Pancratium maritimum*, Amaryllidaceae, phenology, reproductive success, breeding system.

Indroduction

The reproductive ecology of the plants of sand-dune ecosystems of the Iberian Peninsula has been little studied. Those studies that exist have been carried out in Mediterranean areas of the southern part of the Peninsula and have dealt with aspects of floral biology, phenology, pollination and dispersal (HERRERA 1985, 1986, 1987a, 1987b, JORDANO 1988).

Pancratium maritimum L. (Amaryllidaceae) is one of the commonest species in communities occupying stable dunes on both the Atlantic and Mediterranean coasts of southern Europe. EISIKOWITCH & GALIL (1971) studied the pollination biology of this species on the coast of Israel, where it is pollinated by sphingid moths. Studies of other species of the Amaryllidaceae have investigated various aspects of sexual system, pollination and dispersal (BRANTJES & BOS 1980, DAFNI & WERKER 1982, MANASSE 1990, BROYLES & WYATT 1991, MANASSE & STANTON 1991).

On the coast of northern Spain, the flowering and fruiting period of *P. maritimum* lasts for several months, and abundant fruits and seeds are produced. It has frequently been reported that individual plants that flower at different times within a long population flowering period show differences in reproductive success (AUGSPURGER 1983, ZIMMERMAN & GROSS 1984, MELAMPY 1987, NYBOM 1989, GALEN & STANTON 1991, OLESEN & WARNCKE 1992, STENSTRÖM & MOLAU 1992, RAMSEY 1995). Furthermore, it has been suggested that long flowering seasons and within-plant flowering asynchrony may have arisen because such systems encourage pollinators to move from one plant to another within the population, thus favouring cross-pollination (see AUGSPURGER 1980, PRIMACK 1980, OLLERTON & LACK 1992, and references therein). However, our observations indicate that there is very little pollinator activity in populations of *P. maritimum* in northern Spain, suggesting that seeds may be produced by some form of autogamy (*sensu* RICHARDS 1986).

In the present study we investigated various aspects of the reproductive biology of a population of *P. maritimum* on the northwest coast of the Iberian Peninsula. Data were collected in 1995 and 1996. Specifically, we investigated a) flowering phenology during 1996, b) variations in female reproductive success (as measured by fruit set, seed production and seed-to-ovule ratio) between years and between subperiods within years, and c) the effects of different modes of pollen transfer (autogamy, geitonogamy and xenogamy) on reproductive success.

Materials and methods

The plant and the study area

Pancratium maritimum L. is a geophyte that grows on sand dunes and related sandy coastal habitats. In Europe *P. maritimum* has a mostly Mediterranean distribution, extending northwards to 47° 30' in West France. The storage organ is a bulb with several brown membranous external tunics. The bulb gives rise to 4–6 leaves and one (sometimes two) scapes that may reach a height of up to 45 cm above ground level. The umbel-type inflorescence comprises (2–) 4–12 white flowers on short peduncles, with a narrow and prominent (5–8 cm long) greenish perianth tube and six exserted stamens. The ovary is inferior and comprised of three fused carpels. The mean number of ovules per flower is 54. The flowers of each scape tend to open one at a time, although occasionally two and very occasionally three open on the same day. Anthesis occurs at dusk: as the flower opens the stamens begin to dehisce, and dehiscence is complete within a few minutes of the opening of a flower. At this time and during the night the flower releases a strong scent. The stigma is exserted, and does not undergo any visible morphological change during the lifespan of the flower. The flower remains open for about 36 h. The fruit is a capsule with loculicidal dehiscence.

The study was carried out in a population of *P. maritimum* in the Corrubedo Dune Complex Natural Park in the southwestern part of La Coruña Province in the region of Galicia in northwest Spain, during the flowering and fruiting seasons of 1995 and 1996. The natural sand-dune vegetation in this area basically comprises three well-defined communities: a) a community of woody species occurring on stable sand and dominated by *Helichrysum picardii* var. *virescens, Artemisia crithmifolia, Scrophularia frutescens* and *Iberis procumbens,* b) a community of monocarpic herbs that appears in early spring on bare sites, the most common species being *Silene littorea, Viola kitaibeliana* and *Erodium cicutarium* subsp. *bipinnatum,* and c) a perennial herb community occurring on seasonally waterlogged soils and dominated by *Juncus acutus, Scirpus holoschoenus* and *Festuca arundinacea.*

Annual mean temperature is 14.6 °C and mean annual precipitation 1 244 mm (data for the Santa Eugenia de Riveira weather station, situated at 25 m above sea level; CARBALLEIRA et al. 1983).

Flowering phenology

An area of 1 400 m^2 was selected and fenced to prevent entry of cattle, rabbits and wild boar. Studies of flowering phenology were carried out in this area, within which a total of 790 individuals of *P. maritimum* were detected. Flowering phenology was not investigated in 1995, though we counted the number of plants within the fenced area that flowered. In 1996, the plants within the fenced area were monitored every three days between late June (start of the flowering season) and early September (end of the flowering season). Since flower lifespan is about 36 h, and since flower age can be estimated accurately, this monitoring strategy allowed us to estimate number of flowers open on each day of the flowering season.

Temporal variation in reproductive success

In 1995 and 1996, to allow evaluation of within-year variation in reproductive success, the flowering period was divided into three subperiods denominated early (E; June), middle (M; July) and late (L; August). In each of these subperiods we randomly selected plants in flower (sample sizes: 10 plants in 1995 E, 10 plants in 1995 M, 10 plants in 1995 L, 27 plants in 1996 E, 44 plants in 1996 M, and 39 plants in 1996 L). Final fruit set (*sensu* GOLDWIN 1992) was estimated for all these plants, on the basis of numbers of fruits counted 20 days after flowering. For laboratory determination of number of seeds per fruit and seed-to-ovule ratio, we collected all fruits remaining on the plants (i.e., all fruits which had not been eaten by herbivores) 50–60 days after flowering, giving sample sizes of 0 fruits for 1995 E, 17 fruits for 1995 M, 17 fruits for 1995 L, 20 fruits for 1996 E, 146 fruits for 1996 M, and 21 fruits for 1996 L.

Pollen transfer mode and sexual system

In 1996, we performed experiments to investigate the effects of pollen origin (same-flower, same-plant-different-flower, or different-plant) on fruit and seed production and on seed-to-ovule ratio. The following treatments were applied (in all cases to plants outside the fenced area):

a) A total of 106 flowers on 31 plants were manually pollinated with pollen from the same flower, then bagged with mosquito netting. All flowers had opened recently and had not received insect visits. Pollination was by removal of the anthers with fine tweezers, the anthers then being brushed gently against the stigmas. Tweezers were cleaned between flowers.

b) A total of 93 flowers on 30 plants were emasculated, manually pollinated (as in treatment a) with pollen from a different flower on the same plant, then bagged with mosquito netting.

c) A total of 105 flowers on 30 plants were emasculated, manually pollinated (as in treatment a) with pollen from a flower on a different plant, then bagged with mosquito netting.

In all the above treatments, pollination was done immediately after the opening of the flower, using pollen from flowers with stamens that had opened recently.

To investigate whether spontaneous autogamy can occur, a total of 118 flowers on 32 different plants were bagged with mosquito netting (treatment d).

In all the above treatments (a–d), the scapes bearing bagged flowers were tied to a stake to minimize movement in the wind. The flowers remained bagged from just before anthesis until senescence.

Finally, a total of 120 flowers on 30 different plants were tagged and monitored without treatment of any kind (control, treatment e).

In all the above experiments (treatments a–e), wherever possible we used the first four flowers to open on each plant, since previous experiments (MEDRANO, unpublished data) have indicated that the fruit set of later-opening flowers may be resource-limited. All experiments were carried out during the peak flowering subperiod (M). Fruit set was determined 20–30 days after bagging. Mature fruits that had survived herbivory were collected 50–60 days after bagging for laboratory determination (stereomicroscope, x 10), of number of seeds and number of aborted ovules in each fruit (n = 86 fruits for treatment a, 71 fruits for treatment b, 82 fruits for treatment c, 37 fruits for treatment d, 66 fruits for control treatment e).

The data on number of seeds per fruit were used to determine Schoen and Lloyd's self-compatibility index (SCI, SCHOEN & LLOYD 1992), which is a measure of the 'success' of self pollen with respect to that of nonself pollen:

$$SCI = Ps/Px$$

Ps = mean number of seeds per fruit after manual autogamous pollination (treatment a), and Px = mean number of seeds per fruit after manual xenogamous pollination (treatment c).

Data analysis

Temporal variation in fruit set, mean number of seeds per fruit and mean seed-to-ovule ration was investigated by two-way model I analysis of variance (ZAR 1996), with the factors *year* and *subperiod*. Note that, in the case of number of seeds per fruit and seed-to-ovule ratio the data for subperiod E were excluded from the analysis, since in 1995 no fruits from this subperiod survived herbivory. The consideration of both factors as fixed (i.e., the use of a model I analysis) was in view of the criteria recommended by EISENHART (1947) cited in BENNINGTON & THAYNE (1994); in addition, and as pointed out by BENNINGTON & THAYNE (1994), two years are unlikely to be representative of a long-term among-years variability and in such cases *year* should be considered as fixed.

Final fruit sets after each of the pollination treatments were compared with the control by chi square heterogeneity tests. To investigate possible differences in number of seeds per fruit and seed-to-ovule ratio, we used one-way analysis of variance (factor *treatment*) followed by Tukey-HSD tests. Fruit set and seed-to-ovule ratio percentage data were subjected to an arcsine-square root transformation before analysis of variance.

Results

Flowering phenology

In 1995, only 99 (12.5%) of the 790 plants in the fenced area flowered, and only 2 (0.3%) produced two scapes instead of one. In 1996, 345 (43.7%) of the plants flowered, and 35 (4.4%) produced two scapes. In 1996, flowering commenced within the fenced area on June 20, peaked on July 15 and finished on September 2 (Fig. 1).

Temporal variation in reproductive success

Considering the fruit set data broken down by flowering subperiod (E, M or L), analysis of variance indicated that subperiod but not year had a significant effect (Table 1a, Fig. 2a). The effect of the subperiod x year interaction was significant at the 5% level indicating that the differences in fruit set between the three subperiods were not consistent between years, which may be due to differences between fruit set in the late subperiod in the two years. However, the mean number of seeds per fruit did not differ significantly either between subperiods or between years nor was the subperiod x year interaction significant (Table 1b, Fig. 2b). Similarly, mean seed-to-ovule ratio did not differ significantly

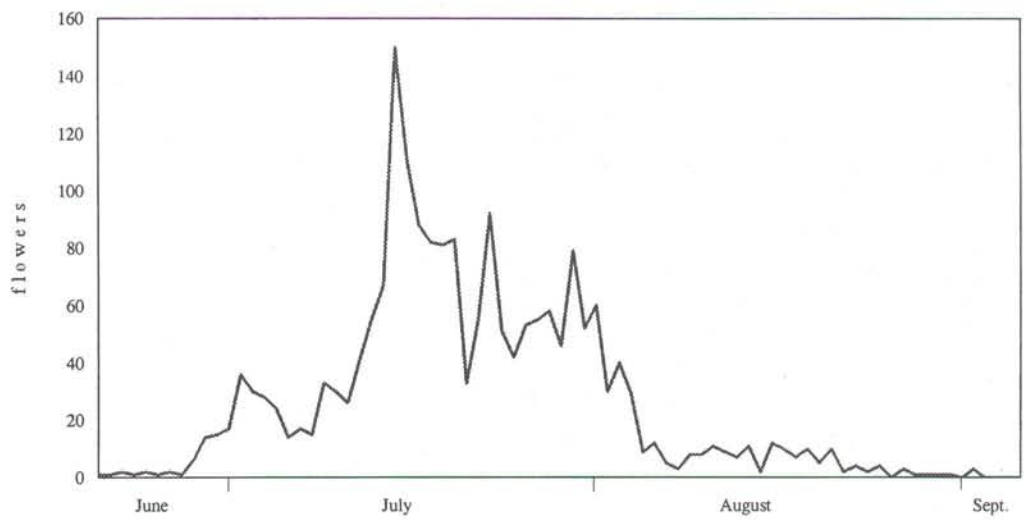

Fig. 1. Flowering phenology of *Pancratium maritimum* in the study area in 1996.

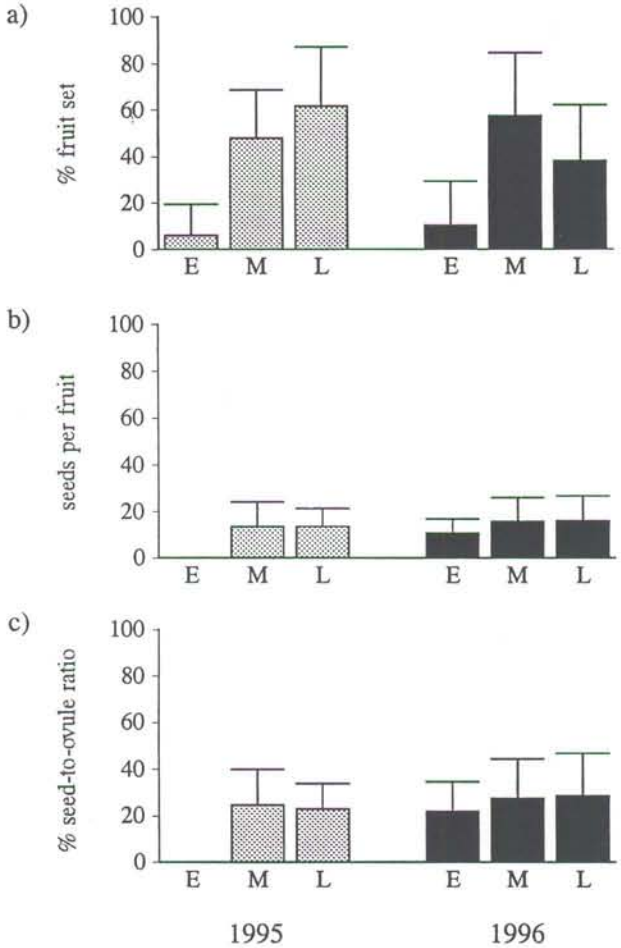

Fig. 2. Fruit set (a), number of seeds per fruit (b), and seed-to-ovule ratio (c) (means + standard deviations) for plants flowering in each of the three flowering subperiods (early, E; middle, M; late, L) in 1995 (grey) and 1996 (black).

either between subperiods or between years, and again the subperiod x year interaction was not significant (Table 1c, Fig. 1c).

Pollen transfer mode and sexual system

Fruit set, mean number of seeds per fruit, and mean seed-to-ovule ratio for the flowers subjected to each of the pollination treatments are shown in Figure 3. Results of statistical analyses of the data for number of seeds per fruit and seed-to-ovule ratio are summarized in Table 2.

Fruits were produced by flowers bagged without manual pollination (treatment d), indicating that spontaneous autogamy can occur in the absence of insect visits. The fruit set of these flowers was significantly lower than that of control flowers (treatment e) ($\chi^2 = 25.55$, d.f. = 1, $p < 0.0001$); however, there were no significant differences in either mean number of seeds per fruit or mean seed-to-ovule ratio (Table 2, Fig. 3).

The fruit set of flowers subjected to treatments a (pollen from same flower), b (pollen from same plant, different flower) and c (pollen from different plant) was in all cases significantly higher than that of the control flowers (a versus e, $\chi^2 = 14.73$, d.f. = 1, $p < 0.0001$; b versus e, $\chi^2 = 14.35$, d.f. = 1, $p < 0.0001$; c versus e, ($\chi^2 = 23.47$, d.f. = 1, $p < 0.0001$). Similarly, both mean number of seeds per fruit and mean seed-to-ovule ratio were significantly higher among flowers subjected to treatments a, b or c than among control flowers (Table 2, Fig. 3). None of the three variables considered varied significantly among treatments a, b and c.

The estimated value of the self compatibility index was 0.91, indicating that the fertilization capacity of self pollen is almost as high as that of nonself pollen.

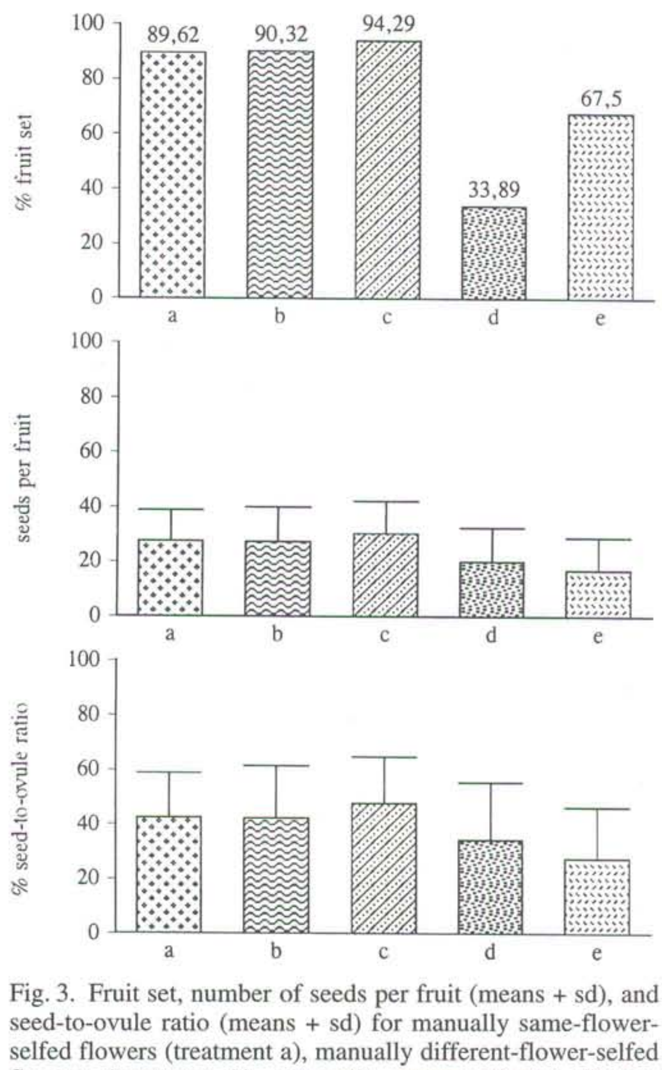

Fig. 3. Fruit set, number of seeds per fruit (means + sd), and seed-to-ovule ratio (means + sd) for manually same-flower-selfed flowers (treatment a), manually different-flower-selfed flowers (treatment b), manually cross-pollinated flowers (treatment c), flowers allowed the possibility of spontaneous selfing only (treatment d) and flowers under natural conditions (treatment e).

Table 1. Results of analysis of variance to investigate the effects of year (1995 or 1996) and flowering subperiod (early, middle or late) on a) fruit set, b) number of seeds per fruit, and c) seed-to-ovule ratio.

Source of variation	SS	DF	MS	F	p
a) Fruit set					
Year	136.04	1	136.04	0.39	0.532
Subperiod	28038.12	2	14019.06	40.47	0.000
Year x subperiod	2738.58	2	1369.29	3.95	0.021
Within + Residual error	46424.11	134	346.5		
b) Seeds per fruit					
Year	130.75	1	130.75	1.25	0.266
Subperiod	1.24	1	1.24	0.01	0.913
Year x subperiod	0.00	1	0.00	0.00	0.998
Within + Residual error	21826.18	208	104.93		
c) Seed-to-ovule ratio					
Year	158.48	1	158.48	1.25	0.265
Subperiod	1.00	1	1.00	0.01	0.929
Year x subperiod	10.84	1	10.84	0.09	0.770
Within + Residual error	263161.68	208	126.74		

Table 2. Results of analysis of variance and subsequent Tukey-HSD tests to investigate the effects of pollination treatment (assisted-selfing, geitonogamy, xenogamy, spontaneous-selfing, control; treatments a–e respectively) on a) number of seeds per fruit and b) seed-to-ovule ratio. (n.s. = p > 0.05)

	DF	SS	MS	F Ratio	p	p (Tukey-HSD)
a) Seeds per fruit	4	8320.54	2080.14	14.529	0.000	
Control vs Assisted selfing						<0.05
Control vs Geitonogamy						<0.05
Control vs Xenogamy						<0.05
Control vs Spontaneous selfing						n.s.
b) Seed-to-ovule ratio	4	7736.84	1934.21	13.574	0.000	
Control vs Assisted selfing						<0.05
Control vs Geitonogamy						<0.05
Control vs Xenogamy						<0.05
Control vs Spontaneous selfing						n.s.

Discussion

The study population of *Pancratium maritimum* has a long flowering period (June–September), though different to that reported by EISIKOWITCH & GALIL (1971) for populations in Israel (July–October). Such differences may be attributable to latitude (OLLERTON & LACK 1992). The long reproductive period, together with the pronounced flowering peak, may indicate a 'satiation strategy' (see JANZEN 1971) for protection against insect attack: the study population suffers intensive predation of fruits and seeds by larvae of the moth *Britys crini* subsp. *pancratii.*

Our results indicate that the fruit set of early-flowering plants was lower than that of late-flowering plants (though the precise pattern differed between the two years of study; see Fig. 2); however, neither mean number of seeds per fruit nor mean seed-to-ovule ratio varied significantly either between years or among flowering subperiods. Previous studies of species with long population flowering periods have generally found that early-flowering plants have greater reproductive success than late-flowering plants (ZIMMERMAN & GROSS 1984, GALEN et al. 1985, LUBBERS & CHRISTENSEN 1986, MULLINS & MARKS 1987, HERRERA 1992, OLESEN & WARNCKE 1992, OBESO 1993, RAMSEY 1995). However, the opposite pattern (i.e., late-flowering plants are more successful) has been reported for some species (GROSS & WERNER 1983, THOMSON 1985). Our results are partially in accordance with those of the latter studies, in that the fruit set of plants flowering in the early subperiod (June) was much lower than that of plants flowering in the middle and late subperiods (July and August); note, however, that although fruit set peaked in the late subperiod in 1995 (in accordance with the "late-flowerers successful" pattern), it peaked in the middle subperiod in 1996 (Fig. 2).

Manual pollination experiments indicated that the fertilization capacity of self pollen is almost as high as that of nonself pollen (SCI = 0.91). In addition, manual pollination (whether with self or nonself pollen) gave both better fruit set and more seeds per fruit than did natural pollination. The relative positions of anthers and stigma in flowers of *P. maritimum* indicate "approach herkogamy" (*sensu* WEBB & LLOYD 1986); i.e., the arrangement is such that pollinators can be expected to contact the stigma first, with that flower's pollen being transferred to the pollinator subsequently, after is has entered the flower in search of the nectar at the base of the corolla tube. In flowers of this type, effective pollination requires the pollinator to be the appropriate size and to enter the flower in the 'correct' manner. In EISIKOWITCH & GALIL's (1971) study in Israel, these conditions were met by legitimate pollinators. WEBB & LLOYD (1986) suggest that herkogamy may have arisen for two reasons: first, to prevent deposition of self pollen (because it interferes with donation and receipt of nonself pollen), and second to prevent self-fertilization. The results obtained in the present study indicate that *P. maritimum* is a self-compatible species which can produce fruits and seeds by spontaneous self-pollination: thus both of the above reasons are in this case plausible.

Although other species of the family Amaryllidaceae with herkogamous flowers have been shown to produce fruits and seeds following manual (assisted) selfing (*Zephyrantes atamasco,* BROYLES & WYATT 1991; *Crinum erubescens,* MANASSE & STANTON 1991; *Sternbergia clusiana,* DAFNI & WERKER 1982), good seed production following spontaneous selfing – as observed in the present study – has not been reported previously. Specifically, spontaneous selfing gave rise to poor fruit/seed production in *Zephyrantes atamasco,* (BROYLES & WYATT 1991) and did not occur in *Sternbergia clusiana* (DAFNI & WERKER 1982).

In their study of *P. maritimum* EISIKOWITCH & GALIL (1971) found that the plants of their study population were incapable of spontaneous selfing and self-incompatible. This suggests that the breeding system of our population of *P. maritimum* differs from that of populations in Israel. Plant breeding system can evolve rapidly and differences often arise between disjunct populations (see WYATT 1988 for a review). Ecologically marginal or geographically peripheral populations are often self-fertile, while populations at the center of a species' range are generally cross-pollinating (WYATT 1988, RAMSEY 1993, RAMSEY et al. 1993, see also references cited in these articles). In Europe, *P. maritimum* has a mostly Mediterranean distribution; the populations in northwest Spain can thus be considered geographically peripheral. Furthermore, EISIKOWITCH & GALIL's results suggest that the pollinator spectrum is relatively broad, and that pollinators are relatively abundant, in their population; this would be expected to favour outcrossing. In our population, by contrast, flowers are very rarely visited by polinators (MEDRANO, unpublished data); under such conditions, self-fertile individuals may have been at a selective advantage.

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