

**PATTERNS OF FRUIT AND SEED SET WITHIN  
INFLORESCENCES OF *PANCRATIUM MARITIMUM*  
(AMARYLLIDACEAE): NONUNIFORM POLLINATION,  
RESOURCE LIMITATION, OR  
ARCHITECTURAL EFFECTS?<sup>1</sup>**

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We investigated patterns of fruit and seed production on inflorescences of a population of *Pancratium maritimum* in northwest Spain over a 2-yr period. Initial findings showed that the earliest opening flowers on an inflorescence are more likely to set fruit and produce more seeds than later opening flowers and that this pattern is maintained throughout the flowering season. Supplementary pollination and flower-removal experiments were performed to investigate whether the observed pattern is attributable (a) to variation in pollen receipt, (b) to sequestration of resources by the earliest flowers on an inflorescence, and/or (c) to “architectural” limitations on the fruit/seed production of later flowers. Supplementary pollination did not improve fruit or seed production by late flowers in either of the 2 yr of study. In flower-removal experiments, the remaining flowers showed improved fruit set and mean number of seeds per flower, by comparison with flowers in the same position on control inflorescences. When all flowers except the latest third were removed, these showed fruit set and seed production similar to those of early flowers on control inflorescences. These results strongly suggest that the observed within-inflorescence patterns of fruit and seed production in *P. maritimum* are mainly attributable to competition for resources (i.e., explanation b), though other adaptive explanations cannot be ruled out.

**Key words:** Amaryllidaceae; architectural effects; floral variation; fruit and seed production; *Pancratium maritimum*; pollen limitation; resource allocation.

In plants in which the flowers are grouped in inflorescences, consistent patterns of within-inflorescence variation in morphological and functional characteristics of flowers are commonly observed. Numerous studies have investigated relationships between reproductive success and within-inflorescence spatial position (proximal or distal) and/or time of opening (early or late) (Stephenson, 1980, 1981; Wyatt, 1982; Bawa and Webb, 1984; Holtsford, 1985; McKone, 1985; Lee, 1988; Solomon, 1988; Schoen and Dubuc, 1990; Berry and Calvo, 1991; Herrera, 1991; Ehrlén, 1992; Karoly, 1992; Goldingay and Whelan, 1993; Obeso, 1993; Vaughton, 1993; Guitián, 1994; Brunet, 1996; Emms, 1996; Guitián and Navarro, 1996; Navarro, 1996; Méndez, 1997; Vaughton and Ramsey, 1997; for a review, see Diggle, 1995). In species with acropetal inflorescence development, the probability of fruit set and/or number of seeds per flower is often lower for distal/late-opening flowers than for proximal/early-opening flowers (Solomon, 1988; Herrera, 1991; Ehrlén,

1992, 1993; Karoly, 1992; Guitián, 1994; Guitián and Navarro, 1996; Navarro, 1996). Less commonly, fruit set is highest in intermediate flowers (Sutherland, 1987) or in distal/late-opening flowers (Goldingay and Whelan, 1993). Some studies of species with basipetal inflorescence development have found higher fruit and seed set in distal/early-opening flowers (Brunet, 1996), while others have found higher fruit and seed set in intermediate flowers (Berry and Calvo, 1991) or proximal/late-opening flowers (Vaughton, 1993; Vaughton and Ramsey, 1997). Rarely, there have been reports of species in which fruit and seed production are independent of position within the inflorescence (Zimmerman and Aide, 1989).

Various nonexclusive hypotheses have been put forward to explain such patterns of within-inflorescence variation in female reproductive success.

1) The “resource competition hypothesis” (Stephenson, 1981; Bawa and Webb, 1984; Nakamura, 1986; Lee, 1988; Thomson, 1989; Guitián, 1994) postulates that the observed patterns are attributable to competition among the ovaries of an inflorescence for a limited amount of resources; fruits initiated early, and/or located close to the source of nutrients, sequester more resources than fruits initiated later and/or located more distally (Lee, 1988).

2) The “non-uniform pollination hypothesis” (Thomson, 1985, 1989; Lee, 1988; Berry and Calvo, 1991; Goldingay and Whelan, 1993; Brunet and Charlesworth, 1995) postulates that the observed patterns may be attributable to variation in pollen receipt over the inflorescence flowering period. Specifically, the relatively low fruit or seed sets of certain flowers on the inflorescence

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may be attributable to insufficient quantity or quality of pollen (Lee, 1988).

3) The “architectural effects hypothesis” (Wyatt, 1982; Lee, 1988; Thomson, 1989; Wolfe, 1992; Diggle, 1992, 1995, 1997) postulates that the observed patterns are attributable to intrinsic (“architectural”) limitations on the reproductive success of flowers in different positions within the inflorescence (Diggle, 1995, and references therein). This hypothesis is based on studies in which the fruit set of late-opening flowers is not affected by the removal of early-opening flowers or the prevention of their fruiting (Sutherland, 1987; Berry and Calvo, 1991).

In the present study we investigated patterns of fruit set and seed production among flowers within umbels of *Pancretium maritimum* L. (Amaryllidaceae) over two reproductive seasons. Our aim was to investigate the extent to which these three hypotheses explain the patterns observed in an umbel-type inflorescence, within which there is temporal but not spatial variation in opening time among flowers (i.e., flowers open at different times but do not vary appreciably as regards distance from the growth axis). Species with inflorescences of this type have been little studied to date (though see Wyatt, 1980). Because a previous study revealed that fruit set varies over the flowering season (Medrano, Guitián, and Guitián, 1999), we took account of possible effects of timing in the population flowering period. Specifically, we aimed to determine whether fruit set and seed set are affected by position within the flowering order on the umbel, and if so (1) whether the observed patterns are dependent on timing in the flowering period and (2) to what extent pollination, resource availability, and/or architectural effects influence the female reproductive success of flowers at different positions within the inflorescence.

## MATERIALS AND METHODS

**The plant and the study area**—*Pancretium maritimum* L. is a bulbous perennial geophyte that occurs on dunes and other sandy coastal habitats. In Europe and North Africa it is present in Morocco, the Iberian Peninsula, and France. In the study area (see below), the flowering period is June to September. *Pancretium maritimum* has an umbel-type inflorescence with 2–14 white flowers, which develop centripetally on a scape ~15 cm long. Plants generally produce one inflorescence per season (occasionally two). Anthesis occurs at dusk and the flower remains open for ~36 h. Depending on the number of flowers on the inflorescence, the time elapsed between anthesis of the first and last flower ranges from 3 to 15 d (since flowers open sequentially, generally one per day, though sometimes two or rarely three per day; M. Medrano, unpublished data). In a previous study, *P. maritimum* was found to be self-compatible and to produce fruits by autonomous autogamy; furthermore, fruit set (though not seed set) varied over the flowering season (Medrano, Guitián, and Guitián, 1999). The mean number of ovules per flower is 56.6 ( $N = 74$  flowers,  $SD = 9.7$ ). The fruit is a capsule with loculicid dehiscence, containing on average 13.6 seeds ( $N = 341$ ,  $SD = 9.8$ ).

The study was carried out in 1996 and 1997 in a population of *P. maritimum* in the Corrubedo Dune Complex National Park in the southwest of A Coruña Province in Galicia (northwest Spain). At this site, *P. maritimum* occurs on stabilized sand as part of chamaephyte communities dominated by species including *Helichrysum picardii* var. *virescens*, *Artemisia crithmifolia*, *Scophularia frutescens*, and *Iberis procumbens*.

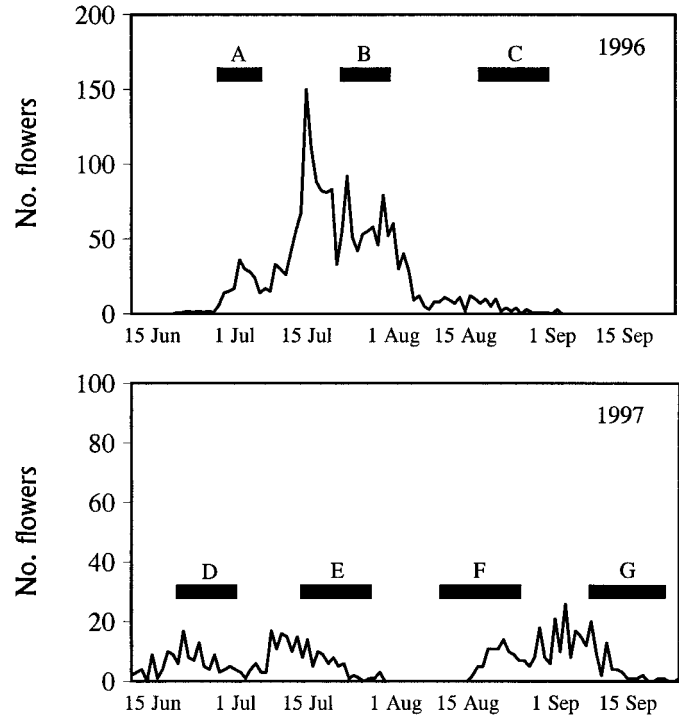


Fig. 1. Flowering phenology of the study population of *P. maritimum* in the 2 yr of study, showing the subperiods (1996 A, B, and C and 1997 D, E, F, and G) defined for the experimental design. Note that fruit set in subperiod D of 1997 was zero in all experimental groups and controls, and this subperiod was therefore excluded from the analyses.

At the nearby weather station of Santa Eugenia de Riveira (25 m a.s.l.), mean temperature is 14.6°C, and mean annual rainfall 1244 mm (Carballeira et al., 1983).

**Experimental design**—To characterize patterns of fruit set in the study population, and to investigate whether these patterns vary over the flowering period (12 and 18 wk in 1996 and 1997, respectively), we divided the flowering period into subperiods, as shown in Fig. 1. Note that the subperiods defined in each year do not correspond, since flowering patterns differed markedly between the 2 yr of study. Note also that fruit set in subperiod D of 1997 was zero in all experimental groups and controls, and this subperiod was therefore excluded from the analyses. Patterns of seed set within inflorescences were investigated in the same plants as those used for the study of fruit set, but only in subperiods 1996-A, 1996-B, 1997-E, and 1997-F. At the end of the reproductive season in both years of study, the study population suffered intense herbivory by larvae of the moth *Brithys crini* subsp. *pancratii* (Noctuidae), with the result that sample sizes in 1996-C and 1997-G were insufficient for analysis of patterns of seed set.

**Open pollination: fruit set**—In both years and in all subperiods, we randomly selected inflorescences (one inflorescence per plant) that initiated and completed flowering within that subperiod, and marked these plants with plastic tags (56 plants in 1996-A, 44 plants in 1996-B, 39 plants in 1996-C, 50 plants in 1997-E, 50 plants in 1997-F, and 54 plants in 1997-G). In all cases, and for each inflorescence considered, we numbered each flower as it opened; after all flowers on that inflorescence had opened, we monitored that inflorescence weekly until 20–30 d after anthesis, recording fruit set in all cases. The total number of flowers monitored was 934 in 1996 and 1227 in 1997; the mean number of flowers per inflorescence was 6.7 (range = 4–11) in 1996 and 7.9 (range = 4–13) in 1997.

*Open pollination: seed set*—We collected a total of 33 “complete” infructescences (i.e., infructescences that had not lost any full-size fruits as a result of herbivory during the maturation process) from the naturally pollinated nonmanipulated plants monitored in 1996 (six infructescences from subperiod A, 27 from subperiod B;  $N = 139$  fruits), and a total of 60 complete infructescences from the naturally pollinated nonmanipulated plants monitored in 1997 (36 from subperiod E, 24 from subperiod F;  $N = 247$  fruits). In all cases infructescences were collected 60–80 d after anthesis of the first flower. The infructescences were taken to the laboratory, and the number of mature and aborted seeds in each fruit was counted with the aid of a stereomicroscope.

*Nonuniform pollination hypothesis: fruit set*—If within-inflorescence patterns in female reproductive success are attributable to differences in amount of pollen received, supply of pollen to all flowers should lead to uniform female reproductive success. To test for this possibility, we carried out supplementary pollination (SP) experiments in 1996 and 1997, randomly selecting 14–19 plants in flower in each subperiod (one inflorescence per plant; 1996-A, 14 plants; 1996-B, 14 plants; 1996-C, 15 plants; 1997-E, 19 plants; 1997-F, 19 plants; 1997-G, 18 plants). As each flower opened, we numbered and pollinated it with a brush containing abundant xenogamous pollen, obtained by collecting recently opened stamens from 10 to 15 plants located at least 5 m away from the recipient plant. The brush-pollination was repeated 24 h later. The flowers were subsequently monitored weekly, and fruit set was noted 20–30 d after anthesis.

*Nonuniform pollination hypothesis: seed set*—We collected a total of 16 complete infructescences (i.e., infructescences not affected by herbivory) from the supplementary-pollinated plants monitored in 1996 (eight infructescences from subperiod A, eight from subperiod B;  $N = 59$  fruits), and a total of 30 complete infructescences from the supplementary-pollinated plants monitored in 1997 (16 from subperiod E, 14 from subperiod F;  $N = 185$  fruits). The infructescences were taken to the laboratory, and the number of mature and aborted seeds in each fruit was counted with the aid of a stereomicroscope.

*Architectural effects vs. resource competition: fruit set*—To discriminate between architectural effects and resource competition among flowers within inflorescences, flower-removal experiments were performed in 1996 and 1997. The 1996 experiments were designed to identify possible variation in these effects over the flowering season: from each inflorescence (one inflorescence per plant; 14 plants in 1996-A, 16 plants in 1996-B, 16 plants in 1996-C), we removed the first three flowers to open (treatment FR<sub>3e</sub>). The 1997 experiments were carried out only in subperiod E: we randomly selected 34 inflorescences (on 34 plants) and removed the first two-thirds of the flowers to open (16 inflorescences; treatment FR<sub>2+1</sub>) or the last two-thirds of the flowers to open (18 inflorescences; treatment FR<sub>1+1</sub>). In all cases (i.e., both in 1996 and 1997), the flowers removed were cut within 24–72 h of anthesis, and the remaining flowers in the inflorescence were brush-pollinated (as described above for treatment SP), to allow us simultaneously to rule out the possibility of effects due to deficient pollination. In both years, the controls were inflorescences from the same subperiod from the SP experiments. [A detailed explanation of the basis for experimental designs of this type (FR<sub>3e</sub>, FR<sub>2+1</sub>, FR<sub>1+1</sub>, controls) is given by Diggle (1997)]. The flowers were monitored weekly, and whether each set fruit was noted 20–30 d after anthesis.

*Architectural effects vs. resource competition: seed set*—We collected a total of 23 complete infructescences from the plants subjected to treatment FR<sub>3e</sub> in 1996 (11 infructescences from subperiod A, 12 from subperiod B;  $N = 65$  fruits). In 1997, we collected 16 complete infructescences from the inflorescences subjected to treatment FR<sub>2+1</sub>, and 16 from the inflorescences subjected to treatment FR<sub>1+1</sub> ( $N = 78$  fruits). The infructescences were taken to the laboratory, and the number of

mature and aborted seeds in each fruit was counted with the aid of a stereomicroscope.

*Data analysis*—In all analyses of factors influencing fruit/seed set, only inflorescences that produced at least one fruit were considered. To allow consideration of inflorescences with different numbers of flowers, flower “position” was in all cases defined as “early” (the earliest third to open), “intermediate” (the middle third), or “late” (the last third). For example, flower number 3 in an 11-flower inflorescence was classified as “early,” and flower number 4 as “intermediate” (see Berry and Calvo, 1991). Unless otherwise stated, statistical significance is taken to be indicated by  $P$  values of  $<5\%$ .

*Fruit set*—To investigate whether the probability that a flower will set fruit varies with position in the inflorescence and, if so, whether the effect of position varies over the flowering season, we used maximum-likelihood logistic regression (CATMOD; SAS, 1992), with the independent variables “position” and “position  $\times$  subperiod.” The data for the 2 yr and for the two modes of pollination (natural or supplementary) were analyzed separately. Subsequent pairwise comparisons between positions were done with  $G$  tests; since these were multiple comparisons, the significance level was corrected for the number of tests (Bonferroni method; Sokal and Rohlf, 1995).  $G$  tests were also used to compare fruit set between flowers from inflorescences subjected to flower removal and their corresponding controls.

*Seed set*—For each position (early, intermediate, and late) and each inflorescence of each treatment (control, supplementary pollination, flower-removal treatments), we calculated mean number of seeds per flower and mean seed-to-ovule ratio, taking flowers that did not set seed into account. For between-position comparisons of mean number of seeds per flower and mean seed-to-ovule ratio, we used nonparametric tests in all cases, since the data were markedly non-normal even after standard transformations (largely because of frequent zero seed set among “late” flowers). Specifically, the effects of position and pollination type on mean number of seeds per flower and mean seed-to-ovule ratio were investigated by Friedman’s analysis of variance, with subsequent pairwise comparisons between positions by Tukey tests for nonparametric randomized-block analysis of variance (Zar, 1996). The effects of flower removal on seed production by the remaining flowers were investigated with Kruskal-Wallis tests.

## RESULTS

*Open pollination—Fruit set*—Data on the fruit set of naturally pollinated flowers (considering only those inflorescences that produced at least one fruit) are summarized for each position and each subperiod in Figs. 2A and 3A. The results of maximum-likelihood logistic regression indicate that in both years the factor “position” had significant effects on the probability that a flower set fruit (1996:  $\chi^2 = 87.1$ ,  $df = 2$ ,  $P < 0.0001$ ; 1997:  $\chi^2 = 134.3$ ,  $df = 2$ ,  $P < 0.0001$ ); the interaction “position  $\times$  subperiod” had a significant effect in 1997 ( $\chi^2 = 24.9$ ,  $df = 4$ ,  $P = 0.0001$ ) but not in 1996 ( $\chi^2 = 7.3$ ,  $df = 4$ ,  $P = 0.12$ ). The results of  $G$  tests indicate that the fruit set of early flowers was significantly higher than that of intermediate and late flowers, except in 1997 subperiods E and F, when fruit set did not differ significantly between early and intermediate flowers (Figs. 2A, 3A). In both years and all subperiods, the fruit set of intermediate flowers was significantly higher than that of late flowers (Figs. 2A, 3A).

*Seed set*—Mean number of seeds per flower and mean

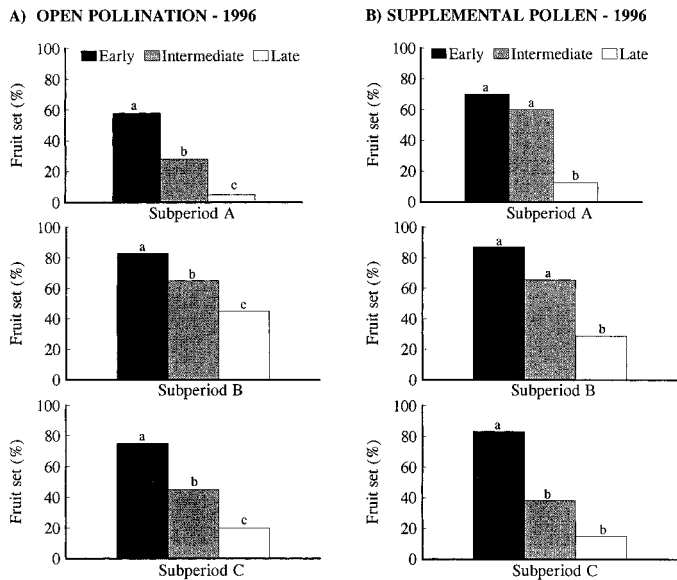


Fig. 2. Fruit set of early (black), intermediate (grey), and late (white) flowers, considering only inflorescences that produced at least one fruit. (A) Open pollination. (B) Supplemental pollination. Data are shown for the three different subperiods considered in 1996 (A, B, and C). Within each subperiod, means with the same letter do not differ significantly (Bonferroni-corrected  $P > 0.0125$ ).

seed-to-ovule ratio under natural conditions are shown for flowers in the three positions, in the subperiods A, B, E, and F of the 2 yr of study, in Figs. 4A and 5A. The results of Friedman's analysis of variance show that mean number of seeds per flower varied significantly with position in the inflorescence in all subperiods of both years of study (1996-A:  $\chi^2 = 7.7$ ,  $P = 0.021$ ; 1996-B:  $\chi^2 =$

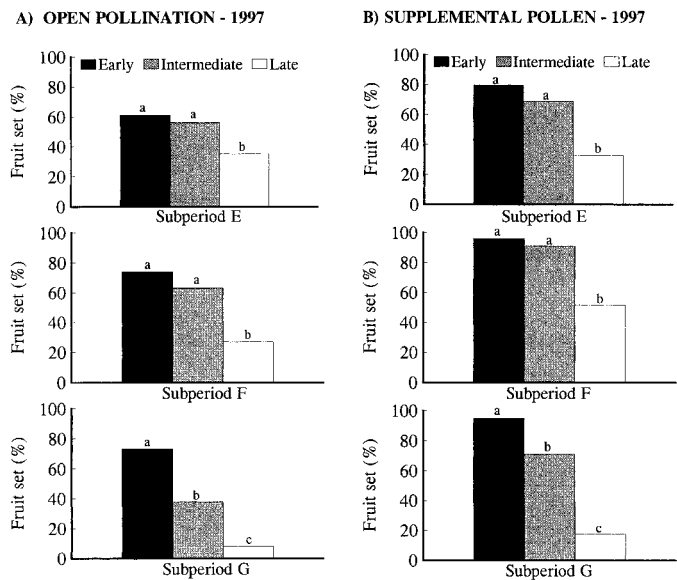


Fig. 3. Fruit set of early (black), intermediate (grey), and late (white) flowers, considering only inflorescences that produced at least one fruit. (A) Open pollination. (B) Supplemental pollination. Data are shown for the three different subperiods considered in 1997 (E, F, and G). Within each subperiod, means with the same letter do not differ significantly (Bonferroni-corrected  $P > 0.0125$ ).

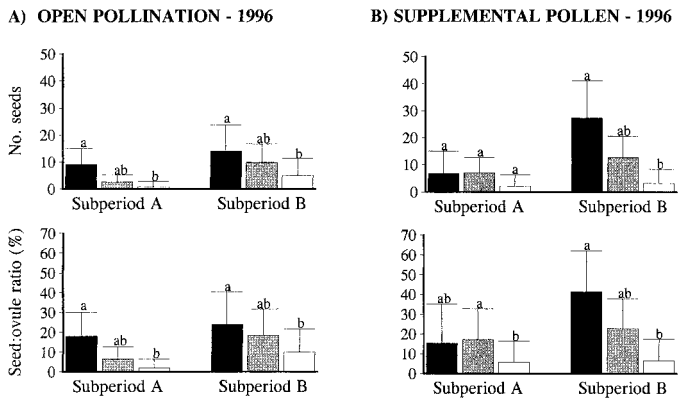


Fig. 4. Mean number of seeds per flower (+ SD) and mean seed-to-ovule ratio (+ SD) among early (E, black), intermediate (I, grey), and late (L, white) flowers, considering only inflorescences that produced at least one fruit. (A) Open pollination. (B) Supplemental pollination. Data are shown for 1996 subperiods A and B. Means with the same letter do not differ significantly at the 5% level.

10.9,  $P = 0.004$ ; 1997-E:  $\chi^2 = 7.6$ ,  $P = 0.022$ ; 1997-F:  $\chi^2 = 21.3$ ,  $P < 0.0001$ ). Similarly, mean seed-to-ovule ratio varied significantly with position in all subperiods except 1997-E (1996-A:  $\chi^2 = 7.7$ ,  $P = 0.021$ ; 1996-B:  $\chi^2 = 9.2$ ,  $P = 0.01$ ; 1997-E:  $\chi^2 = 4.5$ ,  $P = 0.108$ ; 1997-F:  $\chi^2 = 19.8$ ,  $P = 0.0001$ ). Pairwise comparisons with Tukey tests indicated that neither mean number of seeds per flower nor mean seed-to-ovule ratio differed significantly either between early and intermediate flowers or between intermediate and late flowers, in any of the subperiods considered (with the exception of 1997 subperiod F, in which both variables were significantly higher for intermediate flowers than for late flowers) (Fig. 5A). However, both variables (mean number of seeds per flower and mean seed-to-ovule ratio) were significantly higher for early flowers than for late flowers in subperiods A, B, and F (Figs. 4A, 5A).

**Nonuniform pollination hypothesis—Fruit set**—Figures 2B and 3B show fruit set in the early, intermediate,

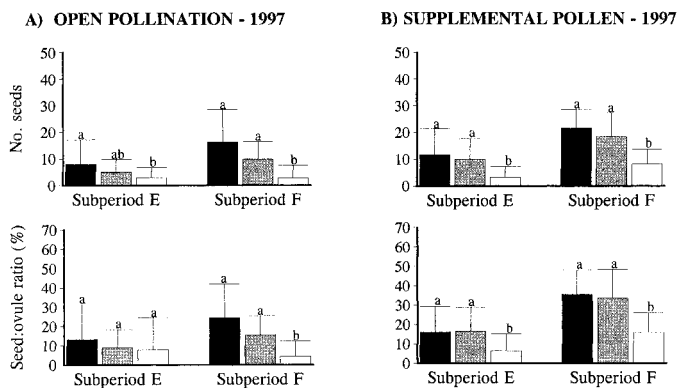


Fig. 5. Mean number of seeds per flower (+ SD) and mean seed-to-ovule ratio (+ SD) among early (E, black), intermediate (I, grey), and late (L, white) flowers, considering only inflorescences that produced at least one fruit. (A) Open pollination. (B) Supplemental pollination. Data are shown for 1997 subperiods E and F. Means with the same letter do not differ significantly at the 5% level.

TABLE 1. Fruit sets of flowers at each of the three positions (early, intermediate, and late) in inflorescences subjected to treatment FR<sub>3e</sub> (i.e., removal of the three earliest opening flowers) and of flowers in the corresponding control inflorescences. These experiments were carried out in 1996. Values in parentheses are numbers of fruits and numbers of flowers, respectively. For each subperiod, the results of *G* tests (for pairwise comparison of fruit set between flowers from treated inflorescences and from the corresponding controls) are also shown.

Subperiod	Treatment	Fruit set (%)		
		Early	Intermediate	Late
A	FR <sub>3e</sub>	—	78.6 (22, 28)	22.7 (10, 44)
	Control	70 (7, 10)	60 (9, 15)	12.5 (2, 16)
	<i>G</i> test		1.63 <sup>NS</sup>	0.83 <sup>NS</sup>
B	FR <sub>3e</sub>	—	100 (27, 27)	53.2 (25, 47)
	Control	87.1 (27, 31)	65.6 (21, 32)	28.6 (10, 35)
	<i>G</i> test		15.58***	5.07*
C	FR <sub>3e</sub>	—	72.7 (22, 16)	41.7 (36, 15)
	Control	83.3 (25, 30)	38.2 (13, 34)	15 (6, 40)
	<i>G</i> test		6.55*	6.88**

NS = not significant, \* *P* < 0.05, \*\* *P* < 0.01, \*\*\* *P* < 0.001.

and late positions for inflorescences included in the supplementary pollination experiments carried out in 1996 and 1997. The results of maximum-likelihood logistic regression show that “position” had significant effects on the probability that a flower set fruit in both 1996 and 1997 (1996:  $\chi^2 = 44.9$ , *df* = 2, *P* < 0.0001; 1997:  $\chi^2 = 87.1$ , *df* = 2, *P* < 0.0001). The interaction “position × subperiod” had a significant effect in 1997 ( $\chi^2 = 13.1$ , *df* = 4, *P* = 0.011) but not in 1996 ( $\chi^2 = 3.9$ , *df* = 4, *P* = 0.426). The results of *G* tests indicate that the fruit set of early and intermediate flowers was significantly higher than that of late flowers in all subperiods of both years, even with supplemental pollination, except in 1996 subperiod C, when fruit set did not differ significantly between intermediate and late flowers (Figs. 2B, 3B). However, the differences between early and intermediate flowers were not always significant (Figs. 2B, 3B).

**Seed set**—The among-position differences observed in seed set under open pollination were maintained when supplemental pollen was applied (Figs. 4B, 5B). Position had a significant effect on mean number of seeds per flower in all subperiods in both years, except in 1996 subperiod A (1996-A:  $\chi^2 = 5.8$ , *P* = 0.055; 1996-B:  $\chi^2 = 10.8$ , *P* = 0.005; 1997-E:  $\chi^2 = 11.5$ , *P* = 0.003; 1997-F:  $\chi^2 = 19$ , *P* = 0.0001). Similarly, position had a significant effect on mean seed-to-ovule ratio in all subperiods in both years (1996-A:  $\chi^2 = 6.3$ , *P* = 0.043; 1996-

B:  $\chi^2 = 10.8$ , *P* = 0.005; 1997-E:  $\chi^2 = 11.7$ , *P* = 0.003; 1997-F:  $\chi^2 = 19.9$ , *P* < 0.0001). Pairwise comparisons with Tukey tests indicated that neither mean number of seeds per flower nor mean seed-to-ovule ratio differed significantly between early and intermediate flowers in any of the subperiods considered (Figs. 4, 5). Considering intermediate and late flowers, no significant differences in either mean number of seeds per flower or mean seed-to-ovule ratio were observed in 1996, except in subperiod A, in which the mean seed-to-ovule ratio was significantly higher in intermediate than in late flowers; in all subperiods of 1997, however, both variables were significantly higher for intermediate than for late flowers (Figs. 4B, 5B). Early flowers consistently showed significantly higher mean number of seeds per flower and mean seed-to-ovule ratio than late flowers, except in 1996-A, in which the *P* value obtained was slightly greater than 5% (Fig. 4B).

**Architectural effects vs. resource competition**—**Fruit set**—In the 1996 experiments, the three earliest flowers were removed (just after anthesis) from treated inflorescences. The mean number of flowers remaining on the inflorescence was 4.9 (range 2–7). In 1996 subperiods B and C, the removal of the three earliest flowers significantly improved the fruit set of both the intermediate and late flowers of those inflorescences (with respect to flowers in the same positions in control inflorescences) (Table 1); in 1996 subperiod A, however, no significant effect was observed (Table 1). In none of the three subperiods did the fruit set of intermediate flowers in treated inflorescences differ significantly from that of early flowers in control inflorescences (subperiod A: *G* = 0.29, *P* = 0.44; subperiod B: *G* = 5.27, *P* = 0.07; subperiod C: *G* = 0.85, *P* = 0.28).

In the 1997 experiments, either all intermediate and late flowers (FR<sub>i+l</sub>) or all early and intermediate flowers (FR<sub>e+i</sub>) were removed from treated inflorescences. The mean number of flowers remaining on the inflorescence was 3.0 (range 2–5) after treatment FR<sub>e+i</sub>, and 2.7 (range 2–4) after treatment FR<sub>i+l</sub>. Treatment FR<sub>i+l</sub> had no significant effect on the fruit set of early flowers (by comparison with control-inflorescence early flowers; Table 2). In contrast, treatment FR<sub>e+i</sub> led to a very marked improvement in the fruit set of late flowers with respect to

TABLE 2. Fruit sets of remaining flowers in inflorescences subjected to treatment FR<sub>i+l</sub> (i.e., removal of the latest two-thirds of flowers) or FR<sub>e+i</sub> (i.e., removal of the earliest two-thirds of flowers), and of flowers in the corresponding positions in control inflorescences. These experiments were carried out in 1997. Values in parentheses are numbers of fruits and numbers of flowers, respectively. The results of *G* tests (for pairwise comparison of fruit set between flowers from treated inflorescences and from the corresponding controls) are also shown.

Treatment	Fruit set (%)		
	Early	Intermediate	Late
FR <sub>i+l</sub>	90.7 (39, 43)	—	—
FR <sub>e+i</sub>	—	—	83.7 (41, 49)
Control	79.6 (35, 44)	68.8 (33, 48)	32.7 (17, 52)
<i>G</i> test	2.18 <sup>NS</sup>		28.44***

NS = not significant, \*\*\* *P* < 0.001.

TABLE 3. Mean (SD) number of seeds per flower and mean (SD) seed-to-ovule ratio of flowers at each of the three positions (early, intermediate, and late) in inflorescences subjected to treatment FR<sub>3e</sub> (i.e., removal of the three earliest opening flowers), and of flowers in the corresponding control inflorescences. These experiments were carried out in 1996 (subperiods A and B). For each position and each subperiod, the results of Kruskal-Wallis tests (*H*; for pairwise comparison of mean number of seeds per flower or mean seed-to-ovule ratio between flowers from treated inflorescences and from the corresponding controls) are also shown.

Variable and flower position	Subperiod A			Subperiod B		
	FR <sub>3e</sub>	Control	<i>H</i>	FR <sub>3e</sub>	Control	<i>H</i>
Number of seeds per flower						
Early	—	6.86 (8.3)		—	27.38 (13.71)	
Intermediate	10.25 (4.51)	7.08 (5.52)	3.02 <sup>NS</sup>	24.82 (10.64)	12.73 (7.93)	4.35*
Late	4.24 (4.82)	2.13 (4.16)	1.79 <sup>NS</sup>	8.49 (7.58)	3.23 (1.42)	3.24 <sup>NS</sup>
Seed-to-ovule ratio (%)						
Early	—	15.4 (19.67)		—	41.41 (20.61)	
Intermediate	22.09 (10.14)	17.24 (15.56)	1.75 <sup>NS</sup>	45.64 (16.27)	22.86 (14.86)	6.89**
Late	8.78 (9.49)	5.81 (10.76)	1.56 <sup>NS</sup>	16.5 (14.05)	6.52 (11.08)	3.82 <sup>NS</sup>

NS = not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ .

control-inflorescence late flowers (Table 2). There was no significant difference in fruit set between the early flowers of FR<sub>i+1</sub> inflorescences and the late flowers of FR<sub>e+i</sub> inflorescences ( $G = 1.02$ ,  $P = 0.31$ ).

**Seed set**—In both subperiods (1996-A and 1996-B), removal of the earliest three flowers of inflorescences did not significantly increase in both mean number of seeds per flower and mean seed-to-ovule ratio in intermediate and late flowers except for subperiod B (Table 3). In both subperiods, the mean number of seeds per flower and mean seed-to-ovule ratio of intermediate flowers from treated inflorescences were similar to those for early flowers from control inflorescences (subperiod A:  $H = 1.44$ ,  $P = 0.23$  for mean number of seeds per flower, and  $H = 1.75$ ,  $P = 0.19$  for mean seed-to-ovule ratio; subperiod B:  $H = 0.21$ ,  $P = 0.64$  for mean number of seeds per flower, and  $H = 0.21$ ,  $P = 0.64$  for mean seed-to-ovule ratio).

In the FR<sub>i+1</sub> and FR<sub>e+i</sub> experiments, early flowers from FR<sub>i+1</sub> inflorescences showed significantly higher mean number of seeds per flower and mean seed-to-ovule ratio than early flowers from control inflorescences (Table 4). Likewise, late flowers from FR<sub>e+i</sub> inflorescences showed significantly higher values for both variables than late flowers from control inflorescences (Table 4). There was no significant difference between early flowers from FR<sub>i+1</sub> inflorescences and late flowers from FR<sub>e+i</sub> inflorescences, either in mean number of seeds per flower (Kruskal-Wal-

lis  $H = 0.12$ ,  $P = 0.73$ ) or mean seed-to-ovule ratio (Kruskal-Wallis  $H = 0.89$ ,  $P = 0.35$ ); in other words, seed production after removal of two-thirds of flowers was not affected by the position of the flowers remaining (early or late) and was in all cases better than that of early flowers from control inflorescences (Table 4).

## DISCUSSION

**Fruit and seed set under open pollination**—Under open pollination the earliest opening flowers of inflorescences of *Pancreatium maritimum* have a higher probability of setting fruit than later opening flowers. We detected clear differences between both “early” and “intermediate” flowers and “intermediate” and “late” flowers. Mean number of seeds per flower and mean seed-to-ovule ratio were also higher for early- than for late-opening flowers; however, statistically significant differences were only detected between “early” and “late” flowers. Moreover, these patterns were maintained in all subperiods of both years of study, although fruit set varied significantly among subperiods in 1996, in accordance with results reported previously (Medrano, Guitián, and Guitián, 1999). In *Petrocoptis grandiflora*, the greater fruit set of early flowers is also maintained throughout the flowering season (Guitián and Navarro, 1996).

Our findings are in agreement with previous studies of other hermaphroditic species with flowers grouped in inflorescences, including for example, *Lupinus luteus* (Van

TABLE 4. Mean (SD) number of seeds per flower and mean (SD) seed-to-ovule ratio of flowers at each of the three positions in inflorescences subjected to treatment FR<sub>i+1</sub> (i.e., removal of the latest two-thirds of flowers) or FR<sub>e+i</sub> (i.e., removal of the earliest two-thirds of flowers), and of flowers in the corresponding positions in control inflorescences. These experiments were carried out in 1997. For each position, the results of Kruskal-Wallis tests (*H*; for pairwise comparison of mean number of seeds per flower or mean seed-to-ovule ratio between flowers from treated inflorescences and the corresponding controls) are also shown.

Variable and flower position	FR <sub>i+1</sub>	FR <sub>e+i</sub>	Control	<i>H</i>
Number of seeds per flower				
Early	21.34 (12.85)	—	11.58 (9.72)	4.87*
Intermediate	—	—	9.98 (7.75)	
Late	—	19.62 (10.47)	3.17 (4.08)	19.65***
Seed-to-ovule ratio (%)				
Early	29.15 (18.24)	—	16.11 (13.24)	5.12*
Intermediate	—	—	16.67 (12.13)	
Late	—	33.13 (16.41)	6.5 (8.64)	19.65***

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .

Stevenick, 1957), *Phaseolus vulgaris* (Tamas et al., 1979), *Catalpa speciosa* (Stephenson, 1979, 1980), *Asclepias tuberosa* (Wyatt, 1980), *Yucca whipplei* (Udovic and Aker, 1981), *Caesalpinia eriostachys* (Bawa and Webb, 1984), *Calochortus leichtlinii* (Holtsford, 1985), *Solanum carolinense* (Solomon, 1988), *Lavandula stoechas* (Herrera, 1991), *Lathyrus vernus* (Ehrlén, 1992), *Banksia spinulosa* (Vaughton, 1993), *Prunus mahaleb* (Guitián, 1994), *Petrocoptis grandiflora* (Guitián and Navarro, 1996), and *Aquilegia caerulea* (Brunet, 1996). Possible proximal causes of the decreasing female reproductive success observed within inflorescences of *P. maritimum*, together with possible ultimate functions of late flowers, are discussed below.

**Nonuniform pollination hypothesis**—Variation in the amount of pollen received does not explain the observed differences in fruit and seed set between early and late flowers, because the differences are maintained when abundant pollen is supplied to all flowers. The patterns observed under natural pollination were maintained under supplemental pollination: the probability of a flower setting fruit was higher for early and intermediate flowers than for late flowers, and both mean number of seeds per flower and mean seed-to-ovule ratio were higher for early and intermediate flowers. Similar results have been obtained with many other species (see, e.g., Holtsford, 1985; Devlin, 1989; Karoly, 1992; Brunet, 1996). In a study of *Agave mckelveyana* (a species in which fruit set under natural conditions is lower for the earliest and most basal flowers in the inflorescence), Sutherland (1987); found that most basal flowers aborted regardless of whether or not supplemental pollen was supplied. In *Lathyrus vernus*, Ehrlén (1992) found that even the addition of outcross pollen had no beneficial effect on the fruit set of late flowers. In some species, by contrast, within-inflorescence patterns of fruit and seed production have been shown to be due to variation in the amount of pollen received (Berry and Calvo, 1991; Goldingay and Whelan, 1993).

Variations in fruit and seed set among flowers within inflorescences may be due to variation in the quality (i.e., source) of pollen arriving at flowers in the various positions and to subsequent selective abortion of fruits (for reviews see Stephenson, 1981; Lee, 1988). Variations in the quality of pollen received by flowers at different positions on the inflorescence have been related to directional movement of pollinators, to the order of development of flowers, and to the degree of within-inflorescence dichogamy (temporal overlap of male and female function) (Wyatt, 1982; Nilsson, 1983; Berry and Calvo, 1991; Brunet and Charlesworth, 1995; Brunet, 1996). In species with protandrous flowers on racemose acropetal inflorescences, for example, it has been found that early flowers have a higher probability of receiving xenogamous pollen than later and more apical flowers because of the pollinators' tendency to move up the inflorescence (Wyatt, 1982, and references therein). The present study did not include experiments designed to assess whether the observed pattern of decline in fruit and seed production in *P. maritimum* might be due to variation in pollen quality. However, two observations argue against this possibility. First, within inflorescences of *P. maritimum*

there is virtually no overlap in flowering periods (i.e., most of the time there is only one flower open, though sometimes two or very rarely three flowers may open on the same day), so that the probability of geitonogamous pollen transfer is low. Second, previous studies have not detected significant differences between selfed and outcrossed flowers in either fruit and seed set (Medrano, Guitián, and Guitián, 1999) or seed dry mass (M. Medrano, unpublished data); *Pancreaticum maritimum* therefore does not appear to show inbreeding depression (at least as regards fertilization, and development and maturation of fruits and seeds).

**Architectural effects vs. resource competition**—The results of our 1996 and 1997 flower-removal experiments indicate that removal of flowers from inflorescences of *P. maritimum* improves the fruit and seed set of the remaining flowers. This suggests that the flowers in an inflorescence compete for resources and that late flowers may act as "ovary reserves." Similar findings have been reported for many other species with flowers grouped in inflorescences, including *Catalpa speciosa* (Stephenson, 1980), *Calochortus leichtlinii* (Holtsford, 1985), *Lavandula stoechas* (Muñoz and Devesa, 1987), *Lathyrus vernus* (Ehrlén, 1992), *Banksia spinulosa* (Vaughton, 1993), *Prunus mahaleb* (Guitián, 1994), *Aquilegia caerulea* (Brunet, 1996), and *Petrocoptis grandiflora* (Guitián and Navarro, 1996).

In 1996, removing early flowers did not significantly increase fruit set, seed production, or seed-to-ovule ratio of either intermediate or late flowers, except for subperiod B. This may simply reflect the fact that infructescence sample sizes were small in this year. By contrast, the 1997 flower-removal experiments, with a larger sample size, showed significant effects.

If removal of "early" (or "early and intermediate") flowers increases the fruit set of "intermediate and late" (or "late" flowers) by only a limited amount (i.e., to a level below that of control flowers), one possible explanation is that an "architectural" effect is acting, i.e., that later opening flowers have intrinsically lower maximum fruit set than early-opening flowers, as has been found in a number of species (Sutherland, 1987; Goldingay and Whelan, 1993), though it has also been suggested that preferentialization among-ovary inequalities in resource distribution, only reversible at early stages in inflorescence development, may be responsible (Solomon, 1988). It has been suggested that architectural effects are attributable to reduced vascular supply to more distal positions, considered an inevitable consequence of indeterminate growth of the floral axis (Wolfe, 1992; Diggle, 1995, 1997). In *P. maritimum*, the latest opening flowers of the umbel are located in the same position with respect to the growth axis as the earliest opening flowers, but floral peduncle length, perianth size, and number of ovules are all greater in early flowers than in late flowers (M. Medrano, unpublished data). However, our present findings indicate that removal of early flowers increased the fruit set of later flowers to levels similar to those of early flowers of control inflorescences, arguing against the architectural effect hypothesis for *P. maritimum*. Similar results have been obtained for species including *Catalpa*

*speciosa* (Stephenson, 1980) and *Banksia spinulosa* (Vaughton, 1993).

Specifically, we found that fruit production by intermediate flowers following elimination of the first three flowers in the inflorescence did not differ significantly from that of early flowers of control inflorescences. The results of our 1997 flower-removal experiments indicate that fruit and seed production after removal of two-thirds of the flowers in the inflorescence were independent of whether the flowers remaining were the earliest third or the latest third. Furthermore, when all except early flowers were eliminated from the inflorescence, these flowers produced more fruits and more seeds than the early flowers of control inflorescences, providing further support for the resource competition hypothesis and suggesting that the earliest fruits (even though they act as resource sinks) would perform even better in the absence of resource limitation.

The number of seeds per fruit and seed-to-ovule ratio did not always show a significant increase when only three early flowers were removed from the inflorescence. Even when two-thirds of the flowers on the inflorescence were removed and abundant pollen was supplied to the remaining flowers, only ~30% of ovules produced seed. This suggests that reallocation of resources within inflorescences of *P. maritimum* occurs largely during the fruit production stage. However, the number of seeds produced per fruit and the proportion of ovules producing seeds may be simultaneously subject to other restrictions that cause low seed production per fruit even when available resources increase.

A number of selective advantages of producing excess flowers, initiated fruits, and/or ovules have been postulated. First, the excess may allow for the quality of fruits and/or seeds to be improved by selective abortion (see above). Second, the excess may act as an insurance against variability in resource availability (including pollinators) and/or herbivore pressure. Third, flowers may achieve reproductive success largely through male function, despite being morphologically hermaphrodite. [For additional explanations see, for example, Stephenson, 1981; Bawa and Webb, 1984; Holtsford, 1985; Nakamura, 1986; Sutherland, 1987; Lee, 1988; Ehrlén, 1991, 1993; Guitián, 1993, 1994.]

Burd (1994) has suggested that, in species with "stochastic pollination," the optimum number of ovules per flower is frequently greater than the mean number of pollen tubes that can successfully develop. In *P. maritimum*, the unpredictability of pollen receipt (possibly related to the scarcity of floral visitors) may have contributed to the evolution of excess ovules and flowers.

An adequate understanding of among-flower or among-inflorescence patterns of variation in hermaphroditic plants requires consideration of male as well as female function, and investigation of whether the flowers of the species in question show any form of sexual specialization (see, e.g., Stephenson, 1981; Bawa and Webb, 1984; Brunet, 1996; and references therein). In the case of *Aquilegia caerulea*, Brunet (1996) suggests that the low fruit set and low seed production of late-opening flowers is partly attributable to these flowers being both morphologically and functionally specialized for pollen production and dissemination. Specialization of late-

opening and/or distal flowers for male function has also been reported in other species (e.g., *Calochortus leichtlinii*: Holtsford, 1985; *Solanum carolinense*: Solomon, 1988; *Myrosmodus cochleare*: Berry and Calvo, 1991; *Solanum hirtum*: Diggle, 1991, 1994). In the present study, we did not take this possibility into account at the experimental design stage, so we are unable to rule out the possibility of specialization of late flowers for male function. However, the fact that potential fruit and seed production by late flowers were similar to that of earlier flowers argues against the possibility of sexual specialization. Nevertheless, we have occasionally found late flowers in which the style is absent or atrophied and that lack viable ovules, suggesting that there may be some degree of specialization for male function (M. Medrano, unpublished observations).

In conclusion, the low fruit and seed production by "late" flowers of inflorescences of *P. maritimum* under natural conditions cannot be attributed to insufficient pollen receipt or to architectural constraints. The principal proximate cause of the decreasing pattern of female reproductive success within inflorescences appears to be competition for resources among the flowers of each inflorescence, with "early" flowers sequestering more resources than "late" flowers.

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