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POLLINATOR ATTENDANCE AND REPRODUCTIVE SUCCESS IN *CISTUS LIBANOTIS* L. (CISTACEAE)

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We studied pollen flow and reproductive success in two different-density stands of *Cistus libanotis*, a self-incompatible species. The pollinator spectrum comprised Hymenoptera, Coleoptera, and Diptera, but their relative frequencies at the flowers differed between stands. The pollen loads carried by insect visitors were from a considerable number of plant species (up to 11 species) apart from *C. libanotis*. Hymenoptera showed the highest activity rate and the highest flower visitation rate and carried by far the highest number of both total pollen grains and *C. libanotis* pollen grains. These factors indicate that Hymenoptera are the most effective pollinators and the major contributors to *C. libanotis* reproductive success. Nevertheless, considering the insect species, a dipteran, the syrphid *Eristalis tenax* appears to be more effective than some Hymenoptera on the basis of its *C. libanotis*–pollen carrying ability. Fluorescent dust dispersal indicated that the neighborhood area for pollen dispersal was different among stands and could change during the flowering season. Considering the reproductive output over the flowering season, differences in pollinator spectrum and in pollen flow among stands did not affect the reproductive success of *C. libanotis* individuals; both fruit and seed set were similar among stands.

Keywords: Cistus libanotis, bees, flies, pollen flow, pollen loads, reproductive success.

Introduction

In flowering plants, gene flow occurs through movement of pollen grains and seeds, with pollen flow often being the major component (Levin and Kerster 1974). In zoophilous plant species, the pattern by which pollen is deposited as a pollinator visits a sequence of flowers strongly influences pollen dispersal distances (Levin and Kerster 1974). Other factors that may affect dispersal include relative flowering time (Campbell 1985), pollen morphology (Heslop-Harrison 1981), flower density (Campbell and Waser 1989), and nectar production rates (Galen and Plowright 1985). Most of these factors affect pollinator attendance, which in turn influences dispersal (Craig 1989).

The distance moved by pollinators is often short (Levin and Kerster 1969; Fenster 1991), but pollen dispersal distance is greater because of pollen carryover (pollen from any single flower is not completely deposited on the next one in sequence; Kerster and Levin 1968; Thomson and Plowright 1980; Waser and Price 1983; Karron et al. 1995*b*). Different groups of flower visitors carry different amounts of pollen (Schemske and Horvitz 1984; C. M. Herrera 1987): for example, Hymenoptera and other insects with long-haired bodies are expected to carry greater amounts of pollen grains than others, such as beetles or flies (C. M. Herrera 1987; Pacini 1992). However, some bees and bumblebees move pollen into their pollen baskets, where it may no longer be available for pollination. In this way, the amount of pollen deposited by a flower visitor is highly variable and is dependent not just on the amount of pollen being carried but also on the length of the visit, the condition of the individual flower, and the behavior of the pollinator during the visit (Pettersson 1991). The contribution to a plant's reproductive success that a visitor makes is determined by both its effectiveness and its visitation rate (Motten et al. 1981). Pollinator effectiveness has been defined in different ways (see Inouye et al. 1994; i.e., effectiveness has been defined as the seed set resulting from a single visit [Beattie 1972]). The visitation rate of a pollinator depends on its abundance or frequency, i.e., the number of individual visitors in a plant population, and on the pollinator's activity rate, i.e., the number of flowers each individual visits per unit time. Thus, a less abundant but very active visitor could account for an equivalent visitation rate compared with that associated with a more abundant but less active visitor.

We examined pollen flow in *Cistus libanotis* L. (Cistaceae) in southern Spain. The large, open flowers of this species, with large-area stigmata and numerous stamens, offer copious and accessible pollen and nectar (Ortiz 1994). We studied the following: (1) flower visitors: spectrum, activity rates, visitation rates, foraging behavior, and the amount and quality of pollen grains they carried; (2) variation in pollen dispersal through the flowering period and among stands, and (3) the effect of these factors on the reproductive success of *C. libanotis*.

Material and Methods

Study Site and Study Species

The study was carried out from 1996 to 1997 in a peniplane at 80–90 m altitude, located ca. 30 km from the sea (lat.

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37°18′–37°20′N and long. 6°30′–6°22′W) in Huelva Province in southwest Spain. The climate is typically Mediterranean, with a mean annual temperature of 16.2°C and mean annual rainfall of 563 mm. Vegetation in the study area consists of a mixed woodland of stone pine (*Pinus pinea* L.) and cork oak (*Quercus suber* L.). The shrub layer is composed mainly of Cistaceae [*Cistus salvifolius* L. and *Halimium halimifolium* (L.) Willk.], Lamiaceae (*Rosmarinus officinalis* L.), Leguminosae (*Genista triacanthos* Brot. and *Cytisus grandiflorus* Brot.), Myrtaceae (*Myrtus communis* L.), and Arecaceae (*Chamaerops humilis* L.).

The species studied, *Cistus libanotis*, is a shrub of 60–150 cm in height; this species is endemic to the southwest of the Iberian Peninsula. It is self incompatible (F. Bastida, unpublished data) and flowers in spring. The white flowers are ca. 30 mm in diameter, have about 70 stamens, and produce nectar that is accumulated in the stamen base. In our study period, the flowers lasted only a day: they opened at ca. 0900 hours, and between 1300 and 1800 hours (depending on pollination), the petals dropped and the sepals closed.

In the study area, *C. libanotis* is locally dominant and forms both dense and sparse stands. The study was conducted in two such stands of *C. libanotis* of about 2000 m^2 each. The stands differed in plant density, 0.5 plants/m^2 versus 4.0 plants/m^2, and were separated by a firebreak that was 15 m wide.

Insect Visitors

In 1996 in both stands, we monitored insect visitors to flowers by 15-min censuses separated by 45-min intervals throughout the day (from 0900 to 1500 hours) at two periods of flowering: middle season, when flower density is the highest (the peak of flowering), and late season, when flower density is much lower (the tail of flowering). Censuses were performed in plants of similar size in which the number of flowers was counted daily; the numbers of insect visits per census were expressed in terms of visits to 100 flowers in order to homogenize the data. Thirty-one censuses were made at each density and flowering period; thus, a total of 31 h of censuses was made. When possible, we recorded activity rates (number of flowers that an individual insect visited per minute). For insects with very little activity, the rate was assigned to one or two discrete classes (<0.1 or ca. 0.1 flowers visited per minute). Visitation rates were estimated in a relative fashion, we defined an index (I_{VR}) accounting for the two components of the visitation rate of an insect species: its frequency at the flowers (F, number of individuals of an insect species relative to the total number of insects included in the census) and its mean activity rate (AR), $I_{VR} = F \times AR$. Insect behavior at the flowers was monitored to determine pollen or nectar foraging.

We analyzed pollen carried on the bodies of floral visitors both qualitatively and quantitatively. Specialized pollen-carrying organs of Hymenoptera were separated before analysis, and pollen grains accumulated in these organs were not considered. For qualitative analysis, a small amount of stained glycerine jelly was pressed to all parts of the body of each insect under a binocular microscope. In the small Coleoptera, all pollen grains were removed in this fashion, thus allowing simultaneous quantitative analysis. The jelly was transferred to a slide, melted, covered with a cover glass, and then sealed with paraffin. Pollen grains were identified and counted, and the frequency of each pollen type was calculated. Identification was accomplished with the aid of a pollen key (Valdés et al. 1987). The following terms were used for pollen grain frequencies: "predominant pollen"—more than 45% of the pollen grains counted; "frequent pollen"—between 16% and 45% were counted; "rare pollen"—between 3% and 15% were counted; and "sporadic pollen"—less than 3% of the pollen grains were counted (Louveaux et al. 1978). For quantitative analysis, other intact insects were used, except in the small Coleoptera (see above). Each insect was immersed in 2 mL of water-detergent solution for 24 h. Then each insect was energetically shaken to remove pollen, and the insect was removed. From each sample, 20 replicates of 5 μL were extracted, their pollen grains were counted, and the number was adjusted for the total volume.

Pollen Dispersal

Pollen dispersal distance was estimated using fluorescent dust, which is reported to mimic pollen grains closely in some systems (Stockhouse 1975; Waser and Price 1982; Webb and Bawa 1983; Waser 1988; Rademaker et al. 1997) and is thus of value for qualitative investigation on pollen dispersal (Thomson et al. 1986). Tracking of fluorescent dust was performed on 2 d at the peak and on 1 d at the tail end of the flowering season in 1996 and on 1 d at peak flowering in 1997. On each day, one source plant was selected from the center of each stand, and the stamens of its flowers were brushed with fluorescent dust. The number of brushed flowers was proportional to the flowering intensity; at peak flowering, about 60 flowers were brushed in each stand, and at the tail of flowering, about 25 were brushed. We censused all receptive flowers present at 2-m intervals, to a distance of 26 m from the source. Dust movements were tracked on pistils at the end of the day, just after flower petals fell. We excised samples of pistils at each 2-m interval in the four cardinal point directions. These pistils were examined in the laboratory under an ultraviolet lamp in order to calculate the proportion of flowers receiving fluorescent dust in each sample. From these data, we calculated the distribution of dispersal distances, taking into account the fraction of receptive flowers sampled at each distance. We used this frequency distribution to calculate the axial variance of pollen dispersal, which is directly proportional to genetic neighborhood area (Crawford 1984; Parra et al. 1993). To calculate axial variance, we assumed that the radial distance to the source of a plant is the midpoint of the interval at which it was located.

Reproductive Success

To determine reproductive success, in 1996, both fruit and seed set were estimated in each stand. Fruit set was studied in 10 individual plants from each stand selected at random; on each plant, from 97 to 507 flowers were marked and the fruits produced were counted. Fruit set values for the selected plants of each stand were pooled and the mean value obtained. Seed set was studied in 30 individuals from each stand selected at random. In each individual, 30 ripe capsules were collected at random, and the numbers of fully developed seeds, aborted seeds, and undeveloped ovules were counted.

Results

Insect Visitors

The spectrum of visitors to *Cistus libanotis* flowers was composed of Diptera (32%), Hymenoptera (32%), and Coleoptera (35%). However, Coleoptera remained for long periods on the same flower, so it is likely that some individuals were counted more than once, as censuses were carried out at 45-min intervals. Thus, the importance of this group may be overestimated. *Exosoma lusitanica* was the most frequent Coleopterans. The Coleoptera observed foraged exclusively for pollen. The most frequent Dipterans were Empidiidae, Muscidae, and Syrphidae (predominantly *Eristalis tenax*), in that order. All the Diptera observed on *C. libanotis* flowers foraged for nectar. Despite the frequency of *Empis*, their behavior indicates that they are not pollinators. They are small and gain access to the nectar from the outer part of the stamens, only rarely touching the stigma. The only Hymenoptera visiting *C. libanotis* flowers were bees, and of these, three species were the most frequent: *Dasypoda crassicornis*, *Dasypoda altercator*, and *Dasypoda* sp. (table 1). Most Hymenoptera foraged both for nectar and pollen; the only exception was *Andrena nitidiuscula*, which gathered pollen exclusively. It has been observed that frequently bee visits were physically deterred by *E. tenax*.

Hymenoptera showed the highest mean activity rate (16.2 ± 1.4 flowers/min), followed by Diptera (3.7 ± 0.7 flowers/min) and Coleoptera (ca. 0.1 flowers/min). However, marked differences were found within each insect order. Of the Diptera, *E. tenax* and Bombyliidae were much more active than the rest, and among Hymenoptera, the activity rates of *Halictus* sp. and *D. crassicornis* were notably higher than those of the other bees (table 1).

Hymenoptera showed the highest visitation rates, measured by the I_{VR} index, followed by Diptera. I_{VR} values for Coleoptera were very low, as might be expected based on their low activity rates (table 1). In the low-density stand, Hymenoptera and Coleoptera were more frequent on the flowers than Diptera, and the reverse was the case in the high-density stand (fig. 1); in this stand, *E. tenax* was very abundant, and thus, bees were frequently ousted from it. These differences between stands in the frequency distribution of insect visitors at the order level were very significant during both the peak (test for independence, $\chi^2 = 15.13$, $P < 0.001$, df = 2) and the tail ($\chi^2 = 20.31$, $P < 0.001$, df = 2) of flowering. Moreover, Hymenoptera were much more diverse in the low-density stand; *A. nitidiuscula* and *Halictus* sp. visited only this stand (table 1). In the high-density stand, there was a general trend for the number of visits to decrease during the flowering period ($\chi^2 = 33.56$, $P < 0.01$; fig. 1), Calliphoridae being the sole exception (table 1). The opposite trend was found in the low-density stand ($\chi^2 = 9.12$, $P < 0.01$); again, some Diptera (Empidiidae and *Syrphus*) were the exception.

Qualitative analyses of pollen carried on insect bodies revealed 20 pollen types belonging to 14 families with markedly different floral types (appendix). All the insects examined bore pollen grains of *C. libanotis*. The main pollen types were *C. libanotis*, *Cistus ladanifer*, *Cistus salvifolius*, *Tuberaria guttata*, *Halimium halimifolium*, *Echium plantagineum*, *Carduus meonanthus*, Lactuceae, and *Silene scabriflora*. Pollen from four anemophilous species (*Pinus pinea*, *Quercus suber*, *Chamaerops humilis*, and Poaceae) were found as sporadic or rare types; because *C. libanotis* stands are located under a canopy of *P. pinea* and *Q. suber*, the presence of pollen grains from these species on insect bodies is probably casual. In general, the number of pollen types found on Hymenoptera (mean 6.6 types) was greater than the number found on Coleoptera (4.5

Table 1

Number of Visitors per Census and per 100 Flowers at Peak and at Tail of Flowering in Low- and High-Density Stands of *Cistus libanotis*, Mean Activity Rates, Relative Visitation Rates, and Foraging Behavior

Visitors	Low-density stand		High-density stand		Mean activity rate	I_{VR}	Foraging behavior
	Peak	Tail	Peak	Tail			
Coleoptera:							
Anthaxia nigritula	3	6	2	0	<0.1	<0.3	P
Cantharidae	6	11	5	1	Ca. 0.1	0.6	P
Exosoma lusitanica	24	40	23	7	Ca. 0.1	0.2	P
Heliotaurus rucicoides	3	7	3	0	Ca. 0.1	0.3	P
Oedemeridae	3	5	2	0	Ca. 0.1	0.2	P
Diptera:							
Bombyliidae	0	0	2	0	4.5 ± 1.5 (2)	2.3	N
Calliphoridae	2	6	0	4	0.9 ± 0.3 (5)	2.5	N
Empidiidae	16	8	37	10	Ca. 0.1	1.7	N
Eristalis tenax	4	6	8	0	6.6 ± 0.8 (13)	28.4	N
Muscidae	8	9	7	6	0.45 ± 0.05 (2)	3.6	N
Syrphidae	1	0	0	0	…	…	N
Hymenoptera:							
Andrena nitidiuscula	5	5	0	0	1 (1)	2.4	P
Dasypoda altercator	13	14	12	5	13.3 ± 0.8 (9)	138.3	P/N
Dasypoda crassicornis	8	12	4	3	25.7 ± 1.4 (9)	164.5	P/N
Dasypoda sp.	16	25	3	2	11.8 ± 0.9 (9)	128.6	P/N
Halictus sp.	0	8	0	0	40 (1)	76.0	P/N

Note. $N = 31$ censuses. Numbers in parentheses are sample sizes. I_{VR} = relative visitation rates. N = nectar foraging; P = pollen foraging.

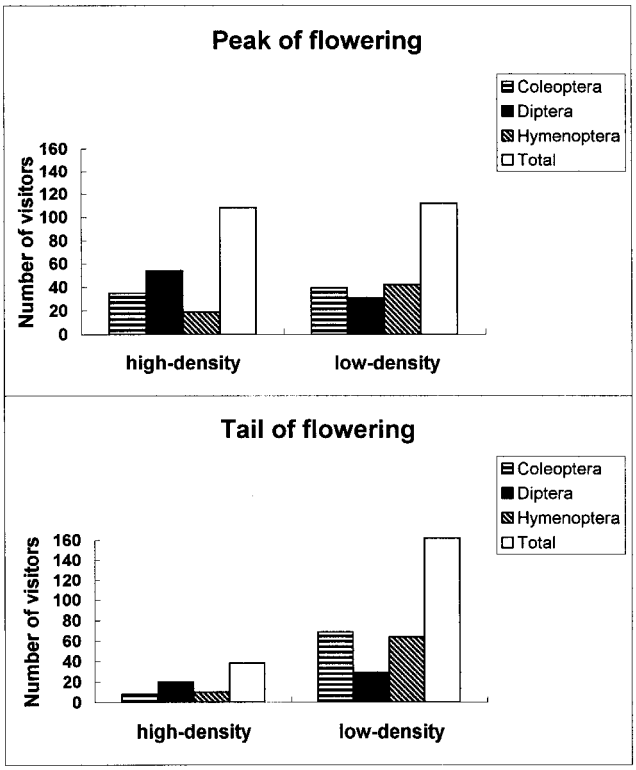

Fig. 1 Number of insect visitors at peak and at tail of flowering in the high- and low-density stands of *Cistus libanotis* in 1996.

types) and Diptera (4.3 types; table 2). However, Oedemeridae (Coleoptera) and *E. tenax* (Diptera) carried as many pollen types as Hymenoptera. Most pollinators carried a predominant pollen type. About 79% of the Diptera analyzed carried *C. libanotis* pollen as "predominant type"; this percentage decreased to 66% in Coleoptera and to 35% in Hymenoptera (appendix).

Quantitative analyses showed that Hymenoptera carried by far the greatest number of pollen grains, with a mean of 16,713 grains (specialized pollen-carrying organs not considered), following by Diptera (1589 grains) and Coleoptera (241 grains; table 2). Of these pollen grains, the proportion of *C. libanotis* pollen was higher in Coleoptera and Diptera than in Hymenoptera (table 2). However, although the proportion of pollen grains of other taxa was very high in Hymenoptera (64.7%), the total number of *C. libanotis* pollen grains was also the highest. Marked differences in the total number of pollen grains and in the fraction of *C. libanotis* pollen carried by the visitors were found within each insect group (table 2). Among Diptera, only *E. tenax* carried considerable numbers of pollen grains. The other Diptera carried numbers of pollen grains that were similar to, or even lower than, those of some Coleoptera (table 2).

Pollen Dispersal

Axial variance of pollen dispersal, and thus genetic neighborhood area, was always higher in the low-density stand at both the peak and the tail of flowering (fig. 2). In the low-density stand, axial variance showed little variation between the different periods studied, whereas in the high-density stand, axial variance was markedly variable, reaching the highest value at the peak of flowering season in 1996 and the lowest at the tail of flowering in 1996 (fig. 2).

Reproductive Success

Fruit set was quite high in all the plants, ranging from 69.5% to 87.8%. Both stands registered similar mean fruit set values, 81.3% in the low-density stand and 78.9% in the high-density stand (table 3). The number of ovules per capsule was markedly variable, ranging from five to 35. Among stands, the number of ovules per capsule was similar, with a mean of about 20 ovules (table 3). Seed set (number of ovules that transform into seeds) was not apparently different among stands, averaging 83.9% in the high-density stand and 85.9% in the low-density stand.

Discussion

The interactions between *Cistus libanotis* and insect pollinators recorded in this study were generalist in nature; the plant species was visited by a variety of pollinating agents that in turn visited other species with diverse floral types. Moreover, the pollinator spectrum of *C. libanotis* showed local differences without variation in female fecundity. These results are in agreement with the idea that unspecificity of plant-pollinator systems seems to be a rule rather than an exception (Herrera 1995; Waser et al. 1996).

Pollinator spectra of other *Cistus* species have been studied in the Iberian Peninsula: Coleoptera, Diptera, and Hymenoptera were always present, but their relative proportions were highly variable among species and sites (Brandt and Gottsberger 1988; Herrera 1988; Bosch 1992; Talavera et al. 1993). At two of these sites, Lepidoptera were also found, but in low proportion (Herrera 1988; Bosch 1992). We have not observed Lepidoptera on *C. libanotis* flowers, but their absence is possibly a consequence of the high nectar concentration of this species in our study site (>70%; Ortiz 1994).

When excluding pollen types that potentially result from contamination, such as *Pinus*, the diversity of pollen types found on every *C. libanotis* pollinator may be attributable to two causes: the insect is visiting different flower species at the same time and/or some of these pollen types are leftover from flowers that were exploited earlier. We do not know the foraging histories of insects, but it is probable that many if not all of the well-represented pollen types come from simultaneously visited sources. It is remarkable that several Cistaceae are among the best-represented types. Cistaceae species have similar floral structures and flowering periods (J. Herrera 1987), so they may compete for the service of the same pollinators (Levin and Anderson 1970; Mosquin 1971). When a pollinator is visiting a large number of heterospecific plants, pollen dispersal distances of a single species decrease (Campbell 1985). In this way, seasonal variation in plant species composition could cause fluctuation in the neighborhood areas during the flowering.

Considering insect orders in the *C. libanotis*–pollinator interaction, Hymenoptera were more promiscuous than other

Table 2

Results of Qualitative and Quantitative Analyses of Pollen Carried on Bodies of Insect Visitors to *Cistus libanotis* Flowers

Visitors	Mean number of pollen grains/individual	Pollen grains of *C. libanotis* (%)	Pollen grains of other Cistaceae (%)	Other pollen grains (%)	Number of pollen types
Anthaxia nigritula	11 (1)	36.4 (1)	0 (1)	63.6 (1)	3 (1)
Cantharidae	102.5 ± 29.8 (4)	55.1 ± 16.7 (4)	30.6 ± 15.5 (4)	14.2 ± 3 (4)	4 ± 1.15 (4)
Exosoma lusitanica	406.2 ± 105.4 (6)	77.1 ± 10.2 (6)	6.6 ± 3.2 (6)	16.3 ± 7.6 (6)	4.3 ± 0.73 (6)
Heliotaurus ruficollis	184.5 ± 113.5 (2)	49.6 ± 22.9 (2)	19 ± 3.5 (2)	31.4 ± 26.4 (2)	4.5 ± 0.7 (2)
Oedemeridae	157.5 ± 46.5 (2)	61.8 ± 21.1 (2)	26.1 ± 18.9 (2)	12.1 ± 2.2 (2)	6.5 ± 0.7 (2)
Total Coleoptera	241 ± 57 (15)	61.6 ± 7.5 (13)	10.9 ± 3 (13)	22.8 ± 5.7 (13)	4.5 ± 0.43 (15)
Bombylius sp.	69 (1)	70 (1)	23 (1)	7 (1)	4 (1)
Calliphoridae	738 (1)	76 (1)	22 (1)	2 (1)	5 (1)
Empis sp.	399 ± 167 (4)	89.4 ± 3.5 (8)	7.5 ± 2.8 (8)	3 ± 1 (8)	2.8 ± 0.42 (8)
Eristalis tenax	4672.8 ± 1327 (6)	50.6 ± 14.2 (6)	42.2 ± 14 (6)	7.1 ± 2.4 (6)	6.3 ± 1.0 (6)
Muscidae	115 ± 68 (3)	67.6 ± 16.3 (3)	3 ± 2.5 (3)	29.3 ± 14.6 (3)	3.3 ± 0.4 (3)
Syrphus sp.	196 ± 77 (5)	67.5 ± 17 (5)	25.4 ± 17.1 (5)	4.8 ± 1.06 (5)	4.8 ± 0.6 (5)
Total Diptera	1588.6 ± 596.6 (20)	71.1 ± 5.9 (24)	20.5 ± 3.6 (24)	7.8 ± 2.4 (24)	4.3 ± 0.4 (24)
Andrena nitidiuscula	5389 (1)	6 (1)	22 (1)	72 (1)	5 (1)
Dasypoda altercator	25,154 ± 22,160 (4)	34.5 ± 12.8 (8)	19.8 ± 8.5 (8)	45.7 ± 14.4 (8)	5.7 ± 0.8 (8)
Dasypoda crassicornis	14,890 ± 10,630 (2)	69.0 ± 3.0 (2)	14.7 ± 3.4 (2)	16.1 ± 0.3 (2)	8 ± 0 (2)
Dasypoda sp.	3010 ± 470 (2)	15.5 ± 3.5 (2)	33 ± 28 (2)	51.1 ± 24.5 (2)	8 ± 0 (2)
Halictus sp.	25,326 (1)	43 (1)	44 (1)	13 (1)	10 (1)
Total Hymenoptera	16,713 ± 8812 (10)	35.2 ± 8.5 (14)	24.4 ± 6.1 (14)	40.3 ± 9.1 (14)	6.6 ± 0.6 (14)

Note. In Hymenoptera, specialized pollen-carrying organs were not considered. In each case, the sample size is given between parentheses.

groups, but they carried more pollen of *C. libanotis* than Diptera, and much more than Coleoptera. The amount and quality of the pollen carried by insect visitors indicate that Hymenoptera could be more effective as pollinators than Diptera and Coleoptera, as it has been reported previously in other plant-pollinator systems (Primack and Silander 1975; Ehrenfeld 1979; O'Brien 1980; Hippa et al. 1981). In addition, Hymenoptera showed the highest flower visitation rate, both because of their high frequency at the flowers and their high activity rates. This fact, together with their high pollen-carrying performance, indicates that Hymenoptera are the major contributors to the *C. libanotis* reproductive success. However, this ought to be taken cautiously because the effect of single visits on pollen deposition on stigmas also depends on insect behavior on the flowers. Moreover, the species within each insect group differed markedly. Taking into account the amount of *C. libanotis* pollen carried by each species, *Halictus* sp., *Dasypoda crassicornis*, and *Dasypoda altercator*, in that order, and, to a lesser extent, *Eristalis tenax* and *Dasypoda* sp., can be considered the most effective pollinators. Thus, a dipteran (*E. tenax*) was more effective than some Hymenoptera. In contrast, other Diptera, such as Muscidae, were as ineffective as some Coleoptera (e.g., *Exosoma lusitanica*). Considering visitation rates of each insect species, the same five species were the most important pollinators, but in a different order: *D. crassicornis*, *D. altercator*, *Dasypoda* sp., *Halictus* sp., and *E. tenax*. Thus, pooling data of individual species into order categories can distort the effects of a particular pollinator species on a plant's reproductive success.

The pollinator spectrum was different in each stand, with Hymenoptera being more frequent in the low-density stand. Bee-mediated pollen dispersal is strongly correlated with plant spacing (Levin and Kerster 1969); therefore, in low-density stands, gene flow (via pollen) caused by Hymenoptera would be greater than in high-density stands. Although the experimental design does not allow a test for any density effect, our results could be explained on the basis of differences in density of individuals among stands. In the low-density stand of *C. libanotis*, axial variance for pollen dispersal, and thus neighborhood area, was greater than in the high-density stand. In the high-density stand, the main flower visitors were Dipterans; thus, the shorter distance of pollen dispersal could also be a result of this difference in the pollinator spectrum.

In the high-density stand, axial variance for pollen dispersal also changed over the season, and the neighborhood area reached the maximum size in middle season. In this case, the marked decrease of insect visits to flowers in late season could account for the short distance of pollen dispersal. In the low-density stand, reduction in the number of insect visits was not observed in late season, and, as would be expected, differences in axial variance for pollen dispersal between the peak and the tail of flowering were not pronounced. The decrease in the number of insect visits observed at late season in the high-density stand probably reflects a reduction in the absolute abundance of pollinators. This reduction could have also happened in the low-density stand, but the very low density of flowers in this stand at this period could allow the maintenance of the number of visits to flowers.

Thus, identity and abundance of pollinators as well as flower density play significant roles in determining dispersal distances and, consequently, neighborhood areas, in *C. libanotis* stands. This fact is particularly important because seed dispersal in *C. libanotis* is extremely limited (F. Bastida, unpublished data), and so pollen flow appears to be the major component of gene flow in this species.

Stand density and time of flowering season were factors affecting the variety of mates among *C. libanotis* individuals. In the low-density stand, *C. libanotis* plants exchanged pollen with more distant individuals than they did in the high-density stand. *Cistus libanotis* is a self-incompatible species, with seeds

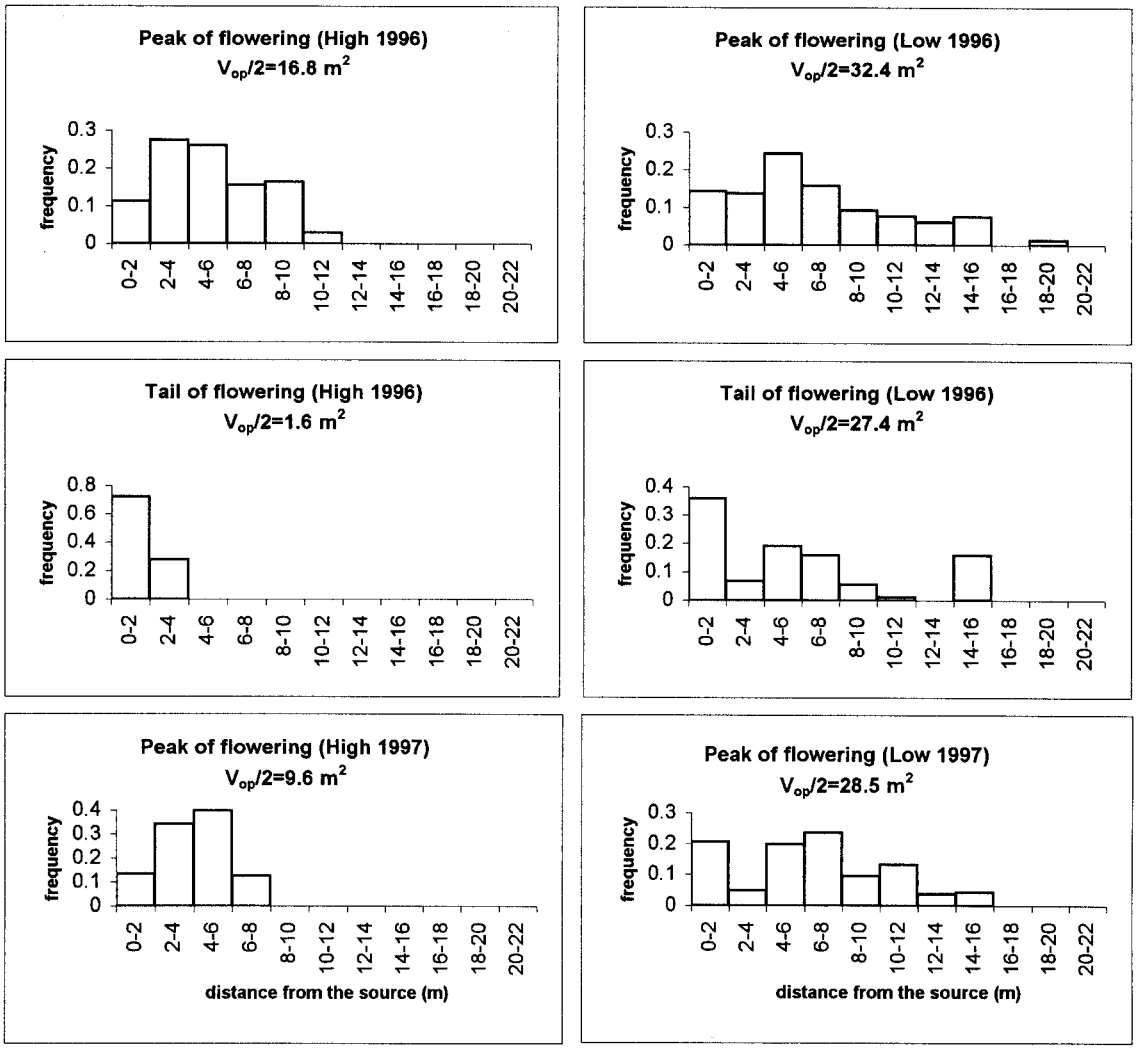

Fig. 2 Frequency distribution of flowers receiving fluorescent dust at different distances from the source plant in both high- and low-density stands of *Cistus libanotis* at peak and at tail of flowering in 1996 and at peak of flowering in 1997. $V_{op}/2$ is the axial variance for pollen dispersal.

dispersing to very short distances; thus, differences in reproductive success between densities resulting from biparental inbreeding could be expected. However, as far as can be inferred from our results, this species did not seem to discriminate between cross pollen on the basis of distance to source plants: fruit set, number of seeds per capsule, and seed set were fairly high in plants growing at low and at high densities. Similar results have been found in other self-incompatible species (Ellstrand et al. 1978; Watkins and Levin 1990). This contrasts with the results of many studies of insect-pollinated self-compatible species, in which a positive correlation between population density and outcrossing has been found (Van Treuren et al. 1993; Karron et al. 1995*a*); in these studies, the low outcrossing rates in sparse populations were attributable to the higher levels of geitonogamous pollinations, because foraging pollinators tend to move short distances (Karron et al. 1995*a*). Negative effects of geitonogamy in self-incompatible species basically number two: reduced pollen dispersal and possibly reduced female fecundity resulting from the dilution of outcross pollen or interference by self-pollen grains (Waser and Price 1991; Snow et al. 1996). However, neither of these negative effects was found in the low-density stand of *C. libanotis*. Pollen dispersal distance was four to five times higher in the low-density stands, and this was probably the result of differences in pollinator spectrum and/or pollinator behavior between densities (Hymenoptera were more frequent in the low-density stand), but in addition, the high pollen production of *C. libanotis* flowers (Ortiz 1991) would make considerable pollen carryover possible. On the other hand, fruit set and seed set were similar between densities, and thus, female fecundity was not affected. Main effects of SI pollen, such as stigma closure or early flower senescence (Waser and Fugate 1986; Waser and Price 1991), are not found in *C. libanotis*. The stigmatic area is large (1.43 mm^2; Herrera 1992), and, in accord with Erdtman (1945), the pollen grain is medium sized (polar axis = 49.1 μm; Fernández and Ortiz 1987), so that the minimum number of pollen grains needed to occupy the stigmatic area is 728. The fruit set of this species was high

Table 3

Reproductive Characteristics of the *Cistus libanotis* Plants in 1996

	Low-density stand		High-density stand	
Characteristics	Mean ± SE	Range (*n*)	Mean ± SE	Range (*n*)
Fruit set (%)	81.3 ± 1.6	69.5–87.7 (10)	78.9 ± 1.4	71.8–87.8 (10)
No. ovules/capsule	20.0 ± 0.4	16.3–23.6 (30)	19.9 ± 0.5	13.6–28.9 (30)
No. seeds/capsule	17.3 ± 0.4	13.4–21.4 (30)	16.7 ± 0.4	12.6–21.1 (30)
Seed set (%)	85.9 ± 0.5	5.6–100 (30)	83.9 ± 0.5	14.3–100 (30)

and similar between stands; that seems to indicate that there is no pollen limitation, as was also reported by J. Herrera (1987). These facts, taken together with the low number of ovules per flower, mean that interference by self pollen is probably low. In fact, the effect of geitonogamy on female fecundity is most evident in pollen-limited populations (Snow 1982; Galen 1985).

The effect of a pollinator visit, from the plant's perspective, is seed production, and this effect is a closer measure of plant fitness than is pollen deposition (Dieringer 1992). However, since seed set in *C. libanotis* seems not to be pollen limited, pollinator preferences probably have a larger impact on male reproductive success than on the female function of its hermaphroditic flowers. Thus, in *C. libanotis*, increasing distance from the pollen source beyond the nearest neighbor does not significantly improve seed production but does increase gene flow via pollen.

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Appendix

Table A1

Pollen Grains Found on the Bodies of the Insects Analyzed Qualitatively

Insect visitor	Predominant pollen	Frequent pollen	Rare pollen	Sporadic pollen
Anthaxia nigritula	…	*Cistus libanotis*, *Echium plantagineum*	Lactuceae	…
Cantharidae	*C. libanotis*	*Cistus ladanifer*	*Pinus pinea*	…
Cantharidae	*C. libanotis*	*C. ladanifer*	*P. pinea*	…
Cantharidae	*Tuberaria guttata*	*C. ladanifer*	*C. libanotis*, *Ranunculus parviflorus*, *Carduus meonanthus*	*Cistus salvifolius*, *P. pinea*
Cantharidae	*C. libanotis*	…	*P. pinea*	*C. ladanifer*
Exosoma lusitanica	*C. libanotis*	Lactuceae	*C. ladanifer*, *C. meonanthus*	…
E. lusitanica	*C. libanotis*	…	…	*P. pinea*
E. lusitanica	*C. libanotis*	…	*C. ladanifer*	*C. meonanthus*, *P. pinea*
E. lusitanica	*C. libanotis*	…	*C. ladanifer*	*P. pinea*, Lactuceae, *C. meonanthus*
E. lusitanica	…	*C. libanotis*, *C. ladanifer*, Lactuceae	…	*C. salvifolius*, *R. parviflorus*, *P. pinea*, *C. meonanthus*
E. lusitanica	*C. libanotis*	…	Lactuceae	*C. ladanifer*, *P. pinea*
Heliotaurus ruficollis	*E. plantagineum*	*C. libanotis*	*C. salvifolius*, Lactuceae	*C. ladanifer*
H. ruficollis	*C. libanotis*	…	*C. ladanifer*, *C. salvifolius*	*P. pinea*
Oedemeridae	*C. libanotis*	…	*C. salvifolius*, *Brassicaceae*	*E. plantagineum*, Lactuceae, *Papaver rhoeas*

Table A1

(*Continued*)

Insect visitor	Predominant pollen	Frequent pollen	Rare pollen	Sporadic pollen
Oedemeridae	…	*C. libanotis*, *C. ladanifer*	*C. salvifolius*, *T. guttata*, *C. meonanthus*, *Eucalyptus* sp.	*P. pinea*
Bombylius	*C. libanotis*	*C. ladanifer*	*P. pinea*	*C. meonanthus*
Calliphoridae	*C. libanotis*	*C. ladanifer*	…	*Quercus suber*, *C. meonanthus*, *P. pinea*
Empis	*C. libanotis*	*C. salvifolius*	*C. meonanthus*	*C. ladanifer*
Empis	*C. libanotis*	…	…	*C. ladanifer*, *P. pinea*
Empis	*C. libanotis*	…	…	…
Empis	*C. libanotis*	…	*C. ladanifer*, *C. salvifolius*	*P. pinea*
Empis	*C. libanotis*	…	…	*P. pinea*
Empis	*C. libanotis*	…	…	*P. pinea*
Empis	*C. libanotis*	…	*C. ladanifer*	*Q. suber*
Empis	*C. libanotis*	…	*T. guttata*, Liliaceae	*C. meonanthus*
Eristalis tenax	*C. ladanifer*	*C. libanotis*	*C. salvifolius*, *C. meonanthus*	*P. pinea*
E. tenax	…	*C. libanotis*, *C. salvifolius*, *C. ladanifer*	…	*C. meonanthus*, *P. pinea*
E. tenax	*C. ladanifer*	*C. libanotis*, *C. salvifolius*	…	*C. meonanthus*, *P. pinea*, *Silene scabriflora*
E. tenax	*C. libanotis*	…	*C. salvifolius*	*R. parviflorus*, *T. guttata*, *E. plantagineum*, Lactuceae
E. tenax	*C. libanotis*	…	*C. ladanifer*, *C. salvifolius*, Lactuceae, *C. meonanthus*, *R. parviflorus*	*Q. suber*, *S. scabriflora*, *E. plantagineum*, *Campanula* sp., *P. pinea*
E. tenax	*C. libanotis*	…	*C. ladanifer*	*P. pinea*, *C. meonanthus*, *Lavandula stoechas*
Muscidae	*C. libanotis*	…	…	*C. ladanifer*, *P. pinea*
Muscidae	*C. libanotis*	*S. scabriflora*	…	*E. plantagineum*
Muscidae	…	*C. libanotis*, *E. plantagineum*	*Halimium halimifolium*, Lactuceae	…
Syrphus	*C. ladanifer*	…	Lactuceae	*C. libanotis*, *P. pinea*, *E. plantagineum*
Syrphus	*C. libanotis*	…	…	*C. salvifolius*, Brassicaceae, *P. pinea*
Syrphus	*C. libanotis*	…	*C. ladanifer*, *C. salvifolius*, *P. pinea*	…
Syrphus	*C. libanotis*	…	*C. ladanifer*	*Campanula* sp., *E. plantagineum*
Syrphus	*C. libanotis*	*C. ladanifer*	*C. meonanthus*	*C. salvifolius*, *E. plantagineum*, *Q. suber*, *Eucalyptus* sp.
Andrena nitidiuscula	*E. plantagineum*	*T. guttata*	*C. libanotis*, *C. ladanifer*	*Campanula* sp.
Dasypoda altercator	*C. libanotis*	…	*C. meonanthus*	*C. ladanifer*, *C. salvifolius*, *S. scabriflora*, *E. plantagineum*, Lactuceae, *P. pinea*
D. altercator	…	*C. libanotis*, *C. ladanifer*, *C. salvifolius*	…	*P. pinea*, *C. meonanthus*, *Q. suber*, *S. scabriflora*

Table A1

(*Continued*)

Insect visitor	Predominant pollen	Frequent pollen	Rare pollen	Sporadic pollen
D. altercator	*E. plantagineum*	…	…	*C. libanotis*, *C. ladanifer*, Lactuceae
D. altercator	*H. halimifolium*	Lactuceae	*C. libanotis*, *E. plantagineum*	*R. parviflorus*, *C. meonanthus*
D. altercator	*E. plantagineum*	*H. halimifolium*	*C. libanotis*	*C. ladanifer*, *Lactuceae*, *Poaceae*, *C. meonanthus*, *P. pinea*
D. altercator	*C. libanotis*	…	*C. ladanifer*	*C. salvifolius*, *Rosmarinus officinalis*, *P. pinea*
D. altercator	*C. libanotis*	*C. meonanthus*	*C. salvifolius*, Lactuceae	*C. ladanifer*, *P. pinea*
D. altercator	Lactuceae	…	…	*C. libanotis*
Dasypoda crassicornis	*C. libanotis*	…	*C. ladanifer*, *C. salvifolius*, *C. meonanthus*, *R. officinalis*	*P. pinea*, Lactuceae, *E. plantagineum*
D. crassicornis	*C. libanotis*	*C. ladanifer*	*C. meonanthus*	*C. salvifolius*, *P. pinea*, *H. halimifolium*, Lactuceae, *E. plantagineum*
Dasypoda sp.	*C. ladanifer*	…	*C. libanotis*, Lactuceae	*C. salvifolius*, *T. guttata*, *Q. suber*, *P. pinea*, *Campanula* sp.
Dasypoda sp.	Lactuceae	*C. libanotis*	*C. ladanifer*, *E. plantagineum*, *P. pinea*	*T. guttata*, *L. stoechas*, *Chamaerops humilis*
Halictus	…	*C. libanotis*, *C. ladanifer*	*C. salvifolius*, *S. scabriflora*	*T. guttata*, *E. plantagineum*, Lactuceae, *P. pinea*, *C. meonanthus*, *Q. suber*

Note. A pollen type was "predominant" when it represented more than 45% of the total number of counted pollen grains, "frequent" when it represented between 16% and 45% of grains, "rare" when it represented between 3% and 15% of grains, and "sporadic" when it represented less than 3% of grains.

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