Reproductive biology of *Cistus ladanifer (Cistaceae)*

S. TALAVERA, P. E. GIBBS, and J. HERRERA

Abstract: The phenology, major floral characteristics, fruiting levels, and breeding system of *Cistus ladanifer L. (Cistaceae),* a common western Mediterranean shrub species, were studied in a southern Spanish population. The white, large (64 mm in diameter) flowers of this shrub appear during spring (March—May) and produce abundant pollen and nectar. In the year of study, flowers lasted up to three days, during which they were visited by a diverse array of insects including beetles, flies, and bees. Hand-pollinations revealed that flowers do not set any seed unless cross pollen is applied to the stigma. Microscopical observations indicate that self pollen tubes grow down the stigma but invariably fail to induce fruit maturation. At the plant level, all estimates of fecundity investigated (number of seeds per capsule, proportion of ovules developing into seed, and proportion of flowers setting fruit) were highly dependent on nearest neighbour distance, with isolated plants setting as little as 0% fruit. In contrast, plants within a clump often transformed into fruit as much as 90% of the flowers. At the population level, seed output was estimated to range between 3,000 and 270,000 seeds per plant during 1991.

The family *Cistaceae* is a very significant element in the Mediterranean flora with five genera *(Cistus, Fumana, Halimium, Helianthemum,* and *Tuberaria)* comprising major components of matorral scrub. The genus *Cistus,* with 16 species, is particularly prominent in such vegetation. The species studied here, *Cistus ladanifer* L. occurs on poor soils in dry habitats in an area from the S of France, the Iberian Peninsula to N Africa (N Morocco and Algeria). In most of this area, *C. ladanifer* has occupied areas of *Quercus* woodland which have been degraded by fire. This species is distinguished by having capsules which open by 10 valves, and young stems and leaves with a resinous exudate which gives the plant a distinctive odour, especially in summer. See HEYWOOD (1978: 108) for an illustration of flowers and capsules.

Despite the ecological importance of the family *Cistaceae* very few studies have been made of the reproductive biology of this group. Most studies have been dedicated to the widespread inter-specific hybridization which occurs in *Cistus* species (BORNET & GARD 1919; DANSEREAU 1941 a, b, 1943), their ecophysiology (MORENO 1982, 1984 a, b), and to the role of fire with respect to the seed banks (TROUMBIS & TRABAUD 1986, TRABAUD & DUSTRIC 1989, CORRAL & al. 1990,

PAPIO & TRABAUD 1990). Aspects related to the pollination biology-breeding systems of some *Cistaceae* have been observed by MOLLER (1883) and KNUTH (1898), and recently by J. HERRERA (1985, 1987 a, b, 1992) and BRANDT & GOTTSBERGER (1988). Outbreeding, inbreeding, and cleistogamy have been reported to occur in various taxa. Few of these studies involved comparisons of hand cross- vs. self-pollinations, or observations of pollen tube growth and post-pollination events. Here we report such studies with the widespread species *Cistus ladanifer* as the first in a series which will examine members of this family. *C. ladanifer* was chosen because of its prominence in the matorrals of the central and SW parts of the Iberian Peninsula (Spain and Portugal), coupled with the fact that its upright, regularly branched growth and persistent woody peduncles allow age and fruiting success to be readily assessed. A further advantage of this species is that it is not associated with introgressive hybridization phenomena which complicate the study of other species in the *Cistaceae.*

Material and methods

Study area. The study was carried out in an area of matorral (37° 18′ — 37° 20′ N and 6° 30′ — 6° 22′ W) near the town of Hinojos, Huelva Province, SW Spain. The area is a peniplane at 80—120 m altitude at ca. 30 km from the sea. The climate is typically Mediterranean, with 90% of the rainfall (mean annual value 563 mm) falling between October and April, with a peak in autumn (October—December) and another in early spring (March—April). There is an average of 15 frost-risk days in December—January, although the summer is hot and dry with temperatures often reaching 45 °C. Mean annual temperature at the site is 16.2 °C.

The vegetation in the study area consists of a mixed woodland of stone pine *(Pinus pinea L.)* and cork oak *(Quercus suber L.),* with *Q. rotundifolia* LAM. occupying upland areas, and *Pyrus bourgaeana* in low lying areas. Stone pine was introduced in the 17th century and now forms dense stands with a shrub layer composed mainly of *Cistaceae, Leguminosae,* and *Ericaceae* in which the former family is dominant. In this area C. *ladanifer* forms extensive, mostly densely aggregated populations but with some isolated individuals scattered over the site. In the aggregated stands the density of individuals may be up to 6-18/m^2. In such dense clumps *Cistus ladanifer is* the only woody species, whilst the more isolated individuals occur with *Halimium halimifolium (L.)* WILLK., *Quercus coccifera* L., and *Chamaerops humilis L.* in upland stands, and with *Cistus crispus L., C. monspeliensis* L., and particularly *C. psilosepalus* SWEET and *C. salvifolius* L., and other matorral shrubs in lower, more humid areas. The studied sample comprised 68 individuals occurring in dense clumps to more isolated plants.

Phenology. Most field work for this study was carried out during the flowering season in 1991, although some additional observations were also done during 1992. The population was visited fortnightly from March 1991 through March 1992 to monitor growth, flowering, fruiting, seed dispersal, and germination. Data on the occurrence of growth, flowering, or fruiting is based on observations of a large number of individuals, whereas dispersal was assessed by noting the presence or absence of seeds in 20 randomly chosen capsules from a minimum of 10 plants. Seed germination was monitored by noting the presence or absence of seedlings within four permanent 0.4 x 0.4 m plots.

Flower characteristics and pollination. To quantify pollen production and estimate pollen-to-ovule ratios, 10 flower buds were collected at random from individual plants and the number of stamens and carpels (ovary locules) counted. The stamens, depending on their position in the flower, have anthers which vary in size and consequently pollen production. Since the ratio of large to small anthers is about 2 : 1, estimations of the average number

of pollen grains per flower were made by macerating two large and one small anther in 1 ml of water-detergent solution, then sampling 10 aliquots of 10 μl from each preparation and counting the number of grains under the microscope. Ovule number was estimated by counting all of the ovules present in two adjacent, intact, ovary locules with the aid of a x 20 dissecting microscope. Estimations of total pollen yield and ovule number were then used to calculate pollen : ovule ratios. Nectar secretion was measured by individually enclosing in plastic bags *23* flowers from three individuals and subsequently sampling these *8, 32,* and *50* h after flowering opening. Nectar was extracted using graduated micropipettes *(5,* 10, and 20 μl), and sugar concentrations measured in a Bellingham and Stanley hand refractometer. Milligrams of nectar sugar were calculated according to the formula proposed by CRUDEN & HERMANN *(1983).*

To monitor floral anthesis, 100 buds belonging to *13* plants were tagged in the afternoon of one day and observed at two-hour intervals from 6:00–18:00 h solar time during the following three days. The complete functional life, which included opening, pollen-shedding, nectar-secretion, and petal-dropping phases, was monitored for all the *55* flowers that opened during the first day.

Floral visitors were censused on a peak flowering date (19 April) using 150–200 flowers of *30* shrubs along a transect of 40 m which extended from one large clump of plants long a line which passed a number of isolated individuals to another, smaller clump. Flowers were monitored at *7:15,* 8:15, 11:15, 13:15, and 17:00 h (solar time). During each census, which lasted ca. *5* min, the number and type of all insects observed on the selected flowers were noted. The behaviour of the insect visitors was studied by means of *30* min observation periods which were made at one clump of individuals at *8:30,* 12:00, and *15:00* h. Collected specimens were either identified to at least the family or sent to specialists.

Breeding system. A number of flowers from 17 individuals were bagged in late bud stage and pollinated by hand on the first day of anthesis with either self- or cross-pollen. Reciprocal pollinations, in which a given individual was first used as the pollen donor and then acted as the recipient, were performed with a total of 10 plants. Crossed flowers were emasculated prior to pollination. A set of flowers on the same plants were tagged and left for natural pollination.

In 1992, a further series of hand self- or cross-pollinations were made, and the pistils of these flowers were removed and fixed in a daily sequence up to eight days after pollination. The sample included pairs of flowers (one selfed and the other crossed) on five different individuals. This material was subsequently studied for pollen germination and pollen tube growth by means of leucoaniline blue stain and fluorescence microscopy (MARTIN 1959). After dissecting each ovary, ovules were removed and rinsed in tap water for an hour. Using NaOH to soften the samples would cause complete darkening of tissues, so this step was bypassed. Rinsed ovules were thus directly placed in a slide with a drop of stain and observed under the microscope.

Flower production and natural fruit-set. A sample of 38 plants was checked at the end of the 1991 flowering period for the number of flowers produced (evident by the persistent, woody peduncles) and number of fruits. Individuals were selected in order to account for within-population variability regarding plant size and location. Thus, the sample included both individuals very close to a conspecific (which are the majority) and a few isolated plants. Average distance to the nearest two conspecifics has been used as an estimate of spatial isolation and to subsequently investigate the relationship between plant location and fecundity.

From the above sample, a subsample of 10 plants was further assessed for seed production. To achieve this, we counted seeds and undeveloped ovules in two adjacent locules per capsule for *8* capsules per plant, as well as the number of locules in these fruits. We then calculated the total number of seeds per fruit, and the proportion of ovules that developed into seed (i.e., seed-set). Unfortunately, the number of undeveloped ovules was

missing for three individuals, so seed-set data are available for only seven plants. Prior to any statistical analyses, variables were checked for normality and transformed as necessary (SOKAL & ROHLF 1981).

Results

Phenology. The life cycle of *Cistus ladanifer* is shown in Fig. 1. Leaves are present only on axes of the previous year. Flowers are initiated during winter at the apex of each vigorous branch produced in the previous year. These axes develop 1—4 (sometimes 5) pairs of slender, opposite branches on each of which are produced 1—3 pairs of leaves and various cordate bracts which enclose a single flower bud. Just prior to anthesis, the pedicels elongate so that by the time the sepals and petals open (see below) the flower is exserted free from the bracts. The flowering phenophase extends over a two-month period from mid-March to mid-May (Fig. 1).

After anthesis, the sepals return to their original position and completely enclose the ovary/young fruit. During fruit maturation the leaves and bracts abscise and the pedicels elongate and lignify. By early summer the fruits are mature and the sepals now fall so that the capsules are exposed at the ends of the woody pedicels (Fig. 1). The main axis of the flowering branch continues to elongate and develop new leaves until the beginning of summer when a dormant period ensues. During summer the fruit capsules begin to open and, by early autumn, seed dispersal occurs following shaking of branches by wind and rain. With the arrival of winter all of
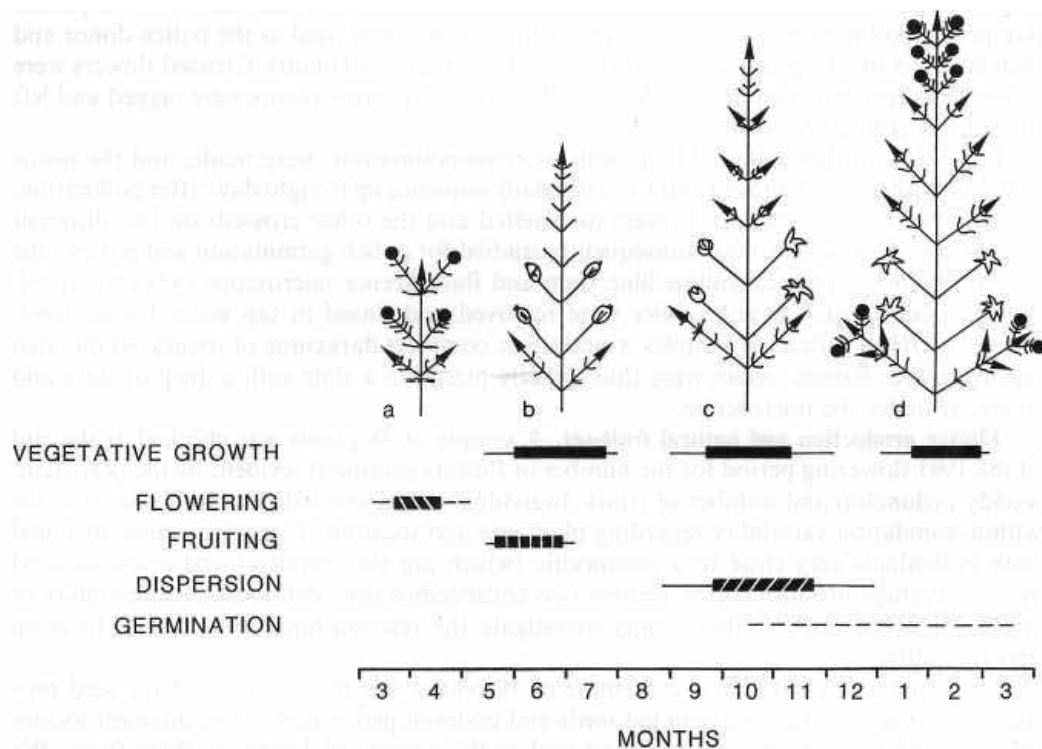

Fig. 1. Phenology of *Cistus ladanifer,* and schematic representations of a branch in successive phenophases. *a* flowering; *b* fruiting; c during seed dispersal; *d* flowering

the seeds have been scattered around the parent plants. Seedlings from the current year seed-crop were observed soon after the first autumn rains.

At the end of August—September, when the high summer temperatures abate and nocturnal dew formation recommences, the plant axes again initiate vegetative growth. During the autumn, each leaf produced at the end of the previous spring organizes an axillary meristem. From such meristems of the lowermost leaf axils, vegetative branches are developed which will produce several flowers in the next cycle, whilst the meristems of the uppermost leaf axils produce unifloral branches (Fig. 1).

Flower characteristics and pollination. The flowers of *Cistus ladanifer* are 55–70 mm in diameter (x = 64.0 ± 1.5, mean ± standard error; N = 14) with white, crumpled petals. These are the largest in the genus *Cistus,* and amongst the largest in the Spanish flora. Only three individuals in the study area presented petals with a basal purple spot which is a commonly encountered polymorphism in some areas. The number of stamens/flower ranged between 178 and 245 (x = 201.6 ± 7.1), and pollen production between 493,594 and 781,830 grains/flower (x = 631,509 ± 38,600). The number of carpels (locules) in a sample of 138 ovaries from 12 individuals ranged between 8 and 11 (x = 9.7 ± 0.1; median = 10). Each locule contained from 78 to 156 ovules (x = 107 ± 2; N = 122). Pollen : ovule ratios varied between 431 and 894 (x = 576 + 44; N = 10).

Flower opening occurred synchronously each day within the population. Initiation of anthesis was signalled when, in late afternoon, the three sepals of each flower began to slacken so that by the end of the day the white crumpled petals were visible. At dawn the following day the petals began to open rapidly so that as the sun rose the flowers were fully open (Fig. 2). At the end of the day the petals reclosed around the ovary until the following morning when all flowers reopened again at sunrise. By the end of the second day a few flowers dropped their petals and the sepals reclosed around the ovary, but the majority of flowers reclosed their petals for the second night. Many of these latter flowers did not open again, but about half of the flowers opened again for a third day during which they too lost their petals.

By the time any flower opens for the first time, the majority of anthers have begun to dehisce and this pollen is readily taken up by the first insect visitors. Nectar is also available from the onset of floral opening and throughout anthesis,
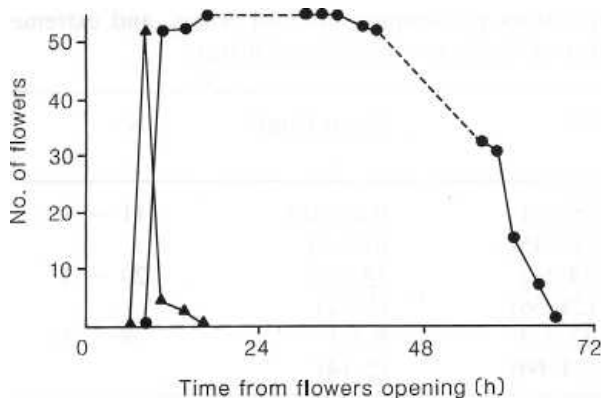

Fig. 2. Rhythm of anthesis of *Cistus ladanifer* flowers. Triangles indicate the pollen-shedding phase, and circles the nectar-secreting phase

but only in measurable quantities after 10:00 h by which time most flowers have been depleted of pollen. Nectar production is reported in Table 1. During the first day of anthesis only small quantities of nectar were produced, with maximum yield during the second day when the flowers were largely pollen-less. The volume of nectar secreted during the third day was about half that produced during the second day of anthesis. The weight of sugar found in two-day old flowers was nearly three times higher than that found in senescing, three-day old ones. Being unprotected, nectar concentrates by evaporation so that at noon concentrations may reach 60% and higher.

Activity of insect visitors to *C. ladanifer* flowers at the study site began ca. 8:00 h (i.e., one hour after the opening of the petals) and continued until approximately 17:00 h. A total of 141 insects were noted of which 16% were *Coleoptera* (mainly *Scarabaeidae, Malachidae, Cerambycidae,* and *Pythidae), 79%* were *Diptera (Calliphoridae, Anthomiidae, Syrphidae,* and *Empididae),* and 4% were *Hymenoptera (Andrenidae, Halictidae,* and *Apidae).* The *Diptera* were mainly nectar feeders and usually occupied a position between the stamens and pistil. The *Hymenoptera* were mainly pollen gatherers and concentrated on the anthers. All of these visitors cross over the central stigma occasionally and so deposit pollen on the papillae. Beetles were usually the last visitors to arrive and they spent long periods in the flowers eating the anthers. The larger species *(Cetonia carthami* subsp. *aurataeformis* CURTIS and *Tropinota squalida* Sco[p].) contact the stigma and so may be occasional pollinators, but the smaller beetles remain between the staminal filaments and rarely contact the stigma.

Breeding system. Results of the hand self- (SP) and cross-pollinations (CP) are given in Table 2. During the first days following pollination, pistils from SP flowers could not be externally differentiated from those in CP ones. Their pedicels, however, began to dry from the fifth day and, thereafter, the ovaries also began to dry up. Such pistils persisted for several more days on the plant since they were supported by the surrounding whorls of bracts. By the 10th to 12th day following pollination, all of the SP flowers had fallen whereas all CP flowers developed fruit. Reciprocal pollinations resulted in fruit being set in all cases (N = 32 flowers).

Table 1. Nectar yield in flowers of *Cistus ladanifer.* All flowers examined after 50 hours were also examined before (after 32 and 8 hours), although the volume of nectar in some of the latter was unquantifiable. Mean values plus-minus standard errors, and extreme values (in brackets) are given. N Number of flowers — number of plants

Flower age (h)	Volume (µl)	%	Sugar (mg)	N
8	1.3 ± 0.2 (0.5—3)	38 ± 1 (33—45)	0.6 ± 0.1 (0.2—1)	11 — 3
32	43.9±5.3 (1—115)	34±2 (21—56)	18±3 (5—72)	20 — 3
50	20.0 ± 5.3 (5—47)	33 ± 4 (21—60)	6 ± 1 (2—14)	8 — 2

Table *2.* Fruit-set following hand cross-, self-, and natural pollination in *Cistus ladanifer.* Two estimates are given of natural fruiting levels: one is based upon flowers from a single day on clumped plants (SD); the other is a pooled average based upon all the flowers produced during the whole flowering season by both isolated and clumped individuals (*WS)*

Treatment	Number of flowers	Number of fruits	Fruit-set (%)	Number of plants
Cross	*44*	44	100	*8*
Self	*39*	*0*	*0*	13
Natural SD	*83*	*79*	*95*	13
WS	*3407*	*2245*	*66*	*38*

In both CP and SP flowers, tubes of ca. 450 sm could be observed in the style within two hours after pollination. However, no pollen tubes were observed within the ovary of SP flowers up to eight days following pollination, nor were ovule penetrations detected in such ovaries (overall sample size N = 1463 ovules from 16 flowers). In CP ovaries, 18% of ovules were penetrated at the first day after pollination and 68% at the second. The proportion of penetrated ovules rose to 88% at the third day, then remained unchanged at approximately 90% until the 8th day (N = 1186 ovules from 16 flowers). Ovules were invariably penetrated through the micropyle.

Flower production, fruit, and seed set. In the study site, most plants were in their second or third year of flowering and, since plants reach flowering by 3—4 years, the population comprised a cohort of flowering individuals of 5—8 years, with the oldest plants being branched, erect shrubs of 3.5 m height. The overall number of flowers produced by individual plants was found to depend both on size/age and location: plants in clumps were often small and opened few flowers, whereas vigorous, more or less isolated individuals produced many. Isolated C. *ladanifer* plants in their third or fourth year of flowering (i.e., seven or eight years old) may open up to 20 flowers per day during the peak of flowering and a total of ca. 300 flowers during the whole flowering season.

Overall, plants in the studied sample produced from 2 to 386 flowers during the 1991 season, while the number of fruits per plant ranged between 0 and 304. All the estimates of fecundity were found to be distance-dependent. Thus, seed yield per fruit varied inversely with nearest neighbour distance (Fig. 3 a; r = — 0.790, p = 0.007). On average, relatively isolated plants set 37 seeds/locule, whereas plants close to other conspecifics produced more than twice as many seeds (92 seeds/locule). This was clearly not due to between-plant variations in the number of ovules in the ovary, since the proportion of ovules developing into seed also correlates negatively with nearest-neighbour distance (Fig. 3 b; r = — 0.871, p = 0.01). To further analyze the relationship between plant location and fecundity, an analysis of variance was performed taking into account both the effect of location (nearest conspecific neighbour within a radius of 8 m or less vs. nearest conspecific neighbour further than 8 m) and the effect of the individual plant (nested under location) on the number of seeds per locule (Table 3). Whereas both factors are significant in
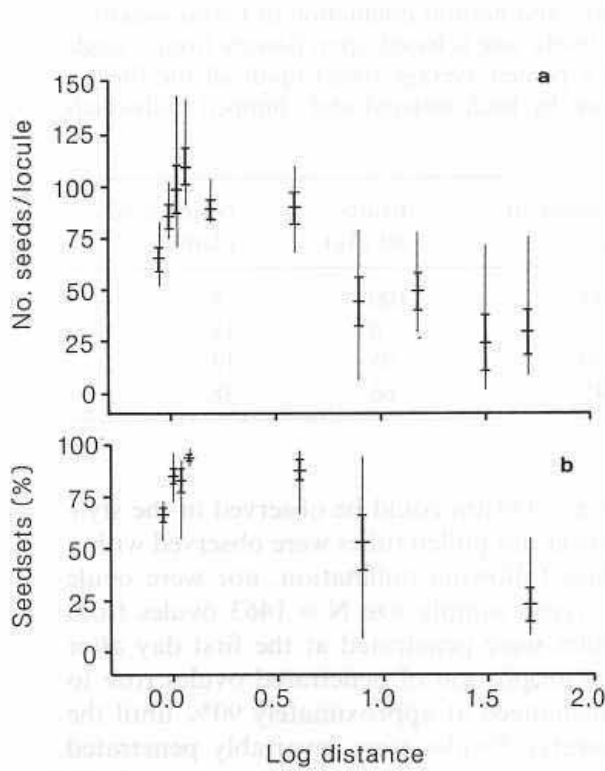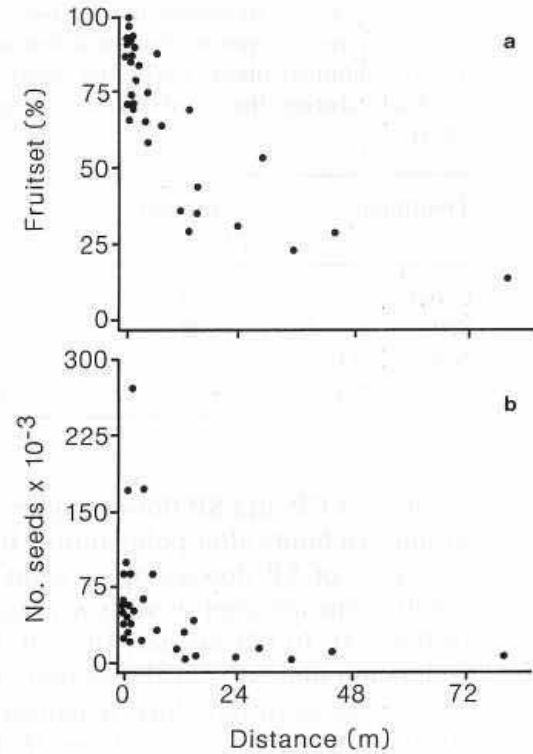
Figs. 3 and 4. *Cistus ladanifer.* — Fig. 3. The relationship between *(a)* seed yield per fruit and *(b)* the proportion of ovules developing into seed vs. nearest neighbour distance. — Fig. 4. The relationship between *(a)* fruit set and *(b)* total seed yield per plant vs. nearest neighbour distance

Table 3. Analysis of variance testing the effect of plant location (nearest conspecific closer than 8 m or beyond that distance) and plant identity (nested under location) on the number of seeds per locule, in capsules of C. *ladanifer. df.* Degrees of freedom

Source	d.f.	Main-square	F-ratio	P
Location	1	115062.6	336.8	< 0.001
Plant (location)	8	3511.0	10.3	< 0.001
Error	150	341.7		

determining the number of seeds/locule, it is the position of the plant with respect to its conspecifics which explains the vast majority of the variance.

Plants converted between 0 and 97% of flowers into fruit. As shown in Fig. 4 a, percent fruiting is also dependent on the distance to nearest conspecific neighbour (r = — 0.876, p < 0.001; see also Table 3). In contrast, fruit-set is largely uncorrelated with flower production (r = 0.002, p = 0.903; arcsin transformed data). The data available also allow an estimate to be made of the number of seeds liberated

by individual plants. To obtain this, we first calculated the product of flower number and percent fruit-set per plant. This value was then multiplied by either 92 seeds per locule (for plants growing in a clump) or 37 (for plants beyond 8 m from the nearest conspecific), and by an average of 9.68 locules per fruit. Estimated in this way, plants liberated from 3,264 to 271,065 seeds (x = 55,279 ± 10,142; N = 32; only medium- to large-sized plants producing 30 flowers or more during the season were used in the computations). Seed yield is even more markedly dependent on nearest neighbour distance (Fig. 4 b) than previous estimates of fecundity such as seed set.

Discussion

Flowers lasting a single day seem to be the rule in the *Cistaceae* studied to date (HERRERA 1987 a, BRANDT & GOTTSBERGER 1988). At the study population of C. *ladanifer,* observations performed in previous years (TALAVERA 1991) and during 1992 (S. TALAVERA, pers. obs.) also indicate that flowers customarily last one day. Consequently, the floral longevity reported here, with virtually all flowers opening for a second day, and many reopening again for a third, seems exceptional. Extended flower duration was probably caused by conditions of relatively low temperature and high humidity before or during the period of study (PRIMACK 1985). This points to the necessity of using tagged flowers to monitor floral longevity. The nectar production established in this study is also notable, since most authors (e.g., J. HERRERA 1985, BRANDT & GOTTSBERGER 1988) have characterized *Cistus* species as principally pollen-flowers with only minute traces of nectar. Given that the flower duration observed in 1991 season was exceptionally extended, the huge amount of sugar secreted (Table 1) should be considered exceptional as well. A generally lower nectar production is also indicated by ORTIZ (1989), who reported that C. *ladanifer* flowers secreted only 1.7 mg/flower/day.

The observation that self pollen can germinate and tubes grow through the stigma without effecting fertilization indicates that C. *ladanifer* has a gametophytic mechanism of incompatibility (GSI; NETTANCOURT 1977). Such a mechanism is probably common in the *Cistaceae,* since other species of *Cistus* as well as species in *Halimium* and *Helianthemum* do not set fruit following selfing (BRANDT & GOTTSBERGER 1988, HERRERA 1992), or do so at a very low frequency (HERRERA 1987 a). Although previous reports have suggested the existence of incompatibility in this family, here it is clearly established for the first time. GSI in *Cistus is* in accordance with the observation that the pollen is in this species binucleate, and is unusual in that the stigma is of the dry type (HESLOP-HARRISON & SHIVANNA 1977). The success of reciprocal pollinations supports the existence of a GSI system (see NETTANCOURT 1977, GIBBS 1986, and BARRETT 1988 for reviews).

The inverse relationship found between plant fecundity and nearest neighbour distance is similar to those found by WYATT & HELLWIG (1979) in *Houstonia caerulea,* a self-incompatible species in the *Rubiaceae,* and by C. M. HERRERA (1985) in *Osyris quadripartita,* a hemiparasitic, Mediterranean dioecious shrub in the *Santalaceae.* In contrast, BAWA & WEBB (1984) report on six self-incompatible neotropical species in which fruit-set was positively correlated with the distance to the nearest conspecific. In C. *ladanifer* the negative correlation would indicate that, even in the presence of self-incompatibility, individuals growing in a clump did not

experience depressed fecundity, probably because pollinators were very abundant and often moved between neighbouring plants. Isolated individuals, on the other hand, would show depressed fruit- and seed-set because of increased within-plant transfer of pollen, and/or decreased visitation rates. In fact, the negative correlation is suggestive of low pollinator mobility, but this would need additional research to be tested.

There were very few isolated plants in the studied population, the vast majority of the individuals therein showing levels of fruit-set near 90%. According to WIENS & al. (1987), this is an exceedingly high value for strictly allogamous plants. Whilst the pollen : ovule ratio observed for this species is low for an outbreeding taxon (CRUDEN 1977), conjectures about the breeding system of C. *ladanifer* based only on fruit-set or P : 0 values would probably have led to wrong conclusions. Undoubtedly, the largely unsophisticated morphology of C. *ladanifer* flowers, together with their highly rewarding nature and spring-flowering contribute to guarantee high visitation rates and extensive pollen deposition on the stigmas. The example of C. *ladanifer is* in sharp contrast with that of *Nerium oleander (Apocynaceae), a* low-rewarding, summer-flowering Mediterranean shrub in which, in spite of self-compatibility, fruit-set is invariably below 5% (HERRERA 1991).

References

BARRETT, S. C. H., 1988: The evolution, maintenance and loss of self-incompatibility systems. — In LOVETT-DOUST, J., LOVETT-DousT, L., (Eds): Plant reproductive ecology, pp. 98-124. — New York: Oxford University Press.

BAWA, K. S., WEBB, C. J., 1984: Flower, fruit, and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. — Amer. J. Bot. 71: 736-751.

BORNET, M. E., GARD, M., 1919: Recherches sur les hybrides artificiels des Cistes. — Ann. Sci. Nat. Ser. Bot. **9:** 71-116.

BRANDT, U., GOTTSBERGER, G., 1988: Flower phenology, pollinating insects and breeding systems in *Cistus, Halimium,* and *Tuberaria* species in Portugal. — Lagascalia **15:** 625-634.

CORRAL, R., PITA, P. M., PEREZ-GARCIA, F., 1990: Some aspects of seed germination in four species of *Cistus* L. — Seed Sci. Technol. **18:** 321-325.

CRUDEN, R. W., 1977: Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. — Evolution 31: 32-46.

HERMANN, S. M., 1983: Studying nectar? Some observations on the art. – In BENTLEY, B., ELIAS, T., (Eds): The biology of nectaries, pp. 223-241. — New York: Columbia University Press.

DANSEREAU, P., 1941 a: Etudes sur les hybrides des Cistes. IV. Correlation des characteres du *C. salvifolius L.* — Canad. J. Res. **19:** 27-39.

1941 b: Etudes sur les hybrides de Cistes. VI. Introgression dans la section *Ladanium.* – Canad. J. Res. **19:** *59-67.*

- 1943: Etudes sur les hybrides de Cistes. V. Le comportement du *x Cistus florentinus* LAM. — Candollea **10:** 9-22.

GIBBS, P. E., 1986: Do homomorphic and heteromorphic self-incompatibility systems have the same sporophytic mechanism? — Pl. Syst. Evol. **154:** 285-323.

HERRERA, C. M., 1985: Predispersal reproductive biology of female *Osyris quadripartita (Santalaceae),* a hemiparasitic dioecious shrub of Mediterranean scrublands. — Bot. J. Linn. Soc. **90:** 113-123.

HERRERA, J., 1985: Nectar secretion patterns in southern Spanish Mediterranean scrublands. — Israel J. Bot. 34: 47-58.

- 1987 a: Flower and fruit biology in southern Spanish Mediterranean shrublands. — Ann. Missouri Bot. Gard. 74: 69-78.

- 1987 b: Biologia reproductiva de algunas especies del matorral de Donana. — Annal. Jard. Bot. Madrid **44:** 483-497.

- 1991: The reproductive biology of a riparian Mediterranean shrub, *Nerium oleander* L. *(Apocynaceae).* — Bot. J. Linn. Soc. **106:** 147-172.

- 1992: Flower variation and breeding systems in the *Cistaceae.* — Pl. Syst. Evol. **179:** 245-256.

HESLOP-HARRISON, Y., SHIVANNA, K. R., 1977: The receptive surface of the angiosperm stigma. — Ann. Bot. **41:** 1233-1258.

HEYWOOD, V. H., (Ed.), 1978: Flowering plants of the world. — Oxford: Oxford University Press.

KNUTH, P., 1898: *Cistaceae.* — In: Handbuch der Bliitenbiologie II, pp. 134-137. — Leipzig: Wilhelm Engelmann.

MARTIN, F. W., 1959: Staining and observing pollen tubes in the style by means of fluorescence. — Stain Technol. 34: 125-128.

MORENO, J. M., 1982: Estudios ecologicos en jarales (Cistion laurifolii): variacion anual de algunos factores del entorno y manifestaciones fenologicas. — Madrid: Fundacion March, Serie Universitaria **180.**

- 1984 a: Estudio ecologico comparado de los jarales de Madrid, I. Variacion anual de la humedad del suelo. — Lazaroa **6:** 105-126.

- 1984 b: Estudio ecologico comparado de los jarales de Madrid, II. Variacion estacional del pH edafico. — Lazaroa **6:** 151-168.

MULLER, H., 1883: The fertilization of flowers. — London: Macmillan.

NETTANCOURT, D. DE, 1977: Incompatibility in angiosperms. — Berlin: Springer.

ORTIZ, P., 1991: Melitopalinologia en Andalucia Occidental. — Tesis Doctoral. Sevilla. Universidad de Sevilla.

PAPIO, C., TRABAUD, L., 1990: Structural characteristics of fuel components of 5 Mediterranean shrubs. — Forest Ecol. Management **35:** 249-259.

PRIMACK, R. B., 1985: Longevity of individual flowers. — Ann. Rev. Ecol. Syst. **16:** 15-37.

SOKAL, **R. R.,** ROHLF, F. J., 1981: Biometry, 2nd edn. — San Francisco: Freeman.

TALAVERA, S., 1991: Flora y polinizacion. In: IV Congreso Nacional de Apicultura, pp. 27-38. — Zaragoza: Diputacion General de Aragon.

TRABAUD, L., OUSTRIC, J., 1989: Heat requirements for seed germination of 3 *Cistus* species in the garrigue of southern France. — Flora **183:** 321-326.

TROUMBIS, A., TRABAUD, L., 1986: Comparison of reproductive biological attributes of two *Cistus* species. — Acta Oecol., Oecol. Plant. 7: 235-250.

WIENS, D., CALVIN, C. L., WILSON, C. A., DAVERN, C. I., FRANK, D., SEAVEY, S. R., 1987: Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. — Oecol. 71: 501-509.

WYATT, R., HELLWIG, R. L., 1979: Factors determining fruit set in heterostylous bluets, *Houstonia caerulea (Rubiaceae).* — Syst. Bot. 4: 103-114.

Addresses of the authors: SALVADOR TALAVERA and JAVIER HERRERA, Departamento de Biologia Vegetal y Ecologia, Universidad de Sevilla, Apartado 1095, E-41080 Sevilla, Spain. — PETER E. GIBBS, Department of Biology and Preclinical Medicine, The University, St Andrews KY16 9TH, Scotland, U.K.