

## Flower variation and breeding systems in the *Cistaceae*

JAVIER HERRERA

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**Key words:** Angiosperms, *Cistaceae*, *Cistus*, *Halimium*, *Helianthemum*, *Fumana*, *Tuberaria*. — Outcrossing, autogamy, cleistogamy, shrublands. — Flora of Spain.

**Abstract:** Fourteen common southern Spanish species in the *Cistaceae* were examined for quantitative variations in floral traits. These included the diameter of the corolla, number and size of anthers, number of ovules, and the size and shape of the gynoecium. The variables were in most instances positively correlated, species with larger flowers having more and larger anthers, more ovules, etc. Shrubs were observed to possess the largest, annuals the smallest, and subshrubs medium-sized flowers. Detailed observations of flower structure and function in a shrub (*Cistus salvifolius*), a spring-annual (*Tuberaria guttata*) and a winter-annual (*T. inconspicua*), revealed substantial variations in the breeding system. While *C. salvifolius* (and probably most woody species in this family) presents self-incompatibility, annual species of *Tuberaria* are self-compatible. In the studied population, *T. inconspicua* plants bore only reduced, cleistogamous flowers with no sign of a corolla. *T. guttata* has chasmogamous flowers that can facultatively self-pollinate.

The *Cistaceae* is a relatively small angiosperm group with about 160 species and a mainly circum-Mediterranean distribution (HEYWOOD 1978), the western part of this area being particularly species-rich (QUEZEL 1981). Plants in this family are mostly showy-flowered shrubs from warm habitats, well adapted to summer drought (MARTIN-BOLANOS & GUINEA 1949). Together with species in the *Lamiaceae* and *Fabaceae* (tribe *Genisteae*), shrubby *Cistaceae* are major and typical constituents of sclerophyllous scrubs that cover vast areas in the Iberian Peninsula and other Mediterranean countries, and often characterize vegetation that develops after disturbance (typically by fire) of evergreen sclerophyllous forests (RIVAS-MARTINEZ 1979).

Studies on species in the *Cistaceae* have mostly dealt with hybridization (DAN-SEREAU 1941, 1943), ecophysiological aspects of seed germination in relation to fire (TROUMBIS & TRABAUD 1986, TRABAUD & OUSTRIC 1989, CORRAL & al. 1990, for example), or growth and distribution (FARMER 1984, BERLINER & al. 1986, AGAMI 1987, among others). Floral biology, on the other hand, could be argued to represent a largely overlooked topic since the extensive review by FRYXELL (1957) gives no data on this family. In fact, characteristics of the reproductive biology of

some *Cistaceae* have been known for long (DARWIN 1877, ASCHERSON 1980 in BRANDT & GOTTSBERGER 1988), and more data have been published recently for a number of taxa including aspects on their phenology (HERRERA 1986, ARROYO 1990), floral biology (HERRERA 1985, 1987 a, b), and pollinators (BRANDT & GOTTSBERGER 1988, HERRERA 1988). Nevertheless, these studies are often community-oriented (see, however, BRANDT & GOTTSBERGER 1988), and since data on *Cistaceae* are scattered among many other plant species, it is difficult to gain a general idea of the reproductive behaviour of the whole family.

This study presents data on the morphological variation of flowers in southern Spanish species of *Cistaceae*, and reports the main reproductive correlates of life-form in this family. It is intended to represent a general view of the reproductive ecology in group, and to make a contribution to the increasingly large body of information on the reproduction of Mediterranean plants. A similar treatment for a number of Mediterranean representatives in the *Ericaceae* has been reported by ARROYO & HERRERA (1988).

### Study area and methods

Field work was carried out on several locations distributed across the western part of Andalucía (southern Spain) during the period 1985–1991. The 14 studied species (see Table 1 for their identities) are representative of all life-forms that occur in the *Cistaceae* (shrubs, subshrubs, and annuals), live in a variety of habitats from coastal areas through mountain ranges, and were selected mostly because of their commonness in the region. Taxonomic nomenclature follows HEYWOOD (1968), except for *Tuberaria* (GALLEGO 1991). In order to investigate additional reproductive traits, not necessarily related to flowers, a smaller subset of 3 taxa was selected. These were chosen among those in the larger sample, and had contrasting life-forms and breeding systems. They included a shrub (*Cistus salvifolius*), a spring-flowering herb (*Tuberaria guttata*), and a winter-flowering herb (*T. inconspicua*). All three species coexisted in a 0.5 Ha study plot located at Reserva Biológica de Doñana (Doñana National Park), a coastal area near the Gulf of Cadiz (a description of this site may be found in HERRERA 1986). Additional field work was carried out during 1991 at a *Cistus salvifolius* population near Aznalcazar (Sevilla province). Voucher specimens are deposited in the herbarium of the Universidad de Sevilla (SEV).

The diameter of 5–10 flowers per taxon was measured to the nearest 0.1 mm. The number of anthers and that of ovules per flower was also counted in 5–10 fixed flower buds for each species under a dissecting microscope. During dissection, the length and width of an anther per flower were measured to the nearest 0.1 mm and subsequently used to estimate anther volume by approximation to a cylinder. The shape and size of the style were also noted, and the diameter of the stigma measured. Since the stigmatic surface was often circular, its area was estimated accordingly.

In the sub-sample of three species, a variety of flower, fruit, seed, and vegetative characteristics was determined. For each taxon, the height of 10–20 individuals was measured, the plants excavated to extract the main roots, and then taken to the laboratory. They were dried to a constant weight, and weighed on an electronic balance. For each species, the length of one sepal and one petal from 10–20 fixed mature flower buds was measured to the nearest 0.1 mm. To estimate the number of pollen grains produced per flower, an anther was squashed on a slide containing a drop of safranin-detergent solution. The whole anther's content was then uniformly extended over the slide and every grain counted under the microscope at a magnification of 400 x . The resulting number was multiplied by the number of anthers in the flower to estimate total pollen production. The number of ovules in the ovary of the same flowers was counted under a dissecting micro -



Table 1. Floral characteristics in 14 species of *Cistaceae*. Flower diameter is in mm, anther size in microlitres, and stigmatic area in mm<sup>2</sup>. Numbers in brackets are standard errors. S Shrub usually higher than 0.5 m; SS subshrub usually lower than 0.5 m; T therophyte. P Pink; W white; Y yellow

| Species                                   | Habit | Flower colour | Flower diameter | Number of anthers | ovules     | Anther size   | Stigmatic area |
|---|-------|---------------|-----------------|-------------------|------------|---------------|----------------|
| <i>Cistus albidus</i> L.                  | S     | P             | 61.7 (1.8)      | 165 (5)           | 69 (2)     | 0.28 (0.09)   | 1.52 (0.28)    |
| <i>C. crispus</i> L.                      | SS    | P             | 38.6 (0.8)      | 181 (10)          | 49 (2)     | 0.16 (0.04)   | 1.45 (0.45)    |
| <i>C. ladanifer</i> L.                    | S     | W             | 77.8 (2.2)      | 156 (3)           | 1166 (121) | 0.72 (0.11)   | 13.79 (0.96)   |
| <i>C. libanotis</i> L.                    | S     | W             | 29.9 (0.6)      | 62 (2)            | 22 (1)     | 0.37 (0.04)   | 1.43 (0.16)    |
| <i>C. monspeliensis</i> L.                | S     | W             | 26.1 (0.7)      | 56 (4)            | 20 (1)     | 0.18 (0.03)   | 0.45 (0.05)    |
| <i>C. salvifolius</i> L.                  | S     | W             | 42.6 (0.8)      | 145 (5)           | 55 (2)     | 0.18 (0.03)   | 2.27 (0.11)    |
| <i>Fumana ercooides</i> (CAV.) GANG.      | SS    | Y             | 16.7 (0.7)      | 29 (2)            | 7 (1)      | 0.05 (0.01)   | 0.35 (0.04)    |
| <i>Halimium commutatum</i> PAU            | SS    | Y             | 22.6 (0.9)      | 37 (2)            | 7 (0.1)    | —             | —              |
| <i>H. halimifolium</i> (L.) WILLK.        | S     | Y             | 32.2 (0.9)      | 96 (4)            | 46 (4)     | 0.25 (0.02)   | 1.88 (0.17)    |
| <i>Helianthemum croceum</i> (DESF.) PERS. | SS    | Y             | 23.9 (0.6)      | 71 (2)            | 18 (1)     | 0.18 (0.01)   | 0.24 (0.11)    |
| <i>He. organifolium</i> (LAM.) PERS.      | SS    | Y             | 13.1 (0.7)      | 40 (1)            | 7 (1)      | 0.11 (0.01)   | 0.20 (0.06)    |
| <i>He. salicifolium</i> (L.) MILLER       | T     | Y             | 10.1 (0.4)      | 4 (0.2)           | 31 (2)     | 0.01 (0.004)  | 0.25 (0.04)    |
| <i>Tuberaria guttata</i> (L.) FOURR.      | T     | Y             | 14.5 (0.6)      | 19 (1)            | 93 (6)     | 0.04 (0.01)   | 0.62 (0.07)    |
| <i>T. inconspicua</i> (THIB.) WILLK.      | T     | None          | 1.1 (0.1)       | 5 (1)             | 33 (5)     | 0.004 (0.002) | 0.19 (0.10)    |

scope, and pollen-to-ovule ratios determined in accordance with these estimates. The length of the fruit peduncle, the width of the capsule, and the number of seeds therein were noted for 20 fruits per species. Seeds from several individual plants were pooled and individually weighed to the nearest 0.01 mg. Seed length was measured on a sample of 20 seeds per species. Estimates of the number of seeds produced per plant were obtained from fruit counts and average number of seeds per capsule.

Three plants of *Cistus salvifolius* were used to perform several experimental manipulations of flowers. Treatments were designed to investigate the dependence on outcrossing for reproduction and included: (1) bagging of flowers with 0.2 mm mesh; (2) removing all stamens and bagging; (3) deposition of self-pollen on the stigma and bagging; (4) deposition of pollen from another individual and bagging; and (5) open pollination. Hand-pollinations in (3) and (4) were done by rubbing 2 dehisced anthers, held with forceps, all over the stigma. Counts on 4 stigmas revealed that the number of pollen grains deposited in this way ranged between 496 and 1115, which is well above the number of ovules in the ovary. The stigmas and styles from several additionally self-pollinated flowers were separated, cleared on NaOH, rinsed in water, and finally stained with decolourized aniline-blue in order to assess the growth of pollen tubes (MARTIN 1959). Preparations were then observed under UV light on a Zeiss-Axiophot microscope. Self-pollinated flowers of *Tuberaria guttata* and *T. inconspicua* were similarly observed for pollen-tube growth.

## Results

**Morphology of cistaceous flowers.** Flower architecture is basically constant in this family, the corollas always fitting the circular, dish-bowl type of FAEGRI & VAN DER PIJL (1979): five free petals define a somewhat concave surface around the androecium and the gynoecium. Petals are predominantly yellow in species of *Halimium*, *Helianthemum*, and *Tuberaria*, while in *Cistus* they may be either pink or white (Table 1). Petals often exhibit dark coloured spots at their bases (for example, *C. ladanifer*, *Tuberaria guttata*), although the size and shade of these spots are highly variable, even among individuals within the same population. In the studied sample the largest flowers are those of *Cistus ladanifer* (more than 70 mm of diameter), while those of annuals are much smaller (Table 1). Most interestingly, the flowers of *Tuberaria inconspicua* from the studied population of Donana showed no sign of a corolla, remained closed at anthesis, and should be considered cleistogamous (see below). Shrub flowers average 45.1 mm of diameter, subshrubs 22.9 mm, and therophytes 8.6 mm, differences being statistically significant (Kruskal-Wallis non-parametric analysis of variance,  $H = 9.12$ ,  $p = 0.01$ ).

Stamens are always yellow, with anthers fixed by their bases to the filaments and opening by longitudinal slits to liberate the pollen. In the genus *Fumana*, the outermost anthers are sterile and do not contain pollen of any kind (either viable or empty), which is exceptional in the family. Among-species variations of anther size are extensive (Table 1), ranging from 0.7 microlitres in *Cistus salvifolius* to 0.004 microlitres in *Tuberaria inconspicua*. The highest number of stamens per flower in the sample occurred in species of *Cistus*, which are usually heavy pollen-producers. The flowers of annuals, on the other hand, may bear as few as 4 stamens on average (*Helianthemum salicifolium*). As shown in Fig. 1, flower diameter and average number of anthers per flower are positively and highly correlated ( $r_s = 0.925$ ,  $p < 0.001$ ; Spearman rank correlation).

There is ample variation among species in the number of ovules in the ovary (Table 1). *Cistus ladanifer* has on average more than 1000 ovules, which is excep-

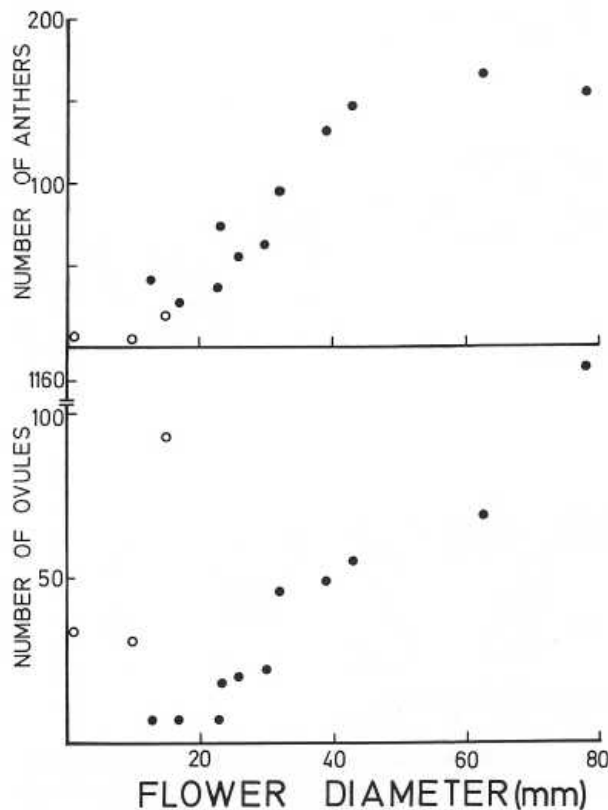


Fig. 1. The relationship between average flower diameter and the number of anthers (top) or ovules (bottom) per flower in a sample of species in the *Cistaceae*. *O* Annual, *•* perennial species

tionally high even for the genus *Cistus*. The smallest numbers of ovules are not found among annuals, but among low shrubs such as *Fumana ericoides*, *Halimium commutatum*, and *Helianthemum origanifolium*, in which the number of ovules is fixed or nearly so. The number of ovules in the ovary is not correlated with flower diameter (Fig. 1;  $r_s = 0.399$ ,  $p > 0.1$ ), this being mostly due to unexpectedly large numbers of ovules among annuals. A highly significant, positive correlation exists, however, if just perennials are considered ( $r_s = 0.970$ ,  $p < 0.001$ ).

There is little if any variation between genera or species regarding the external morphology of the ovary, which is always approximately spherical. There is, however, extensive variation regarding the style and the shape of the stigma (Fig. 2). Species of *Helianthemum* and *Fumana* have relatively long and slender styles terminated by stigmas which are smaller than the diameter of the ovary. In *Cistus*, *Halimium*, and *Tuberaria* the style is often short or nonexistent, while the stigma is a globular body made up of long papillae, with a diameter similar to that of the ovary. The only exceptions in this regard within the genus *Cistus* are the pink-flowered *C. albidus* and *C. crispus*, which have long styles and relatively small stigmatic areas (Table 1). The size of the stigma is positively correlated with average number of ovules in the ovary ( $r_s = 0.703$ ,  $p < 0.01$ ).

Figure 3 displays the relationship between the number of anthers and that of ovules per flower. This plot is based on individual flowers, not on species averages, and no effort has been done to identify particular taxa. Rather, differences associated to life-form are emphasized. In both perennials and annuals the number of

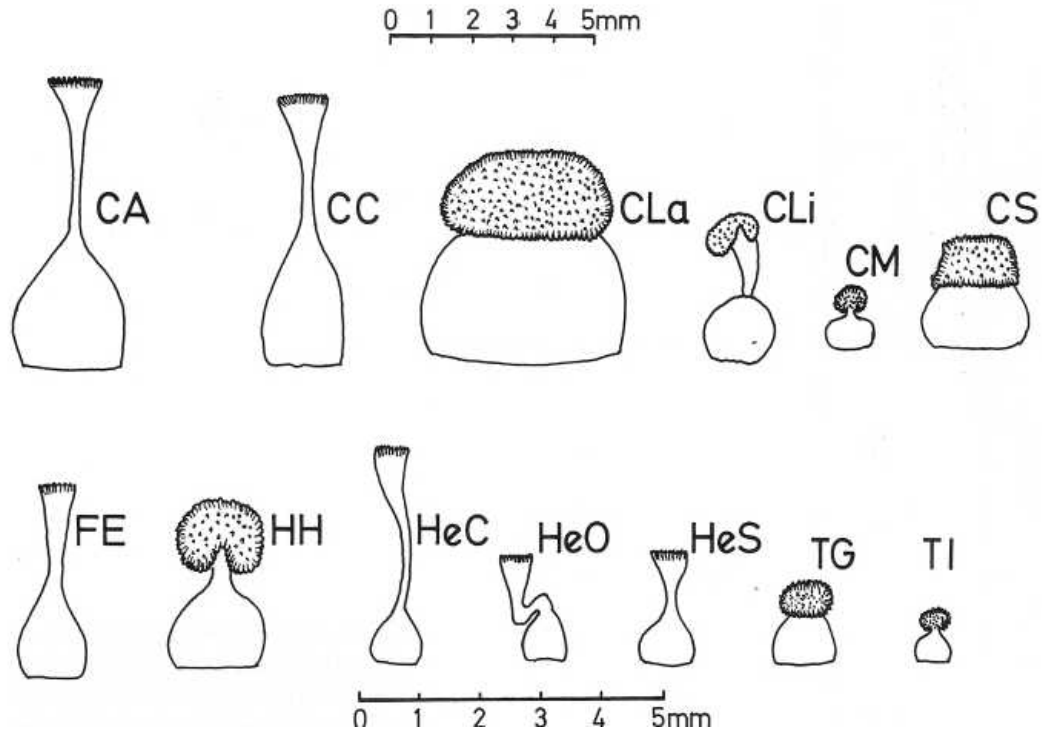


Fig. 2. Varying shapes and sizes of the gynoecium in a sample of species in the *Cistaceae*. CA *Cistus albidus*, CC *C. crispus*, CLa *C. ladanifer*, CLi *C. libanotis*, CM *C. monspeliensis*, CS *C. salvifolius*, FE *Fumana ericoides*, HH *Halimium halimifolium*, HeC *Helianthemum croceum*, HeO *H. organifolium*, HeS *H. salicifolium*, TG *Tuberaria guttata*, TI *T. inconspicua*

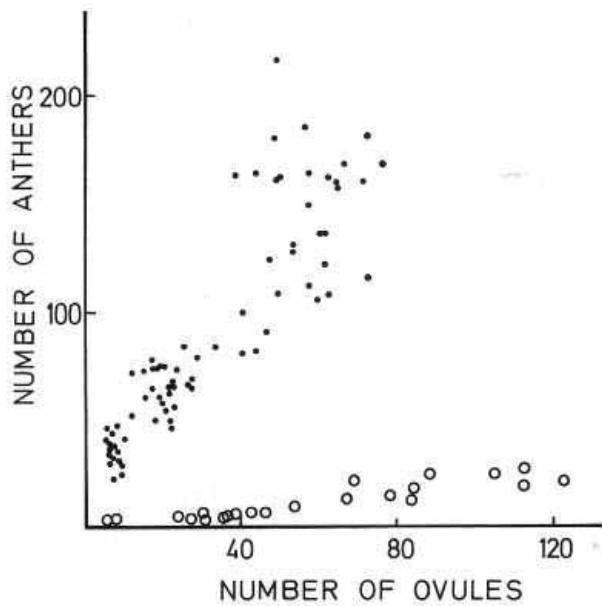


Fig. 3. The relationship between anther and ovule number in flowers of *Cistaceae*. Species are the same that appear in Table 1, except for *Cistus ladanifer* which is not included. • Perennials, 0 annuals



ovules per flower and that of anthers are positively correlated ( $r = 0.894$  for perennials and  $r = 0.924$  for annuals;  $p < 0.001$  in both cases). Nevertheless, the anther-to-ovule ratio of perennials averages  $3.5 \pm 0.2$  (mean  $\pm$  standard error;  $n = 93$ ) while among annuals there is just  $0.2 \pm 0.01$  anthers per ovule ( $n = 25$ ). These differences are highly significant ( $t = 9.688$ ;  $p < 0.001$ ) implying that, for a given number of ovules per flower, perennials devote much more energy to perform male function (and presumably outcrossing) than annuals.

**Reproductive correlates of life-form.** Table 2 reports on a number of quantitative variables, mostly related to reproduction, in a shrub (*Cistus salvifolius*), a spring-annual (*Tuberaria guttata*), and a winter-annual (*T. inconspicua*). Not surprisingly, the shrub shows very high values for most variables when compared to annuals, although in fact *T. inconspicua* and *T. guttata* averages are also often significantly different.

For all variables related to size in Table 2, *Cistus salvifolius* has the largest and *Tuberaria inconspicua* the smallest mean. *C. salvifolius* has larger flowers, fruits, and seeds. It also has more pollen per flower, and a higher pollen-to-ovule ratio. The overall number of seeds produced per plant (Table 2) is much higher for the shrub species than for the annuals, this resulting mainly from *C. salvifolius* having set much heavier fruit crops (more than 250 fruits per plant on average). The number of seeds per capsule is relatively unimportant in determining final seed output per plant.

To compensate for the substantial differences in plant size between *C. salvifolius* and the species of *Tuberaria*, a relative measure of seed production (the seeds produced per mg of plant mass, i.e., the relative reproductive effort, RRE) has been computed. This magnitude is dramatically higher for annuals (Table 2) and, among these, *T. inconspicua* shows higher RRE than *T. guttata*. This suggests that, for a similar size of the plant, the cleistogamic species liberates many more seeds than the facultative selfer (*T. guttata*). This can be graphically assessed in Fig. 4, where seed outputs per plant have been plotted against plant masses. Since both annuals share a similar range of plant sizes, a comparison by covariance analysis could be meaningful (SOKAL & ROHLF 1981). In this analysis, the effect of the factor "species" is highly significant ( $F = 21.995$ ,  $p < 0.001$ ; log-transformed data), which demonstrates that the cleistogamous annual has a relative seed output that is higher than that of the facultatively self-pollinating species.

The high pollen-to-ovule ratio of *C. salvifolius* (Table 2) is consistent with a breeding system in which outcrossing dominates. This correlates with the fact that flowers do not set fruit unless cross pollen is deposited on the stigma (Table 3). The site of operation of self-incompatibility, however, is unclear. Microscopic observations indicate that self-pollen germinates massively on the stigma after two hours, and that pollen tubes do in fact grow down the stylar tissue. Unfortunately, the trajectory of pollen tubes inside the ovary could not be exactly determined because of insufficient clearing of these tissues associated to low emission of fluorescence.

The observation of pollen-tubes in the ovaries of *Tuberaria* species, on the other hand, presented no such technical difficulties. In these taxa, tubes were clearly observed to reach ovules soon after self-pollination. In *T. inconspicua*, self-fertilization is invariably achieved in the bud: anthers, which are in close contact with

Table 2. Characters of habit, flowers, fruits, and seeds in species of *Cistaceae* with varying life-forms and breeding systems. *Cistus salvifolius* is an obligately outcrossing shrub, *Tuberaria guttata* a facultatively self-pollinating annual, and *T. inconspicua* an annual with only cleistogamic, obligately self-pollinating flowers. Numbers in brackets are standard errors

| Character <sup>1</sup> | <i>Cistus salvifolius</i> | <i>Tuberaria guttata</i> | <i>Tuberaria inconspicua</i> |
|------------------------|---------------------------|--------------------------|------------------------------|
| Plant height (mm)      | 689 (49)                  | 224 (12)                 | 234 (16)                     |
| Plant mass (mg)        | 194200 (82900)            | 216 (23)                 | 172 (48)                     |
| Sepal length (mm)      | 13.2 (0.5)                | 3.7 (0.1)                | 2.4 (0.1)                    |
| Petal length (mm)      | 11.6 (0.7)                | 3.1 (0.1)                | 0                            |
| Peduncle length (mm)   | 17.1 (1.1)                | 11.3 (0.4)               | 5.0 (0.7)                    |
| Pollen/flower          | 103760 (6947)             | 5538 (1041)              | 1031 (51)                    |
| Pollen-to-ovule ratio  | 1908 (143)                | 56.7 (7.9)               | 4.9 (0.8)                    |
| Capsule width (mm)     | 9.4 (0.2)                 | 5.1 (0.2)                | 3.2 (0.1)                    |
| Seed length (mm)       | 1.3 (0.03)                | 0.53 (0.01)              | 0.49 (0.01)                  |
| Seed mass (mg x 100)   | 94.0 (4)                  | 5.40 (0.23)              | 4.32 (0.23)                  |
| Seeds/capsule          | 50.3 (3.9)                | 74.6 (8.0)               | 14.4 (0.8)                   |
| Fruits/plant           | 252.7 (113)               | 14.3 (1.2)               | 51.8 (10.1)                  |
| Seeds per plant        | 12700 (5669)              | 495 (42)                 | 746 (144)                    |
| RRE <sup>4</sup>       | 0.06 (0.01)               | 2.94 (0.3)               | 5.04 (0.4)                   |

<sup>1</sup> Among-species differences of means are significant at  $p < 0.05$  for all variables, except for that between *T. guttata* and *T. inconspicua* for plant height and mass.

<sup>2</sup> Measured in the bud stage.

<sup>3</sup> Estimated by multiplying the number of fruits by the average number of seeds per fruit.

<sup>4</sup> RRE = number of seeds divided by plant mass.

the stigma inside the closed flower, shed their pollen directly onto the stigma and, as soon as it becomes receptive, fertilization takes place. In the chasmogamous *T. guttata* the stigmatic surface of most open-pollinated flowers remains clean of self-pollen during the 4—5 hours of anthesis, but self-pollination takes place as soon as petals are shed and sepals fold over the gynoecium, thus causing the anthers to contact the stigma. Not surprisingly, thus, plants of *T. guttata* transform into fruit



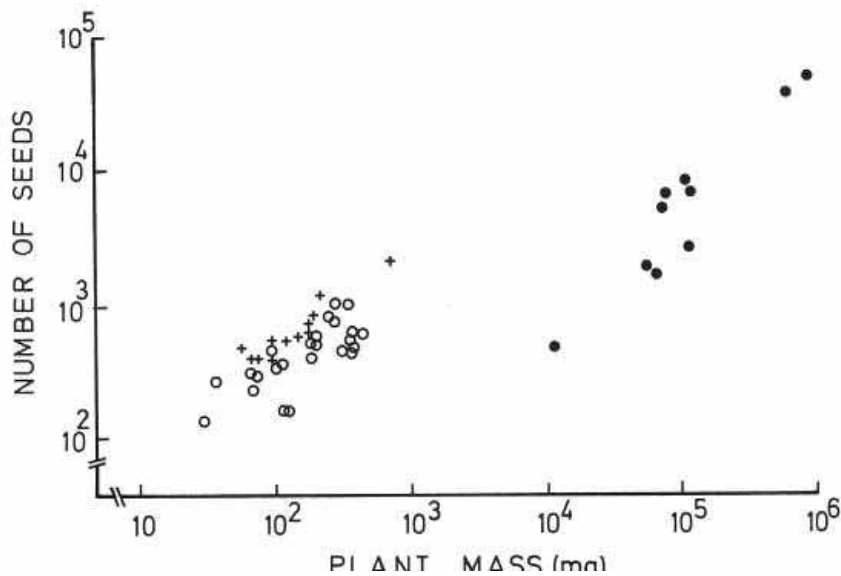


Fig. 4. The relationship between plant dry mass and the number of seeds produced by individuals in three species of *Cistaceae*. • *Cistus salvifolius*, ○ *Tuberaria guttata*, + *T. inconspicua*

Table 3. Results of experimental manipulations on *Cistus salvifolius* flowers designed to ascertain its dependence on outcrossing for reproduction. Three individual plants were involved in each of the treatments

| Treatment                          | Flowers | Fruits | Seeds/<br>fruit |
|------------------------------------|---------|--------|-----------------|
| Unpollinated (Bagged)              | 6       | 0      | —               |
| Emasculated<br>and bagged          | 6       | 0      | —               |
| Hand self-pollinated<br>and bagged | 6       | 0      | —               |
| Hand crossed<br>and bagged         | 6       | 6      | 50 (5)          |
| Open pollinated                    | 6       | 5      | 34 (8)          |

' Values are means followed by standard errors in brackets.  $t = 1.616$ ,  $p = 0.157$ .

80—100% of flowers even if the whole plant is caged to exclude pollinators, while in *T. inconspicua* fruit set is invariably near 100% (HERRERA 1992).

### Discussion

All the large shrubs in the *Cistaceae* studied to date possess showy, highly polliferous flowers that depend on insect vectors (mostly bees and beetlets, HERRERA

1988) for setting fruit under field conditions. HERRERA (1987 a) reported that bagged flowers of five species set from 0 to 1% fruit (*Cistus libanotis*, 0.2%; *C. salvifolius*, 0%; *Halimium commutatum*, 0%; *H. halimifolium*, 1 %; *Helianthemum croceum*, 0%). All the evidence indicates that regular autogamy is unlikely. Furthermore, hand self-pollination has been demonstrated to be ineffective in inducing fruit development in *C. salvifolius* and *Halimium commutatum* (HERRERA 1987 b, and Table 3 of the present paper). The study by BRANDT & GOTTSBERGER (1988) also states that flowers of *Cistus crispus*, *C. ladanifer*, *C. salvifolius*, and *Halimium commutatum* fail to set fruit following hand self-pollination. Taken together, all indicates that some form of self-incompatibility exists in the perennial, woody species. The strictly allogamous nature of cistaceous shrubs is also associated with other features such as the high pollen-to-ovule (HERRERA 1987 a) and anther-to-ovule (this paper) ratios. Often, P : 0 ratios of the studied *Cistaceae* fall within the range which, according to CRUDEN (1977), characterizes xenogamous species (about 2000 or higher). Note that P : 0 comparisons are particularly meaningful when made among taxonomically related taxa (PRESTON 1986). The association between perennial habit and reproductive systems dominated by outcrossing is general in many angiosperm groups (STEBBINS 1957, JAIN 1976).

Within the family, therophytes represent the lower end of the observed gradient in flower size, anther number, anther volume, stigma size (Table 1), and anther-to-ovule ratio (Fig. 3). Pollen-to-ovule ratios are also extremely low (Table 2). All this suggests that selfing is a common phenomenon among annuals. In *Tuberaria guttata*, for example, the intensity of fruiting of caged plants is virtually identical (HERRERA 1992) to that of freely pollinated individuals, pointing to flowers being not just self-compatible, but autogamous. BRANDT & GOTTSBERGER (1988), however, stated that self-pollinated flowers of this species from a population in Portugal failed to set any fruit. The possibility of within-species variations in breeding system demands further study.

Complete independence from pollinators for reproduction occurs in *Tuberaria inconspicua*, an inbreeder with cleistogamous flowers. The occurrence of cleistogamy in the *Cistaceae* was reported long ago for species in *Lechea* and *Helianthemum* (DARWIN 1877), and *Halimium* (LORD 1981), all of which sometimes bear reduced, cleistogamous flowers. In the Donana population of *T. inconspicua*, plants bore no chasmogamous flowers, although individuals in other populations may do so (GUINEA 1954). In general, the proportion of cleistogamous and chasmogamous flowers is known to be under environmental control, with low light, frost, or water stress increasing the number of cleistogamous flowers (SCHEMSKE 1978, LORD 1981, TRAPP & HENDRIX 1988). The population studied in Donana experienced extremely unfavourable conditions (plants lived on sandy soil, and were shaded by shrubs of *Cistus salvifolius*). This could explain the complete absence of chasmogamous flowers.

An intriguing point appears when observing the proportion of ovules that develop into seed in *T. inconspicua*. While ovaries have on average 33 ovules, capsules bear just 14 seeds (42%; Table 1, Table 2). This is striking since autogamous therophytes are known to mature into seed virtually every ovule in the ovary (WIENS 1984). Given that fertilization of all ovules in this species is undoubtedly assured

by cleistogamy, it is likely that the low number of seeds per capsule is accounted for by abortion of developing embryos due to environmental or genetic factors.

Quantitative floral traits such as the diameter of the corolla, or the number of anthers per flower, among others, are continuous, highly correlated variables in the *Cistaceae* (Figs. 1, 3). Species with larger flowers also have more and larger anthers, more ovules, etc. Furthermore, variations in the number and/or size of the reproductive organs run parallel to variations in life-form, which in turn results in certain plant habits being associated to particular breeding systems. It is a known fact that autogamous derivatives usually differ from outcrossing progenitors in many floral features, mainly related to the size and number of flower parts (ORN-DUFF 1969). The *Cistaceae* is another example of how flower reduction associates to changes in the breeding system. Reproductive assurance under conditions unfavourable for pollination is considered to be the main advantage of self-pollination (see WYATT 1988 for a review), and the same is probably true for the annual, autogamous species in this typically Mediterranean family.

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Address of the author: J. HERRERA, Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apartado 1095, 41080 Sevilla, Spain.

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Introduction

Study area and methods

Results

Morphology of cistaceous flowers.

Reproductive correlates of life-form.

Discussion

References

Table 1: Floral characteristics

Table 2. Characters of habit, flowers, fruits, and seeds

Table 3. experimental manipulations on *Cistus salvifolius* flowers

Fig. 1. relationship flower diameter and number of anthers

Fig. 2. shapes and sizes of the gynoecium

Fig. 3. The relationship anther and ovule number

Fig. 4. relationship plant dry mass and the number of seeds