# Reproductive ecology of *Cneorum tricoccon* L. (Cneoraceae) in the Balearic Islands

## ANNA TRAVESET

*Institut d'Estudis Avançats de les Illes Balears, CSIC, Crtra. de Valldemossa Km. 7'5, 07071-Palma de Mallorca, Spain*

This paper examines some aspects of the reproductive biology of *Cneorum tricoccon* L. (Cneoraceae), a Mediterranean relict shrub which evolved under tropical conditions during the Tertiary. The breeding system, the flowering and fruiting phenology, and the variability in fecundity within and among populations of this plant were examined in the Balearic Islands. The plant is andromonoecious, and pollen from male flowers appeared to be more fertile than pollen from hermaphrodite flowers. There was no limitation of pollen, and xenogamous crosses produced more fruit than geitonogamous ones. The efficiency of male flowers suggests that their use increases plant fitness, thus maintaining such a breeding system. Flowering time is unusual compared with other species in the habitat; there is synchrony among individuals, and flowers are produced almost continuously from November through June. Floral sex ratio (number of hermaphrodite flowers: total number of flowers) varied greatly both through the flowering season and between years and was not consistent through time, suggesting that sex expression may be determined more by factors such as resource status of the plant than by genetic factors. Fully developed fruits are observed from December to July. Fecundity varied among individuals depending upon plant size and was consistent during the three years of the study (1992–1994). Fruit crop also differed strongly among sites. The greatest, most vigorous and thus most fecund plants are found in some populations of Mallorca island, especially at high altitudes. In other Balearic islands with low altitudes (<200 m), such as Cabrera, individuals are always short, less leafy and less fecund.

ADDITIONAL KEY WORDS:—andromonoecy – fecundity – phenology – sex expression – western Mediterranean.

## CONTENTS

## INTRODUCTION

The genus *Cneorum* L. (Rosidae, Cneoraceae) consists of only two species with a very restricted distribution (Heywood, 1985). *Cneorum tricoccon* L. is found in

the western Mediterranean area (Balearic Islands, some localities in the eastern and southern Iberian Peninsula, south-eastern France, Sardinia, Liguria and Tuscany) (Bolós, 1958) whereas *Cneorum pulverulentum* L. (included in the genus *Neochamaelea* by some botanists; cf. Heywood 1985) is endemic to the Canary Islands. A third species, *Cneorum trimerum* (Urb.) Chodat, was described from the flora of Cuba (Chodat, 1921) but has recently been reported to be a synonym of *C. tricoccon* (Lobreau-Callen & Jérémie, 1986).

*Cneorum tricoccon* is an interesting species mainly because it belongs to a group of plants of the Mediterranean flora (Müller, 1933) that did not evolve in the extant ecological conditions, but that has been selected out of a diverse array of species which evolved under a warm, summer-rain, tropical climate in the Tertiary environments (Raven, 1973; Axelrod, 1975; Herrera, 1985). Nevertheless, little is known about its reproductive biology. The only available data on this subject come from a preliminary and unpublished study carried out by Sunyer (1991). An earlier paper on this plant (Daumann, 1974) examined some aspects of its pollination such as the presence of septal nectaries and identified some insect pollinators. As far as I know, no information is available on the reproductive biology of the other congeneric species, *C. pulverulentum*.

The main goals of this study were: (1) to examine the natural history and breeding system of the plant, (2) to describe the flowering and fruiting phenology, (3) to find out whether floral sex ratio is consistent through time, and (4) to determine the intra- and interpopulation variability in flower and fruit production.

*Study site*

The study was carried out mainly in Mallorca and Cabrera islands, although additional observations were made in other islands of the Balearics. The phenology of the plant was studied in Cabrera (southern Mallorca), with an area of about 1130 ha and a maximum elevation of 172 m. This island is covered by Mediterranean scrubland, with a vegetation dominated by *Pistacia lentiscus, Phillyrea* spp., *Olea europaea, Juniperus phoenicea, Euphorbia dendroides, Erica multiflora, Rosmarinus officinalis* and *Cistus* spp. *Pinus halepensis* is also commonly found in some parts of the island. *Cneorum tricoccon* is found scattered throughout the island, and although it is not a clonal plant, it usually grows in patches. The plant breeding system was examined in a population at Pontiró (UTM 31T DD 81 8 82 7), on Mallorca. Here, the dominant vegetation consists of *Olea europaea, Pistacia lentiscus, Rhamnus alaternus, Cistus* spp. and *Cneorum tricoccon*. Measurements of plant size and fecundity were also recorded in this area and in another population in the southern coast of Mallorca, Cap Blanc (UTM 31T DD 78 7 63 5). The vegetation in Cap Blanc is also Mediterranean scrubland and the predominant species are the same as in Pontiró except for *R. alaternus*.

METHODS

A total of 31 individuals was marked in Cabrera on February 2, 1992, and monitored until mid July. In each visit to a plant, the number of buds, male and hermaphrodite flowers, and also the number of developing and mature fruits were recorded. Plant height and maximum crown diameter were measured

in each individual. In 1993, the same plants (except one that died) plus 24 supplementary individuals were also monitored from January 26 through June 26. The sex ratio was estimated for each plant by dividing the total number of open hermaphrodite flowers recorded during the censuses by the total number of open flowers, which was also recorded in each census. In the census, fresh male flowers on the ground (recently dropped) were also counted.

In 1993, plant size and fruit crop were measured in 25 individuals from Cap Blanc (Mallorca). The following year, those same variables were recorded for 20 individuals at the other Mallorcan population, Pontiró.

On December 2–3, 1993, hand-pollination experiments were performed at Pontiró in order to determine differences in fertility depending upon the pollen source. A group of 26–30 flowers from each of eight plants were used for the five different treatments and for the control group. Four treatments consisted in pollinating flowers, which had been emasculated before anthesis, with pollen from: (1) male flowers and (2) hermaphrodite flowers from individuals other than the experimental plant (xenogamy), and from (3) male flowers and (4) hermaphrodite flowers from the same individual (geitonogamy). The fifth treatment examined whether there is selfing within a flower (autogamy); flowers in this group were bagged before opening and were not emasculated. To determine if there is anemogamy, another group of 53 flowers from a total of six individuals were emasculated and covered with cloth bags which allowed pollen but not insects to pass through. The number of fruits produced was recorded on February 2, 1994.

Data on filament and style length were gathered from a total of 30 flowers of each sex. The flowers were of the same age and collected from six individuals in Cabrera. The number of pollen grains per flower had been estimated by Sunyer (1991) and this was not repeated here. The method employed by this author consisted in diluting the contents of the three anthers of each of 17 hermaphrodite and 24 male flowers in $1000 \, \text{mm}^3$ of water, and counting, under the microscope, the pollen grains in a subsample of such dilution.

All statistical analyses were performed using the statistical package SAS (1987). The procedures ANOVA and GLM were used to test for differences in the reproductive parameters measured between flower sexes, and for differences in plant size, and fecundity among populations. The angular transformation was used to normalize the proportions before the analysis. The procedure CORR was employed to obtain Pearson and Spearman's rank correlations between variables. All means are accompanied by the standard deviations unless otherwise indicated.

## RESULTS

### Natural history of the plant

*Cneorum tricoccon* L. is a small (usually $<1 \, \text{m}$ tall) evergreen shrub found normally within the coastal maquis. The flowering period is usually from January through April, although it can start as early as late October and last until the beginning of June (personal observation). The flowers are yellow, about 7 mm long and 2 mm wide and are located individually in the axils of the superior leaves of branches. The number of stamens and carpels is usually

TABLE 1. Reproductive parameters measured to compare hermaphrodite and male flowers of *C. tricoccon*. Mean and standard deviation for each characteristic are shown, number of flowers, *n*, is given in parenthesis. *** $P = 0.0001$. †Data from Sunyer (1991)

| Characteristic | Hermaphrodites | Males | Significance |
|---|---|---|---|
| Mean style length (mm) | 5.59±0.38 (30) | 3.50±0.43 (30) | $F_{1,48} = 655.9$*** |
| Mean filament length (mm) | 4.52±0.32 (30) | 6.29±0.44 (30) | $F_{1,48} = 365.4$*** |
| Mean number of pollen grains† | 5753.1±1917.7 (17) | 5443.7±1814.6 (24) | $F_{1,39} = 0.32$ ns |

three, although either two or four are found occasionally. Sometimes, only one or two of the three locules of the syncarpous ovary develop. Within each locule there are two ovules (inserted more or less above one another). The mature fruit is indehiscent, but falls easily apart into three pieces each of which mostly contains two one-seeded compartments. See Boesewinkel (1984) for a detailed description of ovule morphology and ontogeny.

Two types of flowers are produced: (a) *hermaphrodite* flowers, bearing a developed ovary, with an elongated pistil which is slightly longer than the stamens, and (b) *male* flowers, without a developed ovary (and thus producing no fruit), with a short pistil, and with the three stamens slightly longer than those in the hermaphrodite flowers (Table 1). Both types of flower are open for about 5 days. Male flowers are easily detached from the plant, and occasionally drop without having opened. The number of pollen grains per flower does not differ between the two kinds of flowers (Table 1), and the pollen appears to be morphologically similar (Fig. 1).

Both males and hermaphrodites produce nectar at the base of the ovary which is collected by bees (*Apis mellifera* L.), several fly (Diptera) species, and small ants, *Plagiolepis pygmaea* (Latr.) (personal observation). Daumann (1974) found different species of bees in the genera *Apis, Ceratina, Halictus* and *Xylocopa* to be the main pollinators of this species in southern France.

The ovaries of the hermaphrodite flowers grow continuously and reach full size several weeks after anthesis. The three cocci (locules) per fruit have a green pulp when immature that becomes red after ripening. No insect seed predators have been found on this species; only a hemipteran has often been observed sucking the fruit pulp (personal observation). Undispersed fruits dry up on the plant and are usually attacked by a fungus that gives them a black colour. This fungus has misled some observers who thought that the mature fruits are black (Bonafè, 1979). Each coccus measures, on average, 4.6±0.4 mm in cross-diameter (*n* = 25). *Cneorum* seeds have been occasionally observed outside ant nests, suggesting that these insects may act as secondary dispersers of the plant (N. Torres, personal communication). The main dispersers of this plant are a lizard, endemic to the Balearics, *Podarcis lilfordi* (Lacertidae) and carnivorous mammals such as spotted genets (*Genetta genetta*) and pine martens (*Martes martes*). The dispersal ecology of *C. tricoccon* is examined in another paper (Traveset, 1995).
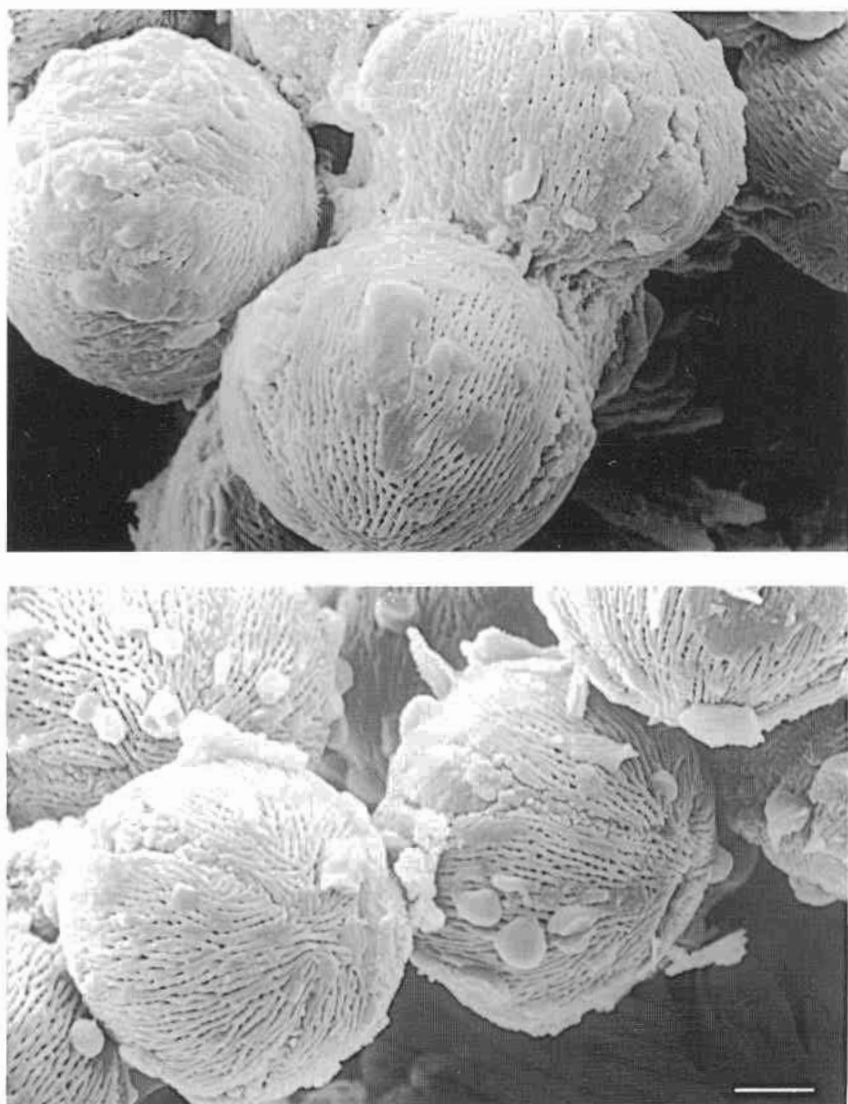
Figure 1. Scanning electron micrographs of the pollen in male (upper panel) and hermaphrodite (lower panel) flowers. Scale bar = 10 μm.

## Breeding system

Figure 2 shows the proportion of flowers that set fruit for each treatment and for the control group (natural pollination). Fruit set in the xenogamous crosses was higher than in the geitonogamous ones (0.60 vs. 0.44, respectively), and pollen from male flowers appeared to be more fertile than pollen from hermaphrodite flowers (0.58 vs. 0.47, respectively). There is some autogamy (7.5%), which probably contributes to the relatively high fruit set in control flowers (67.5%). Wind did not appear to be a pollinator vector, as none of the emasculated flowers, in which insect visitation was prevented, set fruit.

Sunyer (1991) had previously reported that there is no agamospermy (asexual reproduction) in this species; he emasculated and covered with paper bags a
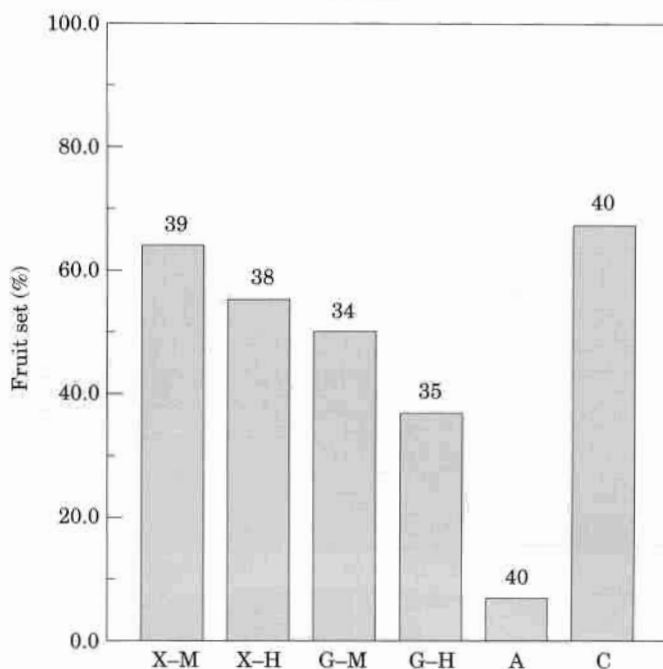
Figure 2. Percentage of flowers that set fruits in the different treatments (X: xenogamy, G: geitonogamy, A: autogamy) and controls (C). Data from the eight plants are pooled since only a maximum of five flowers per plant could be used for each treatment. The number of flowers monitored is given on the top of each column. H: hermaphrodites; M: males.

total of 55 flowers from 10 individuals finding out that none of them produced any fruit. This author performed the cross-pollinations in a population near Cap Blanc (Mallorca)—although using pollen only from male flowers—and found also that xenogamous crosses produced a greater proportion of fruits than geitonogamous ones (89.5% vs. 77.8%). He found greater selfing (36.7%) than that reported here and also a higher fruit set in control flowers (89.8%).

### Flowering and fruiting phenology

Figure 3 shows the flowering phenology of *C. tricoccon* during 1992 in Cabrera. Flower buds were present from January (perhaps even before) through May, the highest peak being in February; by the end of April, an increase in the number of buds was observed relative to the previous census, which may be considered a second (although short) flowering peak. Both male and hermaphrodite flowers appear simultaneously and are both found throughout the flowering period. At any given time, however, the number of males may be higher than the number of hermaphrodite flowers, or vice versa. So, for instance, at the end of April of 1992, there were more male than hermaphrodite flowers (Fig. 3).

In 1993, the flowering phenology was similar to that observed in 1992, although the second short peak of buds occurred about two weeks later (by mid-May). Both sexes were also found simultaneously, and sex ratio varied through time too. By March 17, the number of hermaphrodite flowers found
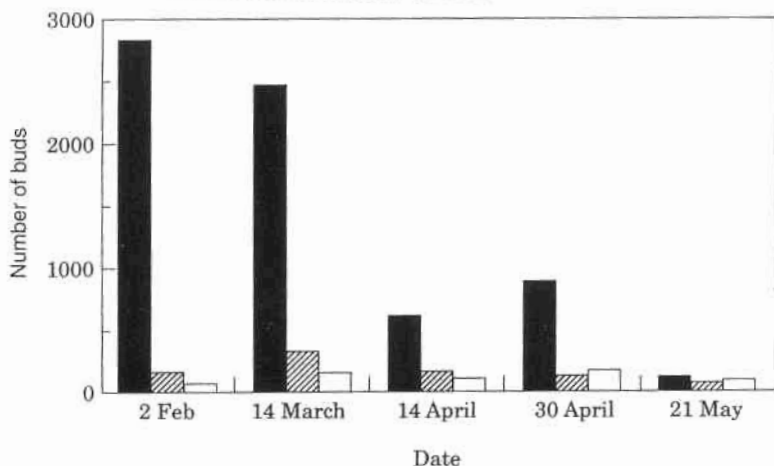
Figure 3. Flowering phenology of *Cneorum tricoccon* in Cabrera island. Data from 1992. *n* = 31 plants. (■) buds; (▨) hermaphrodites; (□) males.

open in the 54 plants monitored was 256 whereas the number of males was 179. By April 20, that ratio was 20:129, and by May 11, it was 310:147.

Fully developed fruits were present in the plants by the end of January both in 1992 and 1993, and remained green until mid-March. At a given time, buds, open flowers and fruits at different stages of development are usually found within an individual. Figure 4 shows the frequency distribution of green and ripe fruits during both 1992 and 1993 seasons. While in 1992 no mature fruits were observed until mid-April, in 1993 there were already ripe fruits by mid-March. The fruits in Cabrera are rapidly removed by lizards as soon as they become reddish (personal observation) which explains why the number of ripe fruits appears to be so low in the censuses. Undispersed fruits tend to remain on the plant, being attacked by fungi or drying up, and can be found attached to the branches up to one year later (personal observations).

### Variability in flower production, sex ratio and fruit crop

The number of flowers produced by an individual in Cabrera during 1992 ranged from 33 to 669, being on average $250.32 \pm 163.62$ ($n = 31$ plants), and was associated with measurements indicative of plant size, height ($r = 0.36$, $P < 0.05$, $n = 30$) and maximum diameter ($r = 0.60$, $P < 0.001$, $n = 30$). Mean floral sex ratio was $0.58 \pm 0.13$ ($n = 31$ plants) in 1992 and $0.55 \pm 0.21$ ($n = 52$) in 1993. A large proportion of plants (c. 35% in 1992 and c. 45% in 1993) produced an almost 1:1 ratio. Only 6.4% and 17% of the plants examined in 1992 and 1993, respectively, were found to produce, in total, a larger quantity of male than hermaphrodite flowers. Sex ratio varied among individuals, from 0.24 to 0.9 in 1992, and from 0 to 1 in 1993. These ratios, however, were calculated from the flowers counted each month and might be slightly biased. Actually, the two plants with a sex ratio of 0 bore some fruits, so they had certainly produced some hermaphrodite flowers, which were closed at the time of census. Likewise, it is unlikely that a plant produces only hermaphrodite flowers and thus a sex ratio of 1 is very rare.
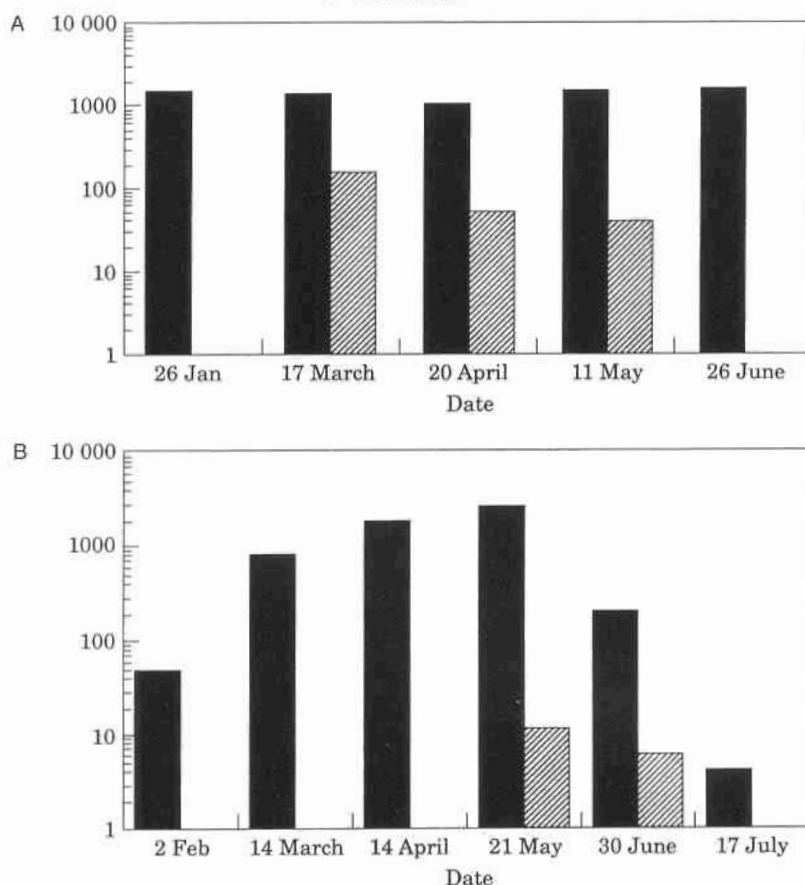
Figure 4. Fruiting phenology of *Cneorum tricoccon* in Cabrera island. Data from 1992 (A, $n = 30$) and 1993 (B, $n = 54$). (■) green; (▨) ripe.

From the 30 plants examined during both years, no consistency was found in floral sex ratio. Plants with higher proportions of hermaphrodite flowers in 1992 did not necessarily produce higher proportions of such flowers in 1993 ($r_s = 0.21$, $P \gg 0.05$). Moreover, sex ratio was not consistently associated with plant size; in 1992, the correlation was not significant ($P \gg 0.05$) while in 1993 sex ratio was related to both plant height and crown diameter ($r_s = -0.45$ and $r_s = -0.42$, $P < 0.05$, respectively).

The total number of fruits produced by a plant during the whole season showed strong variation, both among individuals and among areas (Table 2). Such variability was largely explained by differences in plant size, tall and wide individuals producing significantly more fruits than short and narrow ones ($r = 0.42$, $P = 0.02$ and $r = 0.80$, $P = 0.0001$, respectively, $n = 30$). A high consistency in fruit production was observed between years; plants that produced more fruits in 1992 also had greater crops in 1993 ($r = 0.59$, $P < 0.001$, $n = 30$) and in 1994 ($r = 41$, $P = 0.03$, $n = 30$); fruit crop in 1994 was quite low (Table 2), but was still closely associated with fruit crop in the same plants during 1993 ($r = 0.73$, $P = 0.0001$, $n = 30$). Total number of fruits produced per plant differed among areas (Table 2; $F_{2,72} = 32.54$, $P = 0.0001$), but the difference

TABLE 2. Plant size and fecundity of *C. tricoccon* in the three populations examined. Mean and standard deviation for each characteristic are shown. *n* is given below the mean in parenthesis

| Characteristic | Cabrera | Cap Blanc | Pontiró |
|---|---|---|---|
| Plant height | 45.8±13.4 (30) | 58.1±17.2 (25) | 64.1±16.7 (20) |
| Maximum crown diameter | 45.8±15.8 (30) | 54.0±19.2 (25) | 79.2±27.0 (20) |
| No. fruits 1992 | 95.4±65.2 (31) | — | — |
| No. fruits 1993 | 51.5±49.1 (52) | 41.7±46.7 (25) | — |
| No. fruits 1994 | 28.9±33.4 (54) | — | 352.7±253.1 (20) |

was significant only between Cabrera and Pontiró (SNK's test). Even though plants at Cap Blanc were somewhat larger than in Cabrera ($F_{2,72} = 9.01$, $P = 0.0003$), the difference in the amount of fruits produced was not significant (Table 2).

## DISCUSSION

*Cneorum tricoccon* has shown to have a functional andromonoecious breeding system, producing staminate (male) flowers, with an undeveloped ovary that never develops into a fruit, and hermaphroditic flowers, with an elongated pistil and stamens that bear viable pollen. Both type of flowers produce equal amounts of pollen grains, as it has been found in other andromonoecious species (e.g. *Solanum carolinense*, Solomon, 1986), and such pollen is morphologically similar between sexes. Pollen from male flowers, however, appears to be more fertile (gives a higher fruit set) than pollen from hermaphrodite flowers. This actually represents an advantage to andromonoecy as both male and female fitness may increase through pollen donation by male flowers (Bertin, 1982). The size of the flowers of the different sexes is the same, and based on the measurements of organ sizes, male flowers use less resources than hermaphrodite flowers; even though data on flower weight were not gathered in this study to document it, male flowers are also less massive, mainly due to the undeveloped ovary and to the much shorter style. Males were thus more efficient at male function, as observed in other andromonoecious species (Solomon, 1986). Such efficiency of male flowers suggests that their use increases plant fitness. Female fitness could be reduced by the production of male flowers in the case that fruit set was limited by the number of fertile ovaries. However, this does not seem to occur in *C. tricoccon* since only 67.5% of the hermaphrodite flowers produced fruit, and hand pollination did not increase this ratio. Fruiting success is probably limited by resources and not by the number of fertile ovaries. The hand pollination experiment showed that it was not limited by pollen either, although this may vary among sites and among years depending mainly upon insect pollinator abundance.

Another advantage that is attributed to the production of male flowers in

andromonoecious species is the attractiveness to pollinators of a large floral display (Symon, 1979; Anderson & Symon, 1989). According to this hypothesis male flowers could increase male fitness through pollen donation and female fitness through attraction of pollinators to the plant as a whole. Male flowers in *C. tricoccon* are probably suitable pollinator attractants, since they bear both pollen and nectar which serve as a reward (personal observation). So far, it is unknown whether the quantity and the quality of nectar differ between the two sexes and whether pollinators discriminate between them.

Autogamy in *C. tricoccon* was found to be quite low (<10% of the monitored flowers set fruit) and is probably prevented by the lower position of the anthers relative to the stigma in the hermaphroditic flowers (herkogamy). Such herkogamy has been viewed in other andromonoecious species which are mostly self-compatible as a means of reducing selfing (Anderson & Symon, 1989).

Temporal differences in the functioning of male and female organs are a common feature of monoecious and andromonoecious taxa (e.g. Thomson & Barrett, 1981; Anderson & Symon, 1989 and references therein; Emms, 1993). However, no evidence of any type of dichogamy was found in *C. tricoccon*. Both flowers sexes open simultaneously, and for about the same time, and are available throughout the flowering period.

Since *C. tricoccon* is self-compatible, a fraction of the seeds produced must come from geitonogamous crosses. The hand-pollinations showed that such crosses gave a fruit set of about 45%. However, when pollen availability is not limiting, as is the case here, selfing probably does not increase fruit set substantially (Spalik, 1991). Geitonogamy may be maintained only if there is no inbreeding depression. If selfed offspring are not equal in viability and fecundity to outbred offspring, geitonogamy is selected against and dioecy may evolve (Thomson & Brunet, 1990). It is unknown, at the moment, how important geitonogamy is in this plant. This probably depends mainly upon the insect pollinator movements and upon plant size. Large, more fecund individuals may have a higher number of flowers visited in succession, thus promoting geitonogamy (Charlesworth & Charlesworth 1987; Thomson and Brunet, 1990; de Jong *et al.*, 1993). An extended flowering period might also influence geitonogamous selfing (de Jong *et al.*, 1993); producing only a few open flowers at one time may force the pollinator to leave the plant sooner. In *C. tricoccon*, this is quite likely to happen as the plant has a long flowering period, and, at any given time, the number of open flowers is always low.

As it has occurred in other species, andromonoecy in *C. tricoccon* has probably evolved from hermaphrodite ancestors, by means of a mutation removing pistils from some hermaphrodite flowers and a subsequent regulation of male flower number (Spalik, 1991). It has been hypothesized that such a breeding system could be maintained because the use of male flowers may allow optimal allocation of resources between male and female functions. The production of male flowers for pollen donation and for pollinator attraction can save resources that can be allocated elsewhere (Bertin, 1982; Anderson & Symon, 1989).

Sex expression was found to be quite variable, as has been reported for other andromonoecious plants (Diggle, 1993 and references therein). This variation may be due to: (1) variation among individuals for genetically fixed patterns to male and hermaphrodite flowers (the so-called 'population level variation' by Diggle, 1993) and/or (2) developmental plasticity of individuals in

a heterogeneous environment ('organismal level variation', *sensu* Diggle, 1993). In *C. tricoccon*, sex ratio varied from almost zero (very few hermaphrodite flowers) to almost one (very few males). This ratio was significantly associated with plant size in 1993 (larger plants had a lower proportion of hermaphrodite flowers) but not in 1992. There was no consistency in sex ratio through time either, thus a plant with a high sex ratio one year may have a low ratio the next one. This contrasts with the results found in other andromonoecious species like *Aesculus californica* (Benseler, 1975), *Leptospermum sooparium* (Primack & Lloyd, 1980), *Aralia hispida* (Thomson & Barrett, 1981) or *Solanum hirtum* (Diggle, 1993). Such lack of consistency in sex ratio in *C. tricoccon* indicates that genetic factors are not as important as environmental ones in determining sex expression. Soil nutrients, light, precipitation, temperature, etc. may all influence to which sex resources are allocated. Emms (1993), for instance, has recently reported that nutrient supplementation in the andromonoecious *Zigadenus paniculatus* increases the proportion of hermaphrodite flowers, and Diggle (1993) has found that sex expression in *Solanum hirtum* is plastic among individuals of the same genotype and is partly determined by the resource status of the individual. Since hermaphrodite flowers in *C. tricoccon* are more expensive to produce than male flowers, we might expect that more vigorous plants, with greater size and fecundity, produce a greater proportion of hermaphrodite flowers. However, this was not observed either in 1992 or in 1993, suggesting that other factors besides resources influence gender. It is possible, anyway, that the changes in sex ratio observed through the season are related, at least partly, to the availability of resources at a given time. As stated by Diggle (1993), the evolution of andromonoecy might in fact depend upon the evolution of a developmental system capable of modifying allocation and sex expression in response to environmental cues, and not only on genetic variability for a fixed trait (a particular proportion of flower types).

Fruit production in *C. tricoccon* varies from a few fruits in the smallest individuals to several hundreds in the largest, most vigorous ones. In Cabrera island, the shrubs are rather short, not exceeding half a metre on average, and producing usually less than one or two hundred fruits. The same has been observed in other Balearic islands such as Illa des Conills, Dragonera, Eivissa and Formentera. In Mallorca, by contrast, much greater individuals are found (sometimes exceeding 1 m in height), especially in populations at high and humid sites such as those in Serra de Tramuntana. Considering that this plant evolved in a warm, summer-rain tropical climate (Müller, 1933), it is reasonable to think that the much drier and cooler conditions found in the present scenario have decreased the vigour and fecundity of this species in most sites.

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