Floral biology of *Cneorum tricoccon* L. (Cneoraceae): an unknown case of andromonoecy

FRANCISCO JAVIER TÉBAR & LEONARDO LLORENS

Abstract

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The floral biology of a natural population of *Cneorum tricoccon* L. (Cneoraceae) from Majorca (Balearic Islands, Spain) has been proven to be andromonoecious, a condition not yet described for this species. The ratio perfect : staminate flowers varied along two consecutive reproductive cycles, being low in the dry year 1990 and high in the humid year 1991. The plants are self-compatible and cross-pollinated by a short number of pollinating insects (mainly Hymenoptera). *Neochamaelea pulverulenta* (Vent.) Erdtm. from the Canary Islands (Spain) has also been recognized as andromonoecious. This means that two of the three representatives of the family are andromonoecious and not hermaphroditic, as previously reported

Keywords: Andromonoecy, Phenology, Pollination, Self-compatibility, Cross-pollination, Balearic Islands, Spain.

Resum

TÉBAR, F. J. & L. LLORENS (1997). Biologia floral de *Cneorum tricoccon* L. (Cneoraceae): un cas desconegut d'andromonoècia. Collect. Bot. (Barcelona) 23: 105-113.

La condició d'andromonoècia ha estat descrita per a una població natural de *Cneorum tricoccon* L. (Cneoraceae) provinent de Mallorca. Hom ha trobat que la relació entre flors perfectes y flors estaminals varia al llarg de cicles reproductors consecutius de manera que va ser més baixa l'any sec de 1990 i més alta l'any següent, més humit. Les plantes són auto-compatibles i són pol.linitzades per un nombre reduït d'insectes (principalment Himenòpters). *Neochamaelea pulverulenta* (Vent.) Erdtm. de les Illes Canàries també ha estat descrita com andromonoica. Això significa que dos dels tres representants de la família són andromonoics i no hermafrodites com fins ara s'havia suposat.

Paraules clau: Andromonoicia, Fenologia, Pol.linització, Auto-compatibilitat, Pol.linització creuada, Illes Balears, Espanya.

INTRODUCTION

Andromonoecy, a partial dicliny phenomenon which manifests itself by the presence of functionally masculine (staminate) and hermaphrodite (perfect) flowers on the same plant, provides the possibility of varying the allocation of resources to male and female function

Francisco Javier Tébar & Leonardo Llorens. Laboratori de Botànica, Universitat de les Illes Balears. Carretera de Valldemossa Km 7,5. E-07071 Palma de Mallorca.

throughout the season (CRUDEN, 1976; SOLOMON, 1985; EMMS, 1993). WILLSON (1983) summarises some of its possible adaptation values: 1. Intensification of the intercrossing; 2. reduction of the depredation of the female organs; and/or 3. intensification of the attractiveness of the flowers on the plant in an economical fashion which benefits pollination. In the same work she concludes, however, that a general conclusive interpretation of andromonoecy is needed.

Andromonoecy is an unusual type of plant breeding system, possessed by about 1.7% of known species (YAMPOLSKY & YAMPOLSKY, 1922). In all probability the different forms of dicliny and particularly andromonoecy are more common than we may think at this time. There are instances of species that were considered to be heterostylous, yet after a review were found to be andromonoecious (LLOYD et al., 1990). In the Mediterranean basin, only the study of plants at the taxonomic level is considered to be advanced. Therefore there exists the possibility that new sexual combinations (such as DENELLE et al., 1987) will be discovered as research in reproductive biology progresses.

This paper attempts to describe the phenomenon of andromonoecy in Cneorum tricoccon L., interpret its function in the context of its reproductive biology under natural conditions and provide information in the understanding of this particular form of sexual expression. Some observations on the sexual expression of Neochamaelea pulverulenta (Vent.) Erdtm. are also reported.

MATERIALS AND METHODS

1. Study organism. Cneoraceae is a family of Mediterranean and American geographic affinities (BORGEN, 1979), which is composed of three species endemic to the western Mediterranean: Cneorum tricoccon L.; the Canary Islands: Neochamaelea pulverulenta (Vent.) Erdtm. ; and Cuba: Cneorum trimerum Chod. The shrub C. tricoccon is well represented in the Balearic Islands, its main centre of distribution (KNOCHE, 1921-23; FONT QUER, 1927; BOLOS, 1958; BONAFE, 1980) although it is also quite frequent in Catalonia, Southern France, Western Italy, Sardinia and Southern Andalusia (COSTE, 1900-06; BOLOS, 1958; PIGNATTI, 1982). In the Balearic Islands C. tricoccon is characteristic of the coastal sclerophyllous brushwoods (BOLOS & MOLINIER, 1958), and mostly occupies shallow soils on limestone. It can also be found at an altitude of 1000 m on soils with similar characteristics.

The sclerophyllous shrub Cneorum tricoccon is of approximately 1 m in height. Leaves are alternate, spatulate (glabrous or semi-glabrous), and dark green. Inflorescences are cymose, and generally with 3 flowers. The flowers are actinomorphous, three and occasionally four-merous, with a yellow subcarpellar nectary disk. Fruits are drupe type, and usually tricoccos. The microclimatology of the localities greatly modifies the flowering period of the populations.

2. Study site. This study was conducted in "Sa Marina de Llucmajor", an area located in the south of Majorca (Balearic Islands, Spain). The area has a thermomediterranean climate (GUIJARRO, 1986; RIVAS-MARTINEZ & COSTA, 1987), with most precipitation occurring in the spring, winter and fall with periods of drought in July and August. The soil of Sa Marina has been classified according to the American system as a Xerothent (U. S. D. A. 1975; RITA & VALLEJO, 1988). The vegetation characteristic of the site is a dense sclerophyllous brushwood mosaic with pastures rich in geophytes.

3. Phenology. The phenology was investigated by regular field observation visits (12 labelled individuals, observed in 1 wk intervals beginning in February 1990). The number
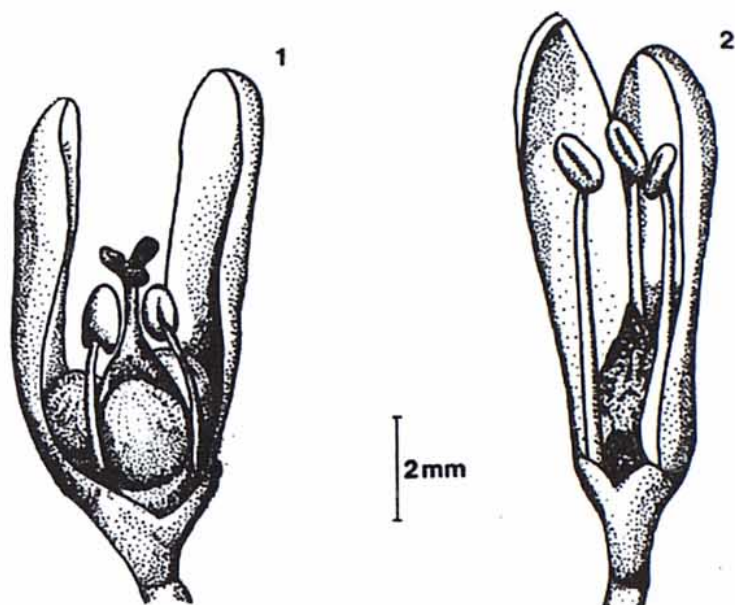
Figs. 1-2. — Flower morphology of *Cneorum tricoccon*. 1. Hermaphrodite flower (without one petal and one stamen). 2. Male flower (with a petal removed).
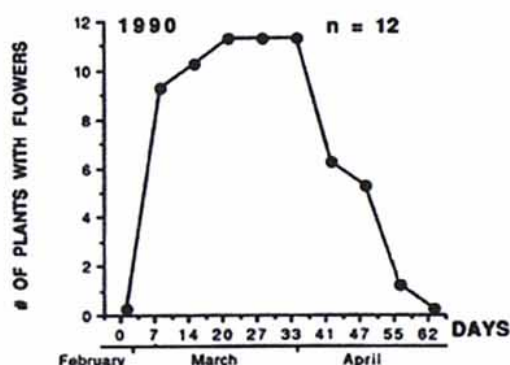

Fig. 3. — Flowering phenology during 1990.

	Sex of the flower	
	Hermaphrodite	Male
Number of ovules	6 ± 0	0
Number of pollen grains	5753 ± 606,9	5444 ± 574,2
P/O	959	-

Table 2. Number of ovules and of pollen grains per flower, and relationship P/O in *Cneorum tricoccon*.

of flowers (both masculine and hermaphrodites) and fruits were recorded for each individual. Beginning March 20 flowers (10 of each sexual expression) were examined on a daily basis to establish the duration of each individual flower. The quotient between the total sum of hermaphrodites and male flowers observed during each visit was calculated. Phenology investigation was repeated the following year with a greater number of individuals (n = 31, including the preceding 12 individuals) with longer intervals.

4. Floral biology. A total of 30 mature flowers (15 of each type) were collected at random at the rate of 1 flower per plant. The sampled flowers were then placed in small airtight containers and transported to the laboratory within four hours where the following variables were then measured: 1. Length of the petal; 2. width of the petal; 3. length of the stamen; 4. length of the pistil; 5. dry weight (60° C to constant weight). Through dissection, the number of ovules per ovary (total 27 all hermaphrodites) and the number of pollen grains per flower (total 41, 24 hermaphrodites, 17 staminates) were counted. Three anthers

were present per flower. After crushing three anthers in 0.5 ml of detergent solution, the number of grains in ten replicates of 5 µl were recorded, with the total number of grains per flower estimated accordingly (HERRERA, 1987, 1991).

5. Fruits. To estimate the average of dry weight of fruit, a total of 40 matured fruits from 12 plants were collected. These were transported to the laboratory where dry weight (60° C to constant weight) was then measured.

	Sex of the flower:			
Character	Hermaphrodite	Male	F	P
Petal lenght (mm) (n = 24)	7.38 ± 1.03	7.02 ± 0.72	2.082	0.1558
Petal width (mm) (n = 24)	2.49 ± 0.25	2.25 ± 0.15	15.565	0.0003
Stamen lenght (mm) (n = 24)	4.29 ± 0.38	5.51 ± 0.61	69.292	0.0001
Ovary lenght (mm) (n = 14)	1.47 ± 0.20	0.95 ± 0.13	66.475	0.0001
Dry weight (mg) (n = 40)	3.66	2.58		

Table 1. Flower morphometry and flower dry weight of the floral morphs (means 1 SD). N = sample size. F statistics and significance levels are from one-way ANOVAs testing for differences between morphs.

6. Pollination treatments. Once observed that male flowers do not bear fruits, the percentage of hermaphrodite flowers that bore fruit was observed in: free branches (natural), those only enclosed in paper bags (autogamy), and by the previous male castration, those which produced fruits (agamospermy) and those pollinated by hand with pollen of the same plant (geitonogamy) and with pollen of another plant (xenogamy), all them also packed in paper (utilising only staminates as donors).

7. Nectar. The flower nectar was extracted and its volume was determined with calibrated 1 µl micropipettes. The concentration of diluted solids, which consisted mainly of sugars (BAKER & BAKER, 1975, 1983; HARBONE, 1982, HERRERA, 1985) was measured (on a weight-weight basis) with a temperature-compensated hand refractometer.

8. Pollinators. During the field visits, all of the pollinating insects observed were collected.

RESULTS

1. Floral variability. The existence of two types of flowers on the same plant is shown, with the one hermaphrodite flower with short stamens and well developed pistil (fig. 1; tab. 1). The masculine flower possesses long stamens and an ovary reduced to a rudiment which lacks the ovules (fig. 2; tab. 1). The perianth of the two forms is also different, with the petals of the flowers with developed pistils being slightly wider (tab. 1). The top posi-
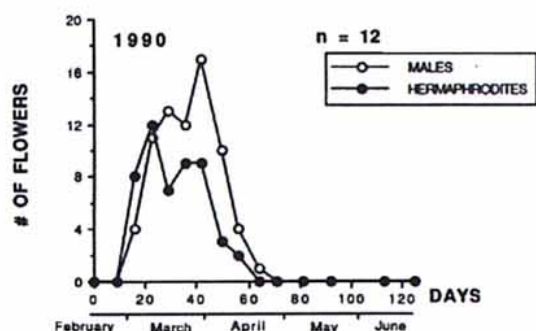
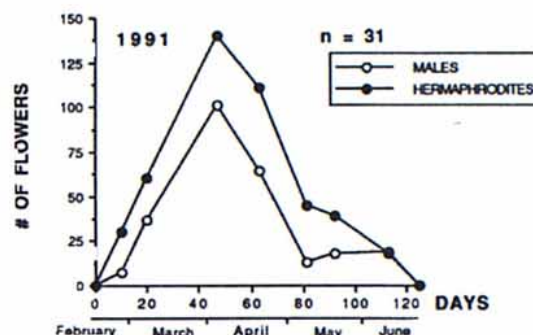Fig. 4.- Flowers of both types during 1990 flo-wering season (n= 12 plants)

Fig. 5.- Flowers of both types during 1990 flo-wering season (n= 31 plants)

tion of the inflorescence is generally occupied by the hermaphrodite flowers while both types of flowers are present at the lateral positions. Within the inflorescence, the sequence of the flowers is centrifugal and the presence of two simultaneous functional flowers is rare.

The brushwood community is composed of malacophyllous and sclerophyllous species. The flower of the *C. tricoccon* is the largest among the sclerophyllous species in the community yet it is smaller than the attraction units of the malacophyllous species of Lamiaceae, Cistaceae and Asteraceae. The size of its flowers and the colourfulness of its yellow corollas give it an intermediate conspicuity in relation to the rest of the sclerophy-llous and malacophyllous species.

Different populations in Majorca, Ibiza and Cabrera (Balearic Islands, Spain) were visi-ted during the blooming season and andromonoecy was confirmed in all of them.

2. Pollen and ovules count. The staminate flowers never produce ovules. Perfect flo-wers always have 6 per flower (2 per carpel). The stamens are inserted at the androgynop-hore and terminate in two-lobed anthers containing four sporangia which open into longi-tudinal slits. Both types of flowers have the same amount of pollen in their three anthers (tab. 2). The grains are identical morphologically in both types: triaperturate, globose, with a slightly furrowed exine layer. According to the pollen ovule ratio (CRUDEN, 1977), the species would fall under facultative allogamous (P/O = 959).

3. Bloom phenology.

3.1. Individual flowers. The perfect flowers last 5-6 days (mean = 5.7, SE. = 0.11; n = 10), while the staminate flowers last only 3-4 days (mean = 3.8, SE. = 0.07; n = 10).

3.2. Population. In 1990, flowers were observed during eight weeks from the beginning of March to the end of April (fig. 3). The intense flowering period (the period with 25% or more flowers observed in a sampling) lasts six weeks, reaching its peak at the end of March.

3.3. Staminate and perfect flowers during two consecutive reproductive cycles. The flo-ral buds start to appear in October and develop slowly until anthesis takes place in February or March. Consequently, the production of flowers is influenced by fall, winter and spring metereological conditions. In the region where this study was carried out, the period September 1989 - June 1990 was dry (as usually occurs) with total precipitation only 488.9 mm. The drought was evident in the community by the necrosis of abundant aerial biomass and the shortening of the blooming time in most of the species, including *C.*

tricoccon. In the 1990-1991 period rainfall was considerably more abundant (total precipitation 714.8 mm) (tab. 3), and the plants in the community did not show any signs of hydric stress.

In both years the proportion of the two types of flowers varied as flowering progressed (figs. 4-5). In the 1990 flowering period, during the first two weeks there were more perfects than staminates. During the third week the opposite occurred and the staminates were more numerous from then until the end of the process. During this year, the rate of perfects: staminates was 0.69 (n = 12). In the second year, the perfect flowers dominated throughout the season, and the rate of perfect: estaminates was 1.76 (n = 31).

Period	S	O	N	D	J	F	M	A	M	J	Total
						Months					
1989-90	123	0.9	71	61.4	82	3.2	29.9	69.4	28.1	20	488.9
1990-91	26.5	152.5	120	13.3	112.2	105	32.6	36.8	105.9	10	714.8

Table 3. Monthly precipitation (in mm) during September - June period 1989-1990 and 1990-1991. During July and August there was no precipitations in both periods.

4. Reproductive system. *C. tricoccon* is not agamocarpous. A high degree of self-compatibility has been observed with considerable geitonocarpic results. The highest fruit production, however, was obtained during the xenogamous pollination tests (tab. 4). The exclusion of pollen vectors tests show that nearly half the flowers produce fruits by autogamy. As can be observed in fig. 1 the stamens of the perfect flowers are at the same level as the stigma, making it easy for the pollen to reach them without the intervention of any external agents. The results obtained through free pollination shows, however, that insects are the most effective vectors in the transportation of pollen.

Pollination Tests	Flowers	Fruits	% hermaphrodite flowers producing fruit
Natural	112	102	91.0
Paper bagged	110	46	41.8
Agamospermy	105	0	0.0
Manual geitonogamy	36	28	77.8
Manual xenogamy	40	36	90.0

Table 4. Results of fertilization experiments in *Cneorum tricoccon*.

5. Reward and flower visitors. During the two research years only occasional visits by the Hymenoptera *Apis mellifera, Halictus tetrazonius, Bombus terrestris* and the beetle *Tropinota squalida* were noted. The yellow color of the corolla, preferable by bees (HARBORNE, 1982) and the production of nectar favor entomophilous pollination. Nectar concentration is of 36.1 ± 1.5 (% w/w ± SE, 10 measurements).

6. Fruits. The dry weight of the fruit is 207.8 mg (n = 50). Compared with those produced by the other plants of the community, it can be considered as a heavy fruit.

DISCUSSION

The result of the pollen-ovule ratio, which include *C. tricoccon* in the facultative allogamous category, do not contradict the results of the hand pollination tests. Both the experiments with bagged flowers and the pollinating insect visits show that the species is basically entomophilous. The main primary attractant is nectar, while size and colour may be considered the secondary ones. The low number of visitors is in line with the little energetic value of its nectar compared with those of other species (mainly of the family Lamiacae) of the community (TÉBAR & LLORENS, unpublished data), and with its small inconspicuous flowers. The flowering period of *C. tricoccon* overlaps those of the majority of cooccurring species, and it appears feasible that the appearance of self-fertilization in *C. tricoccon* may be related to the competition for pollinators, as has been suggested for other taxa (e. g. : WYATT, 1983). The yellow flowers, which acts in plant communities as a neutral color, usually are preferred by diverse unspecialized pollinating insects (KEVAN, 1983), as occurs in *C. tricoccon*. Its open floral architecture allows easy access to the nectar which permits the plundering by non-pollinating insects (as probably occurs with *Tropinota squalida*) something which does not occur in flowers with closed corollas. The above results show that the pollination system of the plant is generalist, making possible autogamous and unspeciallized entomophilous pollination. This provides the plant with an extensive range of possibilities which can be exploited in alternating fashion.

Neochamaelea pulverulenta (the Canarian representative of the family) as well as *C. tricoccon*, are self-compatible (P. Maya, pers. com.). Island floras are characterized by a relatively high proportions of species with inconspicuous and poorly specialized flowers and different mechanisms increasing out-breeding (EHRENDORFER, 1979). All these characters are present in *C. tricoccon* and probably can be generalized to the other representatives of the family.

Up to the present it was accepted that *C. tricoccon* was a strictly hermaphrodite plant. Thus we find ourselves with an up till now unknown case of andromonoecy. The difference in the size of the stamens also indicate the existence of heteroandry. The only known evidence of having observed these floral characteristics in the past is found in two works on the Flora of Italy (FIORI & PAOLETTI, 1933; PIGNATTI, 1982) were the two types of flowers are illustrated in the same way. But both works, however, state that all the flowers are hermaphrodites.

With respect to *Neochamaelea pulverulenta*, we only have brief observations of alive plants during their blooming period (populations of Güimar and Punta Teno, Tenerife Island, Spain). However, they are enough to recognize an analogous sexual dimorphism of their flowers of *C. tricoccon* and we can state that andromonoecy is the sexual system of the European Cneoraceae representatives. To clarify the sexual expresion of the family, it will be very important the study of *Cneorum trimerum* from Cuba, the third species.

Genetic and environmental components are found in any phenotypical variation. Our observations suggest that there is a strong environmental influence in the variation of the sex expression. This has already been observed in other taxa (JAIN, 1976; WYATT, 1983; SOLOMON, 1985; DIGGLE, 1993; EMMS, 1993). The existence of dimorphous flowers allows subtle accommodations of the sexual expression of the plants in relation to environmental opportunities and requirements (COX, 1988). In this particular instance, conditions of favorable water status serve to increase the production of perfect flowers, while an unfavorable

water status have quite the opposite affect. The abscission or abortion of the pistil has been interpreted as an adjustment of the plant progeny to the level of available resources in each reproductive cycle (LLOYD, 1980; STEPHENSON, 1980; AKER, 1982, JORDANO, 1988). This is considered a physiological answer mechanism to the environmental factors, such as precipitation, whose variations have a direct effect on the condition of the plant (JORDANO, 1988).

As has been observed in *C. tricoccon* and in several andromonoecious species, hermaphrodite flowers occur in physiologically favoured positions, while the male flowers are in later, less optimal positions (LLOYD, 1980). The perfect flowers are heavier, more morphologically complex and remain functional longer than the staminates. The production of the perfects, therefore, means a greater investment of resources for the plant. An andromonoecious plant will maintain a limited number of perfect flowers according to the environmental conditions present, "rennouncing" so that the gynaecium of the surplus may mature. This type of adjustment can only be acceptable to a plant with elevated and secured, free pollination rates, such as is the case with *C. tricoccon*. The optimization of the fructification yield signifies a double saving of resources: in the production of gynaecia and in the subsequent maturation of the fruits, all without posing a threat to fruit production. Because of the large fruit biomass, any mechanism which limits production is extremely useful. In this regard, several authors have already indicated that andromonoecy is common in species with large and costly fruits (PRIMACK & LLOYD, 1980; BERTIN, 1982).

Acknowledgements

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