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On the Reproductive Biology of the Dwarf Palm, Chamaerops humilis in Southern Spain

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ABSTRACT

Chamaerops humilis is a dwarf palm which inhabits evergreen forests and xerophytic scrub communities around the Mediterranean region. It is reported that the species is dioecious and presumably wind-pollinated in southern Spain. Nevertheless, female flowers sometimes secrete nectar, and both male and female inflorescences attract weevils which feed on pollen and young fruits. It is hypothesized that, being anemophilous at present, *C. humilis* bears traits related to an earlier insect-pollinated condition.

A recent review of pollination studies in the Palmae (Henderson 1986) demonstrates that the information currently available on the reproductive characteristics of *Chamaerops humilis L.*, the only palm native in S. W. Europe, is even scarcer than that on many tropical species. Quite disappointingly, not a single recent paper on C. *humilis* reproduction is cited in Henderson's review. The purpose of this paper is to contribute to the knowledge of the biology of a palm which, in spite of its abundance in the Mediterranean area, has never been the subject of interest for investigators.

Study Area and Methods

Data reported here are the result of observations carried out in southern Spain on wild populations of C. *humilis* during the years 1983 through 1987. Most observations were made at the Donana Biological Reserve—a sandy coastal area (20 m a.s.l.) with a Mediterranean climate near the Atlantic Ocean in southern Spain. For further details on the vegetation and climate of Donana the reader should refer to Herrera (1986, 1987).

The population was visited at weekly intervals during the years 1983 and 1984. Flowering phenology, sex ratios, and flower visitors, together with morphological features of inflorescences and flowers were recorded in a total of 11 clumps (putatively different individuals). Details of anthesis and phenology were gathered from a sample of 45 inflorescences. Additional observations were carried out in populations distributed across southern Spain. Maximum distance between two populations was 400 km.

Habitat and Habit

Chamaerops humilis (Palmito) in southern Spain commonly grows in the understory of *Quercus rotundifolia* (Evergreen Oak) forests, which represent the potentially climatic vegetation in the area. Due to its vigorous sprouting, however, C. *humilis is* very tolerant of disturbance. It may survive after heavy deforestation, fires, and pasturing, and it appears in nearly every stage of degradated vegetation. Because of that, it is a very common plant in forests and shrublands from sea level to mountain ranges up to 1,000 m. *C. humilis* dominates the highly xerophytic scrub inhabiting coastal arid zones of southeastern Spain with less than 300 mm of rain per year on average (Cape of Gata), but it also grows on the wettest, Atlantic slope of the region where precipitation may average more than 2,000 mm per year. The Dwarf Palm has no obvious preferences regarding type of soil or substratum, since it equally occupies sandy areas, rocky

1. *Habit of Chamaerops humilis L.*

basaltic, granitic or limestone hillsides, and rich, deep soils on marginal areas.

C. humilis has an underground rhizome which produces shoots with palmate, sclerophyllous leaves. Eventually, old shoots develop an unbranched trunk up to 2 m high, covered by a fibrous "bark" and terminated by a crown of leaves. Such a growth habit is quite uncommon and more often plants remain shrubby, leaves starting their development under the level of soil surface and, as they grow, the whole plant becoming a semispherical structure of palmate leaves up to 1 m high. Usually the rhizome forms new shoots around the oldest one so that the individual becomes a clump of vegetatively generated shoots (Fig. 1).

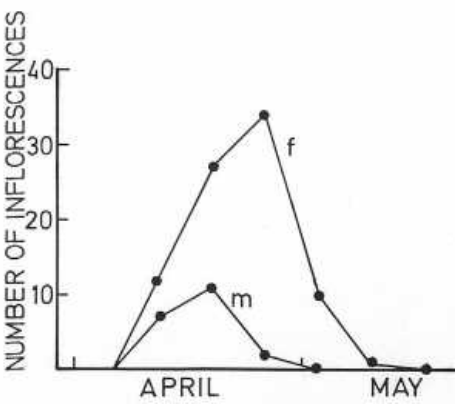
Breeding System

The plant has sometimes been described as polygamodioecious, that is, it is supposed to bear unisexual and, sometimes, bisexual flowers (Amaral Franco 1980). Nevertheless, every southern Spanish wild population checked by me during 1983—1987 behaved as completely dioecious. Not a single hermaphroditic flower was found. In the more thoroughly studied population of Doñana, sex of inflorescences produced by 11 clumps, which account for the whole population in a relatively large area, was assessed during 1983—1984 (Table 1). Inflorescences of only one sex were produced inside each clump and, moreover, clumps producing male inflorescences during 1983 did likewise during 1984. In a parallel way, those clumps with female inflorescences during 1983 behaved as females also during 1984. Consequently, sex expression was unchanged from one year to the next in the population. Sex ratio of female to male clumps was 2.3 in both 1983 and 1984 (Table 1). The ratio of female to male inflorescences was 2.9 in 1983 and 4.4 in 1984. Female biased sex ratios seem to be the rule, which may account for low levels of fruit set observed (see below).

Table 1. Number and sex (f; female, m, male of inflorescences produced by Chamaerops humilis *clumps during two consecutive years.*

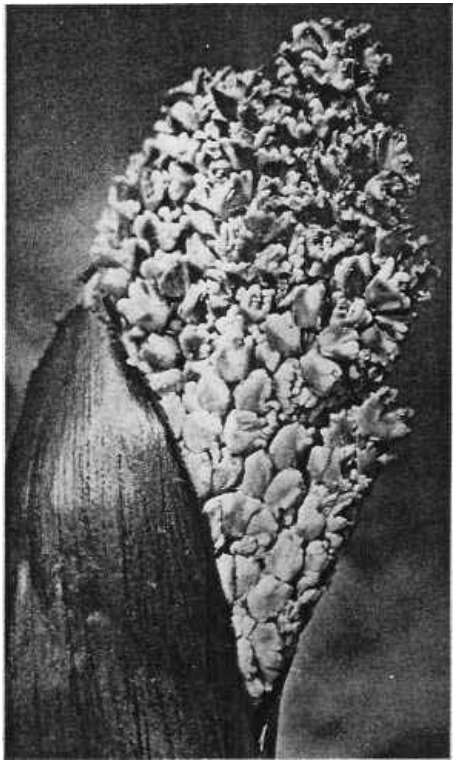
	1983		1984	
Clump	No. of Inflorescences	Sex	No. of Inflorescences	Sex
1	3	f	7	f
2	3	m	3	m
3	0	—	14	f
4	6	f	6	f
5	1	f	0	
6	7	f	7	f
7	28	f	32	f
8	9	m	7	m
9	7	f	18	f
10	28	f	70	f
11	15	m	15	m
Overall	80	f	154	f
	27	m	35	m

Chamaerops humilis blooms once a year, during the period of maximum flow-



2. Flowering phenology of *C. humilis.* f, female; m, male inflorescences.

ering activity of the Mediterranean shrub communities at low elevations (early spring; Herrera 1986). Figure 2 shows the blooming period of male and female plants separately in 1983. There was a delay of seven days between male and female flowering peaks, with males reaching peak bloom earlier. Also, the female-biased structure of the population is easily appreciated.

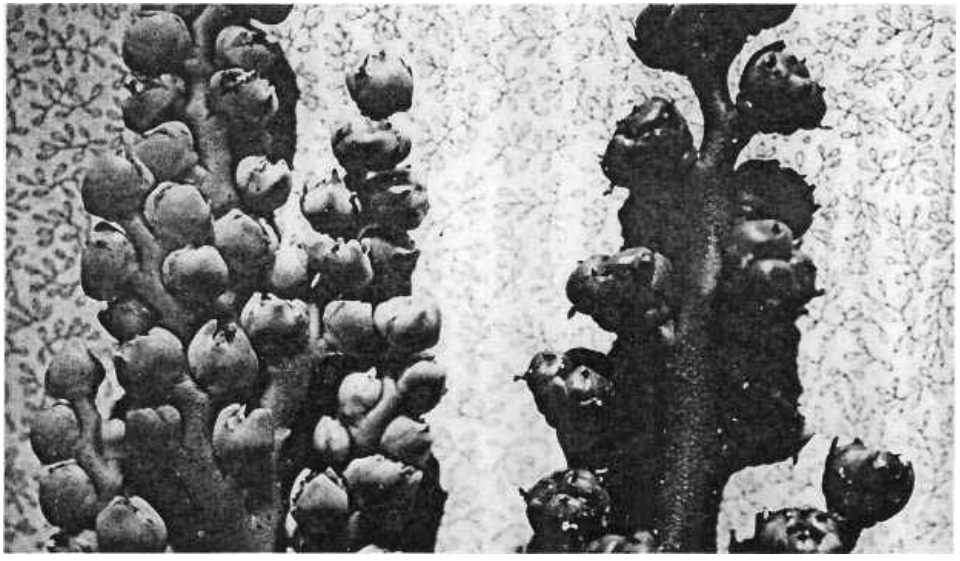


3. Male inflorescence of *C. humilis.*

Inflorescences and Flowers

Male flowers are 4—5 mm in diameter, with three sepals united in a low cupule with three pointed tips, and three ovate petals joined slightly at the base. Filaments of the anthers are expanded and united basally. No sign of a pistillode is found in staminate flowers. They are borne in branched inflorescences up to 20 cm long which commonly appear at ground level (Fig. 3). The number of flowers per inflorescence shows substantial variability (x = 154 ± 24, n = 10, range 40-300). The whole male inflorescence is yellow, produces a faint odor, and liberates large amounts of dry pollen which is carried away from the anthers by the wind. Although flower anthesis is quite synchronous the pollen-shedding phase of any inflorescence extends for about seven days. Herrera (1987) reports on each male flower shedding 214,000 grains of pollen on average. There is no nectar secretion, but pollen-seeking insects are often found on male inflorescences (see below).

Female flowers (Fig. 4) are 3—4 mm in diameter and have three free carpels and six staminodes. The number of flowers per inflorescence ranges from 38 to 90 (x = 57 ± 5, n = 12). Newly opened flowers and inflorescences are yellow but, as pollination takes place, they rapidly become green. Since flowers open sequentially from the top to the bottom of the inflorescence, it is very common to see inflorescences where the top half is green, with flowers no longer receptive, while the lower half is yellow and the flowers on it still receptive. The duration of a female inflorescence ranges from seven to fifteen days. Some



4. Female inflorescences of C. *humilis*. Left, inflorescence with yellow receptive flowers. Right, view of an inflorescence with developing ovaries, ten days after anthesis.

female flowers were found to secrete nectar which, measured on a weight-weight basis with a hand refractometer, yielded 27% sucrose equivalents. Accurate quantification of the amount of nectar secreted was precluded by the fact that it did not accumulate anywhere but simply glided onto the base of rachis. Nectar secretion was by no means widespread in the population, as it was observed in just few clumps. A variety of insects were attracted to the nectar which included ants *(Lasius niger* L., *Tapinoma erraticum* Latr., *Plagiolepis schmitzii* Forel and *Camponotus lateralis Oliv.)* and, especially beetles. A single unidentified species of Curculionidae 4 mm long, *Derelomus chamaeropis (Fab.)*, accounted for the vast majority of insects. The same weevil has been found in every *Chamaerops humilis* population checked for insect visitors all through southern Spain, from the drier to the moister sites. The weevils crawl over the flowers and often slip inside the prophyll. They consistently appear at both male and female plants (up to twenty insects per inflorescence). When on male flowers they eat and get dusted with pollen.

In a female flower of C. *humilis* each of the three free carpels may develop into a drupaceous fruit. Thus, the true fruit should be considered a "polydrupe" which may comprise 1—3 drupes. Nevertheless, the term fruit will hereafter be applied to the drupe, which in fact behaves as an independent dispersal unit. Fruits are dull-yellow to brown when ripe and contain a single, stony seed (mass 780 mg on average) covered by a fibrous mesocarp which smells strongly of rancid butter. Table 2 displays fruit set in seven female clumps, with differences between initiated and ripe fruits being due to predation by (1) *Derelomus* weevils during the early stage of development (up to 10 mm in diameter) and (2) rodents when fruits had reached their definitive size (up to 25 mm). Developing ovaries eaten by weevils were hollow, showed a large hole on their surface and, after turning black usually fell to the ground. In four clumps some fruit were initiated while in only two there were fruits

which escaped predation. 1.32% of the carpels initiated a fruit, but only 0.14% reached maturity. Thus, losses of fruit due to predispersal predation lowered the original fecundity by a factor of ten.

Discussion

Observations have shown that the species can be considered truly dioecious. Occasional existence of populations with a different breeding system cannot be ruled out but, undoubtedly, polygamodioecy (Amaral Franco 1980) is far from being common. It is interesting to note that a cultivated specimen grown from seed and not suffering water stress in any moment of the year has been observed to bear inflorescences which are sometimes entirely male and other times bear male together with bisexual flowers (Herrera, pers. obs.). It is likely that the assertion that this species is polygamodioecious is based on observations of cultivated plants. The above mentioned plant departed much from the reproductive behavior in the wild since, in addition to the spring flowering period, it exhibited another blooming episode during the summer.

Chamaerops humilis male inflorescences shed vast amounts of powdery pollen which is readily transported by the wind. On the other hand, female flowers sometimes secrete nectar, and both types of inflorescence are visited by curculionid beetles. The question arises, thus, whether the species is insect- or wind-pollinated. It would be difficult to give an unequivocal answer, however, as it appears that the plant shares traits of both anemophily and entomophily. The weevils acted as predators of developing fruits, so I have the feeling that their role as pollinators, if any, should be negligible. *Derelomus chamaeropis* is closely associated with the flowers of C. *humilis* in the Mediterranean region (Lesne 1926, Lepesme 1947 *in* Henderson 1986) but they probably should not be considered pollinators, but unspecialized parasites of flowers and fruits.

Table 2. Flower and fruit production, in female clumps of C. humilis *during 1983.*

Clump	Number of Flowers	Number of Fruits Initiated-Ripe
1	171	0-0
4	342	6-0
5	57	0-0
6	399	0-0
7	1,596	36-18
9	399	124-0
10	1,596	15-2
Overall	4,560	181-20

In his review on palm systematics and ecology, Tomlinson (1979) stated that dioecy is often associated with wind pollination. More investigation is needed before we can affirm categorically that *C. humilis* is anemophilous, but it seems likely that wind-pollination is in fact operating in southern Spanish populations. Nectar secretion by some female plants may represent little more than an ancient trait comparable to the existence of staminodes void of pollen in the female flowers. These traits may have been significant long ago to the reproductive biology of the plant but no longer functional in extant populations. C. *humilis* belongs to a set of Mediterranean shrub species whose families show strong tropical affinities (e.g., Anacardiaceae, Santalaceae, Oleaceae). It is but an example of the often dioecious shrub taxa which compose the "tropical element" of Mediterranean vegetation (Quezel 1985). This set of taxa, including C. *humilis,* existed well before the establishment of the Mediterranean climate (Raven 1973, Axelrod 1975), so it is likely that during the Tertiary they lived under a tropical climate. Only recently would C. *humilis* have undergone adaptations to more seasonal ecological conditions which favored the existence of drier and more open habitats such as sclerophyllous forests. The shift to dioecy and wind-pollination may have occurred recently enough

to make the pollination mode appear ambiguous.

Acknowledgments

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