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Low fruit set in the abundant dioecious tree *Clusia hilariana* (Clusiaceae) in a Brazilian restinga

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Abstract

Clusia hilariana (Clusiaceae), a dioecious tree, is an important nurse plant in the open, patchy restinga vegetation of coastal sandy plains in northern Rio de Janeiro (SE-Brazil). Although highly abundant locally, we found low production of fruit and viable seeds in open-pollinated as compared to hand-pollinated flowers. Reward from flowers of both sexes was resin, which was produced in higher quantities in male flowers. Flower visitors, including honeybees, were infrequent. We argue that low sexual reproductive success was due to inefficient pollen transport, and that vegetative propagation may contribute significantly to the high abundance of plants of this species.

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Introduction

The genus *Clusia* is widely distributed in the neotropics and comprises ca. 250–300 species. Most *Clusia* species are dioecious (Bittrich and Amaral, 1996), such as in the case of *Clusia hilariana* Schltdl. This species reportedly occurs from southeastern (Rio de Janeiro and Espírito Santo states) to northeastern (Bahia and Pernambuco states) Brazil (Mariz, 1974). In the open, patchy *restinga* vegetation of the sandy coastal plains of northern Rio de Janeiro state, *C. hilariana* is the most abundant tree species (Dias et al., 2005; Scarano, 2002). This *restinga* physiognomy typically has hemispherical islands of vegetation, sepa-

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rated from each other by white sand; trees of *C. hilariana* often occupy central positions in these islands and serve as nurse plants for a number of other plant species (Dias et al., 2005; Duarte et al., 2005; Scarano, 2002). Moreover, this evergreen tree has obligate crassulacean acid metabolism (Scarano et al., 2005) and plays an important role in nutrient cycling in the restinga (Scarano et al., 2004).

We have recently found that an exceptionally high proportion (37%) of the 27 most abundant plant species in this physiognomy (i.e., the open, patchy restinga vegetation) are dioecious, including *C. hilariana* (Matallana et al., 2005). This was unexpected given that the local flora in this geologically young habitat is predominantly originated from the neighbouring Atlantic rain forest (Araujo, 2000; Scarano, 2002). Since dioecious plants demand vectors for cross-pollination, it appeared improbable that pollinators would follow the

migration of plant species from a mesic forest to a harsh coastal environment. These findings have prompted us to start a long-term endeavour to examine the reproductive biology of dioecious plants in the restinga. C. hilariana was chosen for this study due to its important ecological role as nurse plant and for its high abundance. Because population dynamics of nurse plants are likely to affect ecosystem structure and function (Connell and Slatyer, 1977; Walker and Vitousek, 1991), reproductive biology of this species has relevance for local conservation and management initiatives. Moreover, although the reproductive biology of some Clusia species native to restinga (Correia et al., 1993, 1999; Lopes and Machado, 1998) and elsewhere (Armbruster, 1984; Bittrich and Amaral, 1996, 1997; Carmo and Franceschinelli, 2002) has been studied, such work is lacking for C. hilariana.

In this paper, we report studies of the pollination success and fruit and seed production of *C. hilariana* over two flowering seasons. Our central question was how high is fruit and seed set for this species. Our prediction followed Antonovics and Levin (1980), who proposed that plants at low densities are visited less frequently than those at higher densities (see also Larson and Barrett, 2000). Thus, we expected that given the high local abundance of *C. hilariana*, fruit and seed set would be high.

Materials and methods

This study was conducted in the Restinga de Jurubatiba National Park (22° 00'-22° 23'S, 41° 15'-41° 45'W), municipality of Carapebus, ca. 200 km north of the city of Rio de Janeiro, within the permanent plots of the International Long Term Ecological Research (Brazil, site 5; Scarano et al., 2004). This restinga comprises more than ten different vegetation physiognomies (Araujo et al., 1998; Duarte et al., 2005). The patchy vegetation dominated by C. hilariana covers ca. 40% of the park. Rainfall is seasonally distributed, with minimum monthly values (41 mm) and soil water deficit during the winter (June-September) and maximum (189 mm) during the summer (December-February). Mean annual temperature is 22.6 °C, mean maximal annual temperature is 29.7 °C in January and mean minimal is 20.0 °C in July (Henriques et al., 1986).

Observations were conducted during two flowering seasons between December 1999 and April 2000, and between November 2001 and March 2002. Hand pollinations were carried out to determine the role of pollen in fruit and seed set using flowers on 18 and 11 female plants, respectively, in the first and second flowering season. All female plants selected had a male plant nearby (ca. 3–8 m) to guarantee a close pollen

source. Flowers on each female plant received one of the following treatments: (1) unpollinated – flower buds were bagged and left unmanipulated to test for agamospermy; (2) hand-pollinated – recently opened flowers were selected, and the androecium of a fresh male flower from different individuals was rubbed on all stigmatic surfaces; (3) open-pollinated - recently senescent, unmanipulated flowers that had been available to pollinators were selected to assess natural pollination. After each treatment, flowers were numbered and enclosed in fine-mesh nylon net bags. These bags had the further advantage of allowing aeration and visualization of fruit maturation and dehiscence, without seed loss (Fig. 1a). Evaluation of fruiting success was based on counts of mature fruits. The fruits were collected at the onset of capsule dehiscence. The numbers of seeds per fruit were counted for all mature fruits (except those that were damaged by ants or lost their bags before collection). The seeds measured ca. 5×2 mm when fully developed; likely viable seeds were easily distinguished from aborted seeds or unfertilized ovules.

In November 1999, all *Clusia* trees in a plot $200 \times 100 \,\mathrm{m}$ were mapped using global positioning system (GPS). The sex ratio was calculated as the number of males relative to the number of females, expressed as a proportion of the total number of flowering individuals. Sex was easily determined visually in the field.

Male and female plants were monitored monthly for bud and flower production, fruit initiation, and fruit maturation. Pollinator visits were observed for trees in the plot. For logistic reasons, our observation of pollinators had to be restricted to 16 h, with observation periods of 30 min to 2 h scheduled from 09:00 to 13:00 only. Foraging behaviour was observed and recorded. Whenever possible, pollinators were collected or photographed for identification.

Results and discussion

Male and female flowers of *C. hilariana* are open, oriented towards the ground, and have a diameter of 4–6 cm. In general, flowers last only 1 day, with female plants producing isolated flowers and male plants having 2–3 flowers per inflorescence. Male flowers have pale rose petals with a deep red base, and the ovoid-shaped androecium is composed of numerous, tightly arranged stamens with apically poricidal anthers (Fig. 1b). Male flowers lack a pistillode, whereas a ring of pink staminodes encircles the gynoecium in the female flowers, which have white petals. The ovary is superior with 7–10 large sessile stigmas (Fig. 1c). Resin is produced by both flowers around and at the base of the androecium and the gynoecium; female flowers have

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