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Reproductive phenology and flower visitors' guild of *Canistropsis microps* (Bromeliaceae) in an Atlantic Rainforest of southeastern Brazil

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The reproductive phenology and guild of the floral visitors of *Canistropsis microps* in an Atlantic Forest area in Ilha Grande, RJ were studied for 4 years. The rates of flowering, fruiting and mortality were related to air temperature, rainfall and photoperiod. To register the flower visitors, observations were carried out for 5 days in each reproductive season. The flowering and fruiting occurred in the rainy season and were positively related to the studied climatic variables, whereas the highest mortality rates occurred in the dry season and were negatively related to the climatic variables. The guild of floral visitors of *C. microps* was composed of Hymenoptera, characterizing the species as a melittophilous plant. These results indicate that the rainy season presents more favourable conditions for investment in sexual reproduction, besides being the period in which potential pollinators have larger population densities and a longer period of activity.

Keywords: Bromeliaceae; Hymenoptera; Atlantic Rainforest; environmental factors; pollination

Introduction

Studies on phenology of a given species gather information on where it establishes, its period of growth, its reproduction and the availability of nutrients (Morellato and Leitão Filho 1992) which, regarding plants, concerns the periods of flowering, fruiting and leaf formation.

Phenological cycles of plants may be related to the dynamics of herbivores (Janzen 1967; Howe and Primack 1975; Feisinger et al. 1985; Bawa 1990; Morellato 1992; Morellato and Leitão Filho 1992; Galetti and Pizo 1996), maximization of pollination (Augspurger 1980, 1981) and competition for pollinators and dispersers (Janzen 1967; Waser 1978a, 1978b; Zimmerman 1980; Borchet 1983; Rathcke 1983; Bawa 1990). On the other hand, several studies have stated that these cycles respond to certain environmental factors, such as the climate of the region (Brown and Kodric-Brown 1979), air temperature (Heide 1982; Reader 1983), a combination of temperature and photoperiod (Hume and Cavers 1982; Neuffer and Hurka 1986), competition for light and nutrients (Janzen 1967), seasonal fires (Howe 1994) and water availability (Aronson et al. 1993). Nevertheless, ecological and environmental factors may act together, influencing the phenology of a plant species directly or indirectly, and establishing

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a phenological pattern for the population of a given species (Lennartsson 1997) or even a community (Snow 1965; Gentry 1974; Stiles 1975; Morellato and Leitão Filho 1992; Araújo et al. 1994; Poulin et al. 1999).

The Neotropical family Bromeliaceae occurs from Patagonia to southern Florida (Benzing 1980, 2000), with the Brazilian Atlantic Rainforest being one of the biomes with the greatest species diversity (Smith and Downs 1974; Martinelli et al. 2008). Apart from the high diversity, these plants provide important resources for associated animal communities in Atlantic Forest areas (e.g. Araújo et al. 1994; Martinelli 1997; Rocha et al. 2004). However, there are few studies addressing the phenology (Araújo et al. 1994; Martinelli 1997; Siqueira-Filho 1998; Pereira and Quirino 2008; Marques and Lemos Filho 2008) and reproductive biology of bromeliads (Heithaus 1979; Reitz 1979; Gardner 1986; Sazima et al. 1989, 1995; Araújo et al. 1994; Van Sluys and Stotz 1995; Siqueira-Filho 1998; Rocha et al. 2000; Almeida et al. 2004; Hmeljevski et al. 2007).

Canistropsis microps (E. Morren ex Mez) Leme is a bromeliad species endemic to the Atlantic Forest of Rio de Janeiro State, in southeastern Brazil (Leme 1998; Martinelli et al. 2008), being common in montane forests. At Ilha Grande, an island on the southwestern coast of Rio de Janeiro State, this bromeliad is abundant (Almeida et al. 1998; Nunes-Freitas and Rocha 2007), especially in better-preserved forested areas. Information available on this species is limited to some aspects of geographic distribution (Fontoura et al. 1991; Martinelli et al. 2008) and taxonomy (Leme 1998), and virtually nothing is known about its reproductive biology or ecology.

In the present study we analysed the phenology of flowering and fruiting of *C. microps* in an Atlantic Forest area at Ilha Grande, Rio de Janeiro state, seeking to identify the extension of its reproductive phenophases (flowering and fruiting) and the effects of environmental factors (temperature, photoperiod and rainfall) in determining these phenophases. In addition, we analysed the guild of flower visitors of *C. microps*, identifying the most frequent species and the variation in visitors' guild composition in successive years during the period of study.

Materials and methods

Study area

The study was carried out from December 1996 to March 2000 in an Atlantic Forest area near Vila Dois Rios, at Ilha Grande municipal district of Angra dos Reis (23°11′ S, 44°12′ W), southwestern Rio de Janeiro State, Brazil. Ilha Grande has a warm and humid climate, with average annual temperature of 22.5°C and annual rainfall of about 2200 mm (data provided by the Central Nuclear Almirante Álvaro Alberto for the municipal district of Angra dos Reis) (Figure 1). The warmer and wetter period occurs from October to April, and the colder and drier period, from May to August (FIDERJ 1978) (Figure 1), although there was no water deficit in the region and therefore there is no defined dry season. Monthly rainfall varied during the study (Figure 2A). Most of the island is covered by dense Atlantic rainforest (Alho et al. 2002) in different levels of regeneration as the result of anthropic disturbances. The study area was located on the seaward side of the island, in an area of primary forest at an altitude of ca. 240 m, and presents relatively little anthropic disturbance. Canopy height varies from 25 to 30 m, with a relatively sparse understorey and a relatively deep leaf-litter layer (50–120 mm depth) (Almeida et al. 1998).

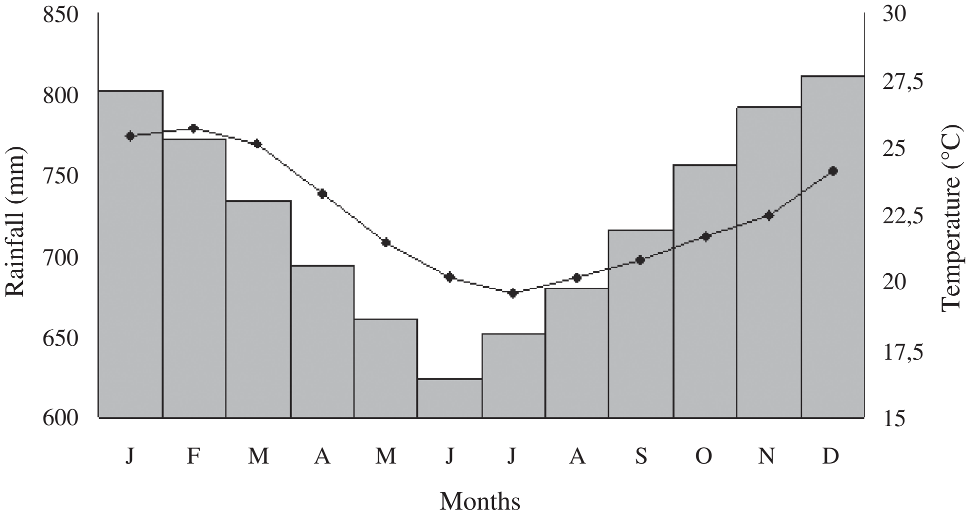

Figure 1. Rainfall (mm; bars) and temperature (line) data for the study area in a 45-year period in the region of Angra dos Reis, RJ, Brazil (source: FIDERJ, 1978).

To study the variation in reproductive phenology of *Canistropsis microps*, we marked 500 adult rosettes with a numbered plastic tape at 20 points in the forest (25 rosettes per point). During 40 consecutive months, we evaluated the phenological state of each individual (flowering, fruiting and proportion of non-reproductive plants), and recorded dead individuals (dried or completely ravaged by herbivores).

We characterized the reproductive cycle of *C. microps*, identifying the periods of the year in which flowering and fruiting occurred, using the frequency of individuals in each phenophase through the months of the study. The frequency of each phenophase was obtained by dividing the number of individuals of each phenophase in a particular month by the total number of marked individuals in that month (excluding the number of dead individuals in a given month). We evaluated to what extent the long-term temperature (°C; average of 45 years), long-term rainfall (mm; average of 45 years), photoperiod (h) (data from FIDERJ 1978), and monthly rainfall during the study period (in mm) (data provided by the Central Nuclear Almirante Álvaro Alberto for the municipal district of Angra dos Reis) affected the frequency of flowering, fruiting and monthly mortality, using Spearman correlation (Zar 1999). For such analyses, because percentages have more a binomial than a normal distribution, we transformed the percentage data into their arcsin of the square root before applying statistics (Zar 1999).

To estimate the proportion of individuals of *C. microps* recruited via clonal growth or via seed germination within the studied population, we established 30 parcels of 4 m^2 (2×2 m) in which we counted the number of rosettes originated by clonal growth, the number of isolated individuals, and the number of young individuals (rosette height < 10 cm) completely isolated from adults and that were originated by seed germination.

Each year, for 5 consecutive days, we registered the times of flower opening and closing, and the amount of time for which flowers remained opened. Observations

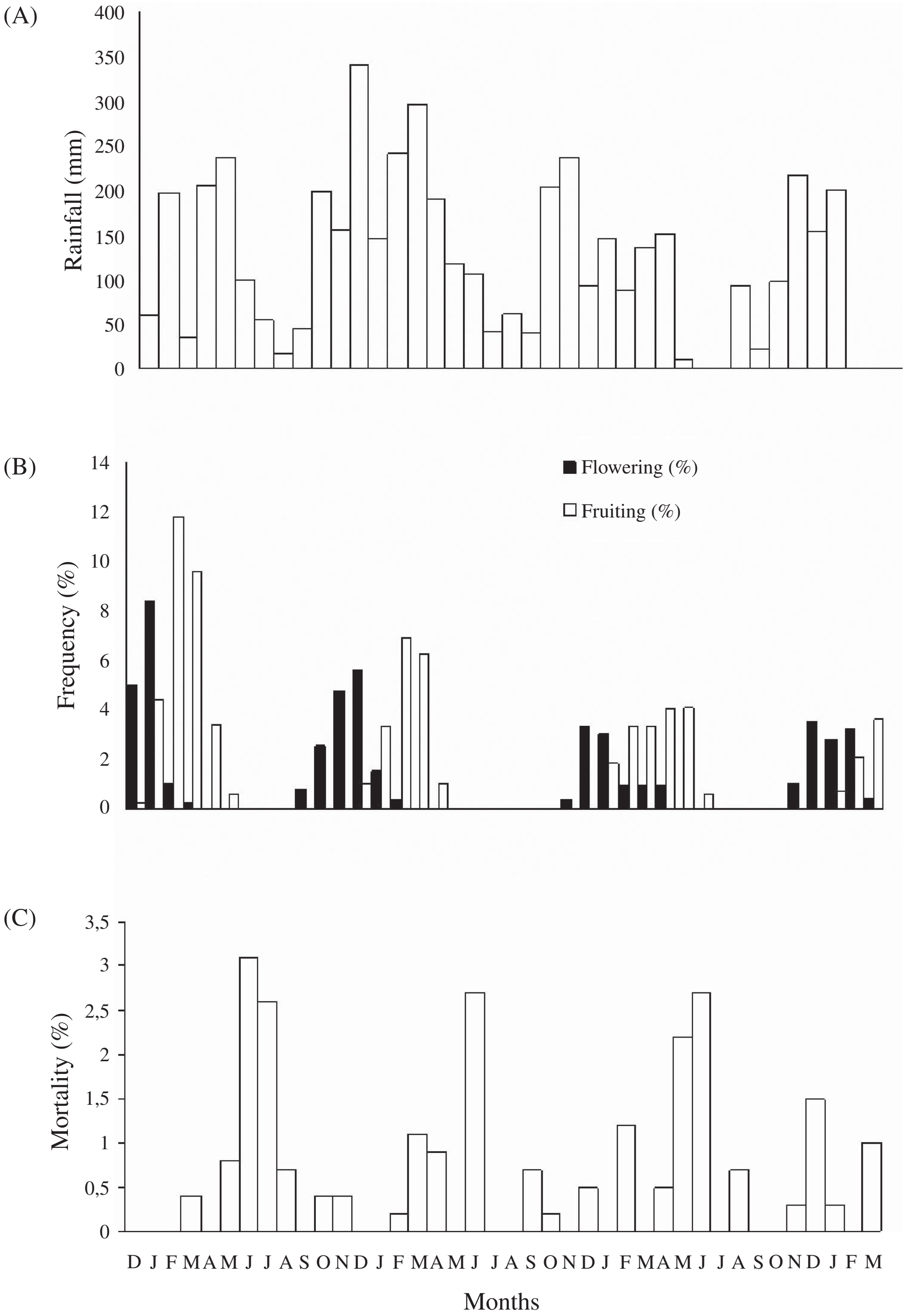

Figure 2. Pluviometric data, phenology and mortality rate of *Canistropsis microps* throughout the period of study (December 1996 to March 2000) in the region of Angra dos Reis, RJ, Brazil. (A) Monthly rainfall (mm) (source: CNAAA); (B) flowering and fruiting frequency of *C. microps*; (C) mortality rate of *C. microps* throughout the period of study.

were made in three different sites from the time before flowers had opened (05:00 h) until after they were already closed (18:00 h), during the peak of flowering in each reproductive season. Through the day, at each hour interval we made two focal observations of 15 minutes (totalling 30 minutes observation at each hour interval of the day), in which we registered the flower visitor species and number of visits of all animals visiting the flowers. In a similar area but distant from that where we made the focal observations, we collected the plant flower visitors using an entomological net for species identification.

For analysis of floral morphometry, we collected 10 flowers of *C. microps* from different inflorescences of different plants to maintain the independence of observations. Using a calliper (precision of 0.1 mm), we measured the height of the flowers, ovary, pistils and style and the depth and diameter of the corolla. The volume of nectar produced during an entire day was sampled with capillary tubes of 10 μl in 10 flowers of 10 inflorescences covered with nylon bags 1 day before flower anthesis. The concentration of sugars (%) in the nectar was obtained with a portable refractometer.

To evaluate the hypothesis that there is a variation in successive years in the composition and heterogeneity of the guild of floral visitors of *C. microps*, we repeated the same sampling methodology in four reproductive seasons in successive years (1996–2000). To each reproductive season, we registered the composition and calculated the richness (S) of floral visitor species. We calculated the heterogeneity of the floral guild visitors in each reproductive season using the Shannon index (H') (Magurran 1988). The similarity in composition of floral visitors among years was estimated using Jaccard's Index (Magurran 1988).

Results

During the study, *C. microps* usually flowered between September and March (Figure 2B), but the individual reproductive period was usually 4 months. The number of flowering individuals of *C. microps* varied among months. In general, the number of flowering individuals in the population at each reproductive season was relatively low: 8.4% (42/500) in the 1996/1997 season; 5.6% (22/461) in the 1997/1998 season; 3.3% (11/433) in the 1998/1999 season and 3.5% (10/396) in the 1999/2000 season (Figure 2B). The frequency of flowering in each month was mainly explained by photoperiod ($R = 0.738$; $N = 40$) and average rainfall ($R = 0.657$) (Table 1).

Fruiting of *C. microps* occurred, in general, from January to June, with a peak in February/March (Figure 2B). In the years of study, the dispersion period occurred

Table 1. Spearman rank correlation values for interaction of phenological phases of *Canistropsis microps* with climatic variables at the Atlantic Forest of Vila Dois Rios, Ilha Grande, RJ.

Phenological phase	Average temperature (°C)	Average rainfall (mm)	Photoperiod (h)	Monthly rainfall (mm)
Flowering	0.564	0.657	0.738	0.241
Fruiting	0.314	0.568	0.258	0.114
Mortality rate	−0.217	−0.282	−0.372	−0.263

in May/June, when all the fruits, mature or not, were dispersed (completely removed from the inflorescence). Mature fruits of *C. microps* were small, orange and without ornaments or thorns. Fruits were aggregated and easily removable from the plant. The frequency of fruiting individuals of *C. microps* was weakly related to the climatic variables (Table 1).

The yearly mortality rate of *C. microps* varied from 0.2 to 2.7%, with a similar variation among years, attaining a maximum value in June 1996 (Figure 2C). The mortality rate was weakly related to climatic variables (Table 1). In general, the mortality rate was highest during the period of the year in which the rainfall and temperature were lower (May–August) and the daylight period was shorter.

A total of 1028 individuals of *C. microps* were counted in the 30 sampled parcels for estimating the frequency of each recruitment type. Of these, 827 originated from vegetative growth (80.4% of the total) and 201 from seeds (19.6%), which corresponds to approximately four individuals originating by clonal growth for each individual originating from seed germination.

The anthesis of *C. microps* started at about 06:00 h, with flowers being completely opened by 07:00 h. The closure of flowers occurred by 16:30 h. The number of opened flowers averaged 1.5 ± 0.5/day/individual ($N = 10$; range 1–4). The total number of flowers per inflorescence varied among individuals, averaging 27.1 ± 7.0 ($N = 10$; range 15–37). The inflorescence of *C. microps* was composed of primary bracts varying in colour from light green to intense purple. The petals were white, with a little green spot in the centre. The flowers of *C. microps* had an average length of 26.8 ± 1.9 mm ($N = 10$). The corolla had an average depth of 19.5 ± 2.0 mm ($N = 10$) and an average diameter of 2.8 ± 0.3 mm ($N = 10$). The anthers were linear, dorsifixed and introrse, with the opening turned to the centre of the flower. Stamens had an average height of 15.4 ± 1.4 mm, whereas the average height of the pistil was 20.4 ± 2.9 mm, with the style averaging 13.8 ± 2.8 mm and the ovary averaging 6.6 ± 1.8 mm in height. The average production of nectar per flower during an entire day was 6.4 ± 2.6 μl ($N = 10$ flowers), whereas the concentration of sugars averaged 38.7 ± 9.0% ($N = 4$ flowers).

In general, the visiting activity in *C. microps* lasted from 6 to 10 hours, varying among reproductive seasons (Figure 3). In all studied reproductive seasons, visitor activity started shortly after the flowers anthesis began (Figure 3), at 06:00 h. The extent of visiting activity varied among the studied seasons, being the shortest (in hours) in the 1999/2000 reproductive season and the longest in the 1998/1999 reproductive season (Figure 3). The peak of visits varied between consecutive years, as did the activity of visitors (Figure 3).

Throughout the years of study, the flowers of *C. microps* were almost exclusively visited by nine species of insects of the order Hymenoptera, belonging to five genera in three subfamilies (Bombinae, Meliponinae and Euglossinae) (Table 2). In only one of the reproductive seasons (1998/1999), did we record a bird visiting the flowers, a male of the hummingbird *Thalurania glaucopis* Gmelin 1788 (Table 2).

Among the species of flower visitors, only *Trigona* spp. and *Euglossa iopoecila* Dressler 1982 were recorded in all four studied reproductive seasons, whereas *Bombus morio* Francklin 1913 was recorded in three (Table 2). Considering all sampled species of flower visitors of *C. microps*, we found pollen grains of *C. microps* only on the bodies of *Trigona* spp. and *Bombus* spp. Those bee species collected pollen and nectar, contacting the anthers and the stigma of the flowers. Field observation showed that all remaining species of Hymenoptera and the hummingbird *Thalurania glaucopis*

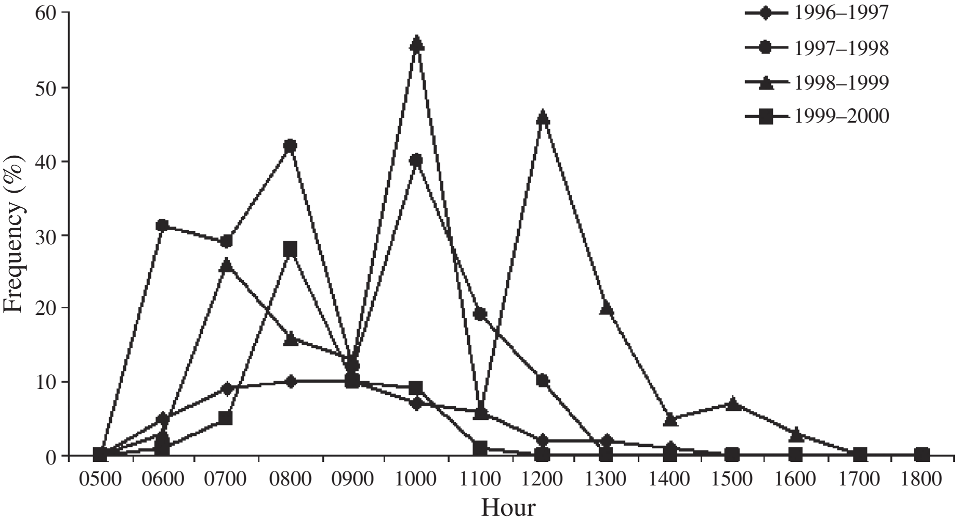

Figure 3. Daily activity of the flower visitors' guild of *Canistropsis microps* during each reproductive season at the Atlantic Forest of Vila Dois Rios, Ilha Grande, RJ, Brazil.

collected only nectar, not touching the flower stigma. The individual of *Thalurania glaucopis* which visited the flowers of *C. microps* during the 1998/1999 reproductive season was captured with an ornithological net just after visiting some flowers. After a careful examination of the bird's body, no pollen grains of *C. microps* were found.

The species composition of the flower visitors' guild of *C. microps* varied among the four studied reproductive seasons (Table 2). The species richness of flower visitors varied from three to seven species depending on the year, and heterogeneity of the visitors guild varied from 0.325 to 0.649 (Table 3). The lowest similarity among the flower visitors' guild was observed between 1996/1997 and 1997/1998 reproductive seasons, whereas the highest similarity was between 1996/1997 and 1998/1999 (Table 4).

Discussion

The present study indicates that *C. microps* is a bromeliad species that does not reproduce continually, but has a reproductive season lasting from September to March, the period of highest rainfall, temperature and photoperiod values in the area. In the period of the year when environmental conditions are more favourable (Sala et al. 1988; Van Schaik et al. 1993), plants tend to initiate their reproductive and vegetative activity, probably in response to an increase in resource availability (Sachs 1977; Morellato 1992), which is expected for plant species occurring in tropical forests (Pandey and Singh 1992; Poulin et al. 1992). This adjustment to the wetter season is also observed in other bromeliad species, as shown by Araújo et al. (1994).

The adjustment of the flowering period of *C. microps* to the wet season may also be explained by its guild of pollinators, which is composed exclusively of Hymenopteran insects. In tropical habitats, a high abundance of arthropods, especially insects, is associated with the moister periods of the year, at which the environmental conditions favour their activity (Janzen and Schoener 1968; Janzen 1973). This would facilitate

Table 2. Number of visits for each species of flower visitor recorded for *Canistropsis microps* at the Atlantic Forest of Vila Dois Rios, Ilha Grande, RJ, during each reproductive season.

	1996/1997	1997/1998	1998/1999	1999/2000	Total
Species	*N* (%)	*N* (%)	*N* (%)	*N* (%)	*N*t (%)
Bombus morio Franklin, 1913	24 (46.2)	0	1 (0.5)	12 (22.6)	37 (7.6)
Trigona spp.*	13 (25.0)	89 (48.6)	153 (76.1)	15 (18.3)	270 (55.2)
Euglossa iopoecila Dressler, 1982	4 (7.7)	43 (23.5)	1 (0.5)	26 (49.1)	74 (15.1)
Hymenoptera 8†	4 (7.7)	0	0	0	4 (0.8)
Melipona quadrifasciata anthidioides Lepeletier, 1836	2 (3.8)	0	9 (4.5)	0	11 (2.2)
Dialictus anisitsianus Strand, 1910	1 (1.9)	0	2 (1.0)	0	3 (0.6)
Hymenoptera 9**	0	51 (27.9)	0	0	51 (10.4)
Bombus brasiliensis Lepeletier, 1836	4 (7.7)	0	0	0	4 (0.8)
Thalurania glaucopis Gmelin, 1788	0	0	35 (17.4)	0	35 (7.3)
Total	52	183	201	53	489

Notes: *N*, number of visits; *N*t, joint number of visits; %, percentage of visits of each flower visitor species in each reproductive season; $\%_t$, total percentage of visits of each flower visitor species for all joint reproductive seasons.

**Trigona fuscipennis* Friese (1908) and *Trigona spinipes* Fabricius (1793) were pooled into *Trigona* spp. because of the difficulties in distinguishing them from one another during field observations.

†Collection was not possible.

Table 3. Richness, heterogeneity and equitability of the guild of visitors and number of flowering individuals in each reproductive season for the population of *Canistropsis microps* at the Atlantic Forest of Vila Dois Rios, Ilha Grande, RJ.

Parameter	1996/1997	1997/1998	1998/1999	1999/2000
Richness (*S*)	7	3	6	3
Heterogeneity (*H*′)	0.649	0.454	0.325	0.452
Equitability (*J*)	33.4%	41.3%	18.1%	41.2%
Flowering individuals	66	31	14	8

the interaction of the flowering period of *C. microps* and its invertebrate pollinators, as has been suggested for other plant species (Borchet 1983).

Canistropsis microps presented an extended flowering period together with a relatively low number of flowers produced per plant per day, which allowed the classification of its flowering as "steady state" type (*sensu* Gentry 1974). This plant flowering

Table 4. Values of Jaccard's Index of Similarity in composition of flower visitors' guild among the four studied reproductive seasons for *Canistropsis microps* at the Atlantic Forest of Vila Dois Rios, Ilha Grande, RJ.

	1996/1997	1997/1998	1998/1999
1997/1998	0.250	–	–
1998/1999	0.625	0.286	–
1999/2000	0.429	0.500	0.500

strategy maximizes the pollen flux among different individuals of the population, preventing self-pollination, because the pollinator is induced to visit a large number of plants to obtain the resources it needs (Gentry 1974). This idea is supported by the fact that each individual plant flowered for 3 months at different moments during the 7 months of the species' reproductive period, with partial overlapping of individual flowering events.

The rate of flowering rosettes of *C. microps* was relatively low and varied along the years of the study, which could be explained by the higher investment of the species in asexual reproduction through vegetative growth. This reproductive strategy is common among the Bromeliaceae (Barracho 1997) and allows a species to colonize a given habitat more rapidly (Zotz 1999; Sampaio et al. 2002), obtaining resources in a more efficient manner (Alpert 1991; Birch and Hutchings 1994; Stuefer et al. 1994; Evans and Cain 1995), especially in heterogeneous environments (Evans and Cain 1995).

The fruiting period of *C. microps* was also adjusted to the wetter season and extended into the drier season, a pattern similar to other species of bromeliads with aggregated-type fruits (zoocoric) (Benzing and Stiles 1998). In this period, *C. microps* could potentially invest in accumulating nutrients, allowing a better maintenance of the fruits and making them more attractive for dispersers in a manner similar to other plant species in the Atlantic Rainforest (Morellato 1992; Morellato and Leitão-Filho 1996).

The negative relationship between adult mortality rate of *C. microps*, and its occurrence in the drier season suggested that in this period of the year the conditions were less favourable to the maintenance and survival of this bromeliad. Also, it is well known that the family Bromeliaceae has monocarpic species that flower only once and after a certain period (depending on the species) degenerate and die (Benzing 1980).

The present study showed that *C. microps* has a guild of flower visitors composed almost exclusively of Hymenopterans, with a total of nine different species visiting its flowers in the study area. Although bees represent the most important group in number and diversity among pollinators in tropical habitats (Bawa 1990), it has been suggested that the main pollinators of bromeliads are vertebrates, especially hummingbirds and bats (McWilliams 1974; Smith and Downs 1974; Sazima et al. 1989; Vogel 1990; Araújo et al. 1994; Van Sluys and Stotz 1995; Martinelli 1997; Sick 1997). Others studies have demonstrated that some species of bromeliads are pollinated or have its flowers visited by insects (Ackerman 1986; Silberbauer-Gottsberger and Gottsberger 1988; Bernardello et al. 1991; Araújo et al. 1994; Siqueira-Filho 1998; Alves et al. 2000; Wendt et al. 2001; Almeida et al. 2004), but in most of them insects are not considered important (McWilliams 1974; Smith and Downs 1974; Sazima et al. 1989;

Vogel 1990; Van Sluys and Stotz 1995; Martinelli 1997; Sick 1997). Our data showed that, for *C. microps*, the guild of flower visitors is composed almost exclusively by insects (all Hymenoptera) concurring with the results obtained by Alves et al. (2000) also in Ilha Grande, who suggested that insects may constitute important pollinators for some bromeliad species.

Canistropsis microps has floral characteristics compatible with melitophily (Silberbauer-Gottsberger and Gottsberger, 1988). Light reflection by the white flowers, in contrast with the colour of the primary bracts (light green to intense purple) would make the flowers of *C. microps* more conspicuous to insects, facilitating their localization and functioning as a mechanism of attraction. This can represent an advantage in the *C. microps* microhabitat, the understorey of the forest, an environment where sunlight availability is relatively limited.

The guild composition, heterogeneity and equitability of flower visitors of *C. microps* varied consistently among consecutive reproductive seasons. This is suggestive that the guild of the plant does not remain homogeneous through time but tends to change between years (or reproductive seasons), which in turn may be a result of the pool of potential visitor species active (and their abundance) at each particular reproductive season of the plant, which is corroborated by the low similarity values obtained between breeding seasons. For tropical environments it has been indicated that abundance, richness and diversity of arthropod species, like hymenopterans, varies with time, usually following a seasonal pattern (with the highest values of the above parameters directly associated with the wet season) (Janzen 1973; Wolda 1977, 1978; Denlinger 1980; Wolda and Fisk, 1981). This seasonality is indicated for different groups of Hymenoptera, such as wasps and bees, which have a well-defined seasonal pattern (Heithaus 1979). As result, *C. microps* guild composition and visitor abundance in each reproductive season would be a function of the hymenopterans active and their species-specific abundance at that time.

We conclude that *C. microps* at Ilha Grande had a seasonal pattern of reproduction that occurs mainly during the rainy season, and is related to the favourable conditions of humidity, temperature and photoperiod during that period of the year. The guild of flower visitors of *C. microps* comprised exclusively Hymenoptera and varied among years. The relationship between flowering and the rainy season, during which there is increased activity of insects, associated with *C. microps* pollination, seems to indicate a strong interaction between these animals and this Bromeliaceae species, increasing the effectiveness of cross-pollinations. However, further studies are needed to assess the efficiency of these floral visitors in the sexual reproduction of *C. microps*.

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