



Anais da Academia Brasileira de Ciências

ISSN: 0001-3765

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Academia Brasileira de Ciências

Brasil

Machado, Isabel C.; Lopes, Ariadna V.; Sazima, Marlies
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Anais da Academia Brasileira de Ciências, vol. 82, núm. 4, 2010, pp. 881-891
Academia Brasileira de Ciências
Rio de Janeiro, Brasil

Available in: <http://www.redalyc.org/articulo.oa?id=327117686010>

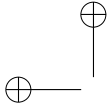
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Contrasting bee pollination in two co-occurring distylic species of *Cordia* (Cordiaceae, Boraginales) in the Brazilian semi-arid Caatinga: generalist in *C. globosa* vs. specialist in *C. leucocephala*

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Manuscript received on June 4, 2009; accepted for publication on March 31, 2010

ABSTRACT

In this study we compare the reproductive biology of *Cordia globosa* and *C. leucocephala* (Cordiaceae, Boraginales) formerly referred to Boraginaceae) to understand the functioning of the floral morphs and the relations with the effective pollinators. The species are synchronopatric, distylic, and self-incompatible. Though they share melittophilous traits, the main visitor and pollinator of *C. globosa* was the generalist and exotic bee *Apis mellifera*, while the one of *C. leucocephala* was the oligolectic bee *Ceblurgus longipalpis*. These two latter species are restricted to the Caatinga of NE Brazil, contrasting with the wide distribution of *Cordia globosa*. While the fruit-set for *C. globosa* was high, independently if the pollen donor/stigma receptor was a pin (long-styled) or thrum (short-styled) individual, in *C. leucocephala* the fruit-set was low and occurred only when a thrum individual was the pollen donor. This raises the possibility of this species moving towards dioecy. The high natural fruit-set of *C. globosa* confirms the generalist bee as its effective pollinator. The low fruit-set after manual crosses in *C. leucocephala* may be due to low pollen viability. Additionally, the low natural fruit-set (two times lower than after crosses) may be related with the foraging behavior of the specialist pollinator.

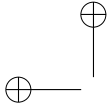
Key words: *Apis mellifera*, Caatinga, *Ceblurgus longipalpis*, *Cordia globosa*, *Cordia leucocephala*, dry forest, heterostyly, oligolecty.

INTRODUCTION

Many species in the Boraginaceae are known to have heteromorphic self-incompatibility system. The occurrence of distyly in *Cordia* L. (traditionally Boraginaceae, but now Cordiaceae) was first recorded by Darwin (1877). Heterostyly is a prominent part of the reproductive system in the genus (Opler et al. 1975, Taroda and Gibbs 1986a, Boshier 1995, Machado and Loiola 2000), although homostyly and functionally dioecious species are also known (Bawa 1974, Opler et al. 1975,

The first descriptions of pollination in *Cordia* go back to the classical publications of Knuth (1898-1900) and Vogel (1954). Bees and butterflies proved to be the main pollinators, although pollination by hummingbirds, wasps, flies, and bats has been also recorded (Machado and Loiola 1970, Percival 1974, Opler et al. 1975, Dobat and Peikert-Holle 1985, Askins et al. 1995, Machado and Loiola 2000).

Cordia globosa Kunth and *C. leucocephala* Lam. belong to the sub-genus *Varronia*, but have differ-



northeastern region of South America (Johnston 1949). In Brazil it is only found in the Caatinga (Taroda and Gibbs 1986a, b, Melo and Sales 2005). Contrastingly, *Cordia leucocephala* is endemic to northeastern Brazil and is restricted to the Caatinga areas and sandy soils (Taroda and Gibbs 1986b, Giulietti et al. 2002, Melo and Sales 2005). Despite its restricted distribution, it has commercial potential as a grazing and ornamental species (Andrade-Lima 1989).

While there are no reports about the pollinators for *C. globosa*, for *C. leucocephala* an oligolectic bee species is suspected to be its pollinator. In 1993, Urban and Moure described a new genus and species (*Ceblurgus longipalpis* – Halictidae) from specimens that visited exclusively the flowers of *Cordia leucocephala* in the Caatinga areas in Pernambuco (I.C. Machado, unpublished data) and Bahia States (C.F. Martins, unpublished data), Brazil. Aguiar and Martins (1994) later captured a large number of individuals of *C. longipalpis* in Paraíba State that almost exclusively visited *C. leucocephala* flowers.

Because of the specific relations between *Cordia leucocephala* and *Ceblurgus longipalpis*, and the total lack of information about the pollinators of *C. globosa*, we aimed to study the floral biology and the reproductive system of these two synchronopatric species. We also described the structure and functioning of the two floral morphs of both species, as well as the relations to their effective pollinators.

MATERIALS AND METHODS

STUDY SITES

Field work was carried out mainly in Sítio Riacho, in the municipality of Alagoinha, Pernambuco State (08°27'S and 36°46'W), Brazil, from 1984 to 1988. Additional data on floral visitors of *Cordia leucocephala* were gathered in 1999 in the municipality of Pesqueira, also in Pernambuco, as well as in 2003 in a protected area within the Fazenda Almas, municipality of São José dos Cordeiros, Paraíba State (7°28'45"S and 36°54'18"W), northeastern Brazil. Field observations of focal plants for both species totalized ca. 260 hours. The vegetation

The main study site (Alagoinha), is located at 762 m a.s.l. and has a very hot, semi-arid climate (BSs'h' – Köppen classification). The average annual temperature is about 24°C (Jacomine et al. 1973), and the annual rainfall ranges between 600 to 700 mm, with a marked dry season that lasts ca. 5 months. The Fazenda Almas site is located in a geomorphological depression zone, 200 to 300 meters below the level of the neighboring Borborema plateau, in a region known as “cariris paraibanos”. The climate is also semi-arid, with irregular annual rainfall totaling less than 600 mm, high solar irradiation levels, low relative humidity, and temperatures ranging between 26 to 30°C (Prado 2003). The dry season is very pronounced and lasts from six to nine months, sometimes extending to 10 months (Governo do Estado da Paraíba/SE/UFPB 1989).

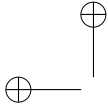
Voucher specimens of both *Cordia* species were housed at the Herbarium UFP at the Universidade Federal de Pernambuco (numbers UFP 04267 and 04276).

PLANT AND FLOWER FEATURES

The phenology of individual flowers, ramets, and of the entire populations of both *Cordia* species were studied by monitoring 20 individuals of *C. globosa* and 20 clumps of 3-4 individuals of *C. leucocephala* (10 with pin and 10 with thrum flowers) during four consecutive years.

Data were recorded concerning the initiation, sequence, and duration of anthesis, as well as floral color and scent emission (or lack of it), floral morphometry, and place and type of the resource. Corolla length and diameter, as well as stigma and anther heights (both measured from the base of the ovary) were measured in 20 flowers from different individuals of each morph. The length of style and filaments and the distance between the stigma and the anthers of both morphs (n = 20 flowers each) were measured in order to determine the function, reciprocity, and complementarity of the morphs, and the effects of morphometric differences on pollination.

We attempted to collect nectar from 20 flowers (bagged at pre-anthesis) using a graduated glass can-



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al. 2005). Flowers and buds used for stereomicroscopic examinations were fixed in alcohol 70%, and schematic drawings were made using a stereomicroscope with camera lucida.

Pollen size and morphology were analyzed in *Cordia leucocephala* to compare brevistylous and longistylous flowers. Slides containing acetolyzed pollen grains were prepared following proposals of Erdtman (1966), and 25 grains, from at least three slides of each floral morph, were randomly sampled and measured (within one week of slide preparation). Pollen viability was verified by using 2% acetocarmine (Dafni et al. 2005) ($n=20$ flowers from 10 individuals; 10 of each morph/species).

Controlled pollination experiments (manual self-pollination and intra- and inter-morph cross-pollinations) were carried out to examine the reproductive system of both species. Entire inflorescences were bagged just before anthesis and anther dehiscence. All controlled pollinations were performed one hour after anthesis initiation. Pollen deposition in all manual-pollination experiments was confirmed by visual inspection of the stigmas with a hand lens. Fruit-set after treatments was compared with fruit-set under natural conditions (control).

FLORAL VISITORS

The behavior (pollination or nectar robbing) of the floral visitors was recorded in the field during observations of focal plants totalizing ca. 100 hours for each species. Observations started at 5:30h a.m. but the visitation time, duration, and frequency of visits were registered from the beginning of anthesis for both species (ca. 7:30h a.m.) until flowers have wilted (ca. 14-15:00h). Photographs were taken of both flowers and bees, and some insects were captured for identification. Vouchers are at the Museu de Zoologia, Universidade Estadual de Campinas-UNICAMP (ZUEC) and at the Laboratório de Biologia Floral e Reprodutiva da Universidade Federal de Pernambuco-UFPE.

RESULTS

PLANT AND FLOWER FEATURES

near *C. leucocephala*, which grows in clumps of individuals. In addition, individuals of *C. leucocephala* were recorded at Fazenda Almas, and also along roadsides. Flowering of *C. globosa* and *C. leucocephala* is uniform, with one major episode per year in three consecutive years. Flowering of both species occurs for a period of three to four months, beginning in January/February (March in the fourth year of observation) and ending in April/May. Both species are heterostylous (distylous), with a 1:1 isoplethic ratio of their floral morphs (brevistylous and longistylous individuals).

The flowers of both species are white, tubular (Fig. 1), infundibuliform (funnel-shaped), and distributed in dense inflorescences (glomerules). About two flowers (*C. globosa*) or eight or more (*C. leucocephala*) flowers per inflorescence were recorded on any given day, emitting a light, sweet odor in the former species and being scentless in the latter. Anthesis starts at 08:00h a.m. in both species, the anthers dehisce shortly after flower opening, and the stigmas remain receptive until 14:00h (*C. globosa*) or 15:00h (*C. leucocephala*). Thus, the flowers are attractive for about six to eight hours. Flowers of *C. globosa* are about four times smaller than those of *C. leucocephala* (Table I). The stamens of *C. globosa* have glabrous filaments of equal length in the flowers of the same morph (Table I, Fig. 1C), and are inserted on the corolla 2.5 to 3.0 mm from its base. Contrastingly, in *C. leucocephala* each morph has three groups of stamens with different filament lengths (Table I), which are inserted on the corolla at different heights (Fig. 1A-B). The distal portions of the filaments and of the corolla tube are covered by trichomes only in the longistylous morph of *C. leucocephala* (Fig. 1A). The style is single apical, terminal, with four stigmatic branches at the apex in both species (Fig. 1). Pollen is spherical, with very different sizes between the two floral morphs. Pollen grains of brevistylous flowers are significantly larger than those of the longistylous flowers (Table I). Pollen viability in both types of flowers is ca. 98% in *C. globosa*, whereas in *C. leucocephala* it is about 60%. The nectary is located at the base of the ovary (Fig. 1), and despite the

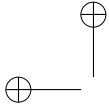
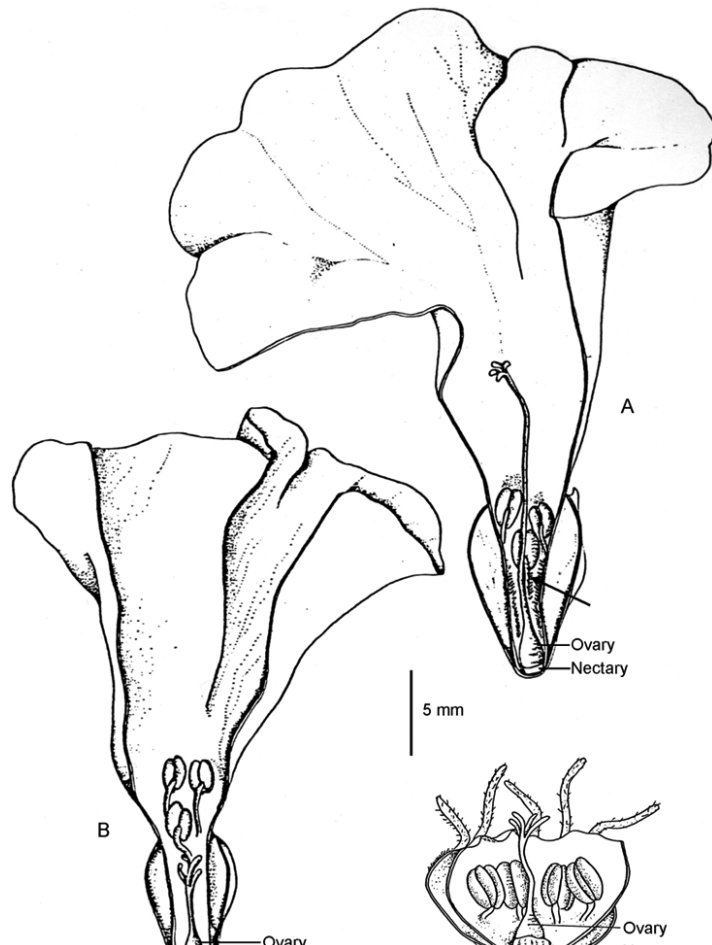
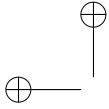


TABLE I
Measurements (mean \pm SD, mm) of short- and long-styled flowers of *Cordia globosa* and *C. leucocephala*, and equatorial diameter (in polar view, μm) of pollen grains (plants from a Caatinga area, Pernambuco State, Brazil).

Species	Corolla (length \times width)	Filaments	Style*	Pollen size (equatorial diameter)
<i>C. globosa</i>				
Short-styled	6.9 \pm 0.4	3.5 \pm 0.4	3.7 \pm 0.3	47.3 \pm 0.7 μm (45-50 μm)
Long-styled	7.0 \pm 0.2	2.0 \pm 0.2	6.4 \pm 0.3	39.5 \pm 0.6 μm (37-42 μm)
<i>C. leucocephala</i>				
Short-styled	35 \pm 0.5 x 28 \pm 1.8	16.6 \pm 1.0; 13.3 \pm 1.6; 9.1 \pm 0.7	6.4 \pm 0.5	63.3 \pm 0.5 μm (60-68 μm)
Long-styled	35 \pm 0.9 x 28.4 \pm 0.5	10.4 \pm 0.5; 7.3 \pm 0.7; 5.5 \pm 0.5	14.7 \pm 0.5	51.5 \pm 0.8 μm (44-58 μm)

*Values correspond to style + stigmatic branches.





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nectar is spread among the trichomes at the base of the filaments (Fig. 1).

Results of pollination experiments are summarized in Table II. In both species, manual crosses between the same floral morph did not cause fruit-set. In *C. globosa*, reciprocal crosses between different floral morphs resulted in a fruit-set of 80% and 70%, while under natural conditions fruit-set was ca. 50%. In *C. leucocephala*, fruit-set was very low under natural conditions (5%). Low levels of fruit-set, though two-fold higher (10%), were also obtained after intermorph crosses – and only when longistylous flowers were the pollen receptors (Table II).

FLORAL VISITORS

The main floral visitor and pollinator of *C. globosa* was the exotic and invasive bee *Apis mellifera* (Fig. 2A), which is responsible for 60% of all visits. Visits started at 07:30h and finished at 14:00h. Individuals of this species visited several flowers of the same plant, remaining on each flower for about three seconds and contacting anthers and stigma while taking nectar. Many individuals foraged on the same floral group of *C. globosa* at the same time. *Trigona spinipes* visited and pollinated *C. globosa* flowers, behaving in a very similar manner as *A. mellifera* and likewise contacting anthers and stigma during nectar uptake. This species was responsible for about 30% of all visits. Other sporadic visitors were *Xylocopa* sp., beetles, and butterflies that only occasionally transferred pollen to the stigma. Contrastingly, only one bee species, *Ceblurgus longipalpis* (Halictidae, Rophitinae), was registered visiting and pollinating flowers of both morphs of *C. leucocephala* (Fig. 2B-C). Their visits started at 08:00h, continued at intervals of 10 to 20 minutes, and finished at 15:00h. This species landed on the inner side of the corolla, and moved into the corolla tube to probe for nectar or to take up pollen. At this time, anthers and stigma were in touch with the ventral part of its abdomen and legs. Visits lasted for about five to seven seconds, and generally the bees visited other flowers of the same inflorescence be-

DISCUSSION

Both *Cordia* species exhibit annual and extended flowering patterns (*sensu* Newstrom et al. 1994). Extended flowering increases the probability of successful crosses, and the observed intra-specific flowering synchrony of both species favors cross-pollination, which is essential for self-incompatible species (Bawa et al. 1990), such as *C. globosa* and *C. leucocephala*.

The isoplethic population structure of both species (about 1:1 distribution of brevi- and longistylous individuals) is common among heterostylous species and results from a strong diallelic system of self-incompatibility (Vuilleumier 1967, Ornduff 1971, Cribb 1979, Sobrevila et al. 1983, Barrett and Shore 1985, Gibbs 1986, Barrett and Richards 1990, Barrett et al. 1992).

Heterostyly in *Cordia* was first recorded by Percival (1877), and distyly can be considered the most prominent feature in the reproductive system in the genus (Percival 1974, Opler et al. 1975, Gibbs and Tarodo 1979, Taimes and Varela 2005). Heterostyly arose independently in a lot of families (Lloyd and Webb 1997), and the occurrence of similar polymorphisms in many distyly species suggests that these morphological patterns are important to the reproductive system (Vuilleumier 1967, Ganders 1979, Yeo 1975, Barrett 1992). The most common polymorphisms associated with heterostyly involve pollen size and amount, and the number and size of stigmatic papillae (Ganders 1979, Barrett and Shore 1985, Barrett et al. 2000). In some species there may also be differences in the shape and position of the corolla tube among the floral types (Ganders et al. 1992).

Thus, the presence of smaller pollen grains in longistylous flowers, contrasting with larger ones in brevistylous, is a common feature of distylous species (Vuilleumier 1967). In *C. leucocephala* these differences are within the variation range reported by Nowicki and Ridgway (1973) for pollen of *Cordia* species in the *Varronia* section.

Furthermore, the presence of trichomes at the basal part of the filaments of the longistylous fl-

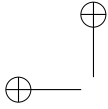


TABLE II
Pollination experiments in *Cordia globosa* and *C. leucocephala* in a Caatinga area, Pernambuco State, Brazil (nFl = number of flowers; nFr = number of fruits; %FS = percentage of fruit set), and estimated percentage of fruit set under natural conditions (NC).

Procedures	<i>C. globosa</i> (nFl/nFr/%FS)	<i>C. leucocephala</i> (nFl/nFr/%FS)
Spontaneous self-pollination	45/0/0	20/0/0
Cross-pollinations:		
Short-styled* × Long-styled	10/8/80	10/1/10
Long-styled* × Long-styled (≠ individuals)	10/0/0	10/0/0
Long-styled* × Short-styled	10/7/70	10/0/0
Short-styled* × Short-styled (≠ individuals)	10/0/0	10/0/0
NC (control)	ca. 50%	ca. 5%

* Pollen donor.

this type of dimorphism is very rare and one can speculate that, if these trichomes were present in brevistylous flowers of *C. leucocephala*, they would hamper the deposition and adherence of pollen grains to the stigmatic lobes.

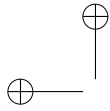
The evident reciprocal correspondence of the style and filaments heights in *C. globosa* and *C. leucocephala* is generally associated with cross fertilization mechanisms mediated by pollinators in most of the heterostylous species (Ornduff 1974, Ganders 1979, Barrett et al. 2000, Castro et al. 2004). In some cases, however, this correspondence may not be perfect (Ganders 1979), such as in *Cordia curassavica* and *C. dentata*, whose style of the longistylous flowers extends only slightly beyond the anthers, while in the brevistylous ones stigmas and anthers are well separated (Opler et al. 1975).

Like *Cordia globosa* and *C. leucocephala*, almost all heterostylous taxa are self-incompatible. In the genus *Cordia*, self-compatibility has only been reported for *C. alliodora* and *C. sebestena*, with all the other species being either distylous (with strongly associated self-incompatibility systems) or dioecious (Opler et al. 1975). Self-compatibility, though rare, does occur in some heterostylous species such as *Oxalis* (Oxalidaceae), *Hedyotis* (Rubiaceae), *Pulmonaria* (Boraginaceae) (Ganders 1979), and *Melochia* (Malvaceae) (Martin 1967). The

Distyly has apparently evolved several times to dioecy in the genus *Cordia*, with *C. inermis* and *C. coloccoca* being considered as intermediate between distylous and dioecious (Opler et al. 1975). In such situations, the longistylous morph would have become pistillate, while the brevistylous became staminate, and an intermediate phase of cryptic dioecy may occur (Opler et al. 1975, Beach and Bawa 1980).

While in *C. globosa* the fruit-set was very similar for both types of crosses [Short-styled (S) × Long-styled (L) and L × S], in *C. leucocephala* a fruit-set after manual crosses was obtained only in the S × L cross (with S as pollen donor), with the reverse cross being unsuccessful. This raises the possibility of this species moving towards dioecy, as observed for some dioecious species of this and other genera (Beach and Bawa 1980).

Fruit-set under natural conditions was low in *C. leucocephala*, and in many other populations no fruits were registered at all (I.C. Machado personal observation, Andrade-Lima 1989, Taroda and Gibbs 1986b, Melo and Sales 2005, Melo and Andrade 2007). This could be due to two reasons: the low pollen viability (60%) and the foraging behavior of the specialist pollinator, which may induce geitonogamy, as discussed below. The low fruit-set after manual crosses in *C. leucocephala* though two-times higher than that obtained



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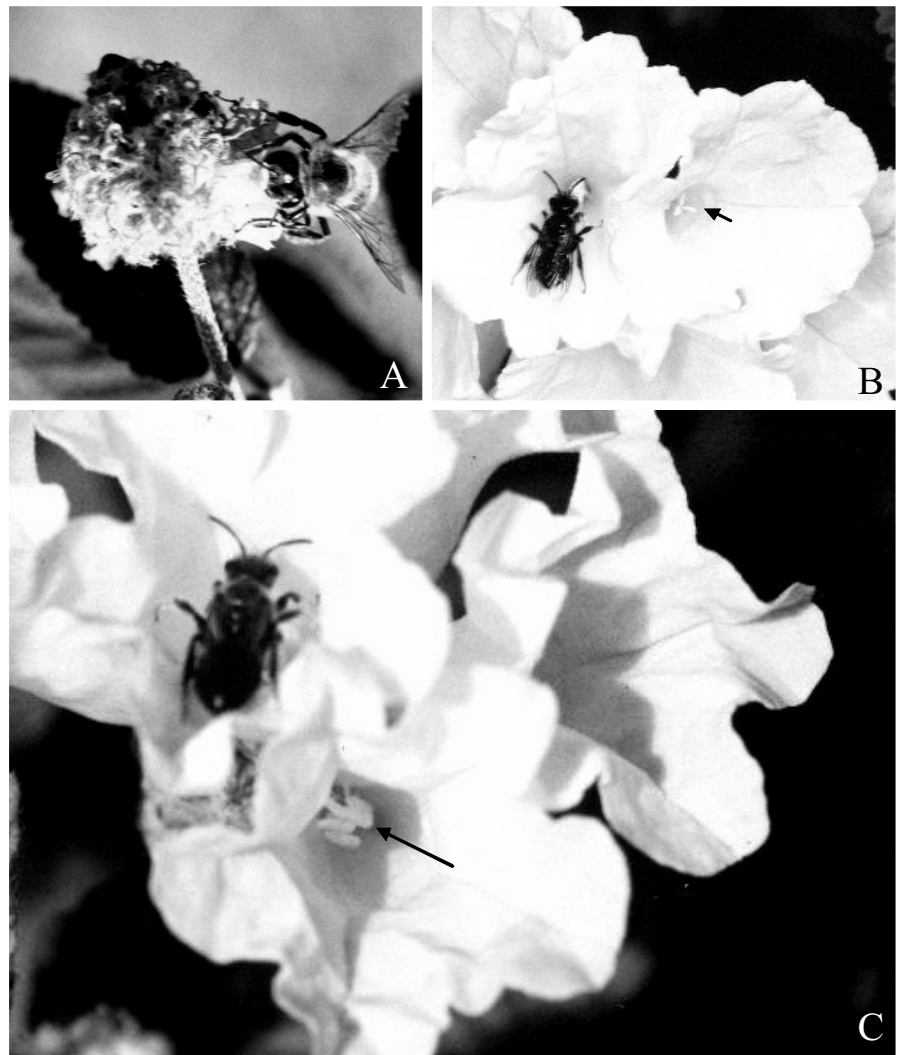
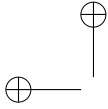


Fig. 2 – *Apis mellifera* visiting *Cordia globosa* flower (A), and *Ceblurgus longipalpis* (Halictidae-Rophitinae) visiting longistylous (B) and brevistylous (C) flowers of *Cordia leucocephala* in a Caatinga area in Pernambuco, Brazil. Arrows point to stigma (B) and anthers (C).

are both melittophilous (*sensu* Faegri and Pijl 1979), with similar floral traits such as color, form, reward, and time of anthesis, they occur synpatrically, flower synchronously, and are pollinated by bees with very different behaviors. The predominance of generalist bee species, such as *Apis mellifera* and *Trigona spinipes*, visiting *C. globosa*, is possibly related to the small flower size. The exclusiveness of the visits of *Ceblurgus longi-*

bees whose long tongues would be able to reach the nectar at the base of the corolla tube. The absence of long-tongued species and the much reduced nectar volume in *C. leucocephala* however, may be responsible for the lack of visitation by long-tongued bees such as *Centris* and *Euglossina* species, and the floral tube (5-7 mm) may limit access to short/medium-tongued bees like *Trigona*, and *Xylocopa* species. Euglossini bees



of scent in flowers of *C. leucocephala* may restrict visits of bees like *Trigona* spp. that are largely attracted by odor (e.g. Nogueira et al. 1999).

The restricted distribution of *C. leucocephala* (endemic to the Caatinga region of northeastern Brazil) may be strongly correlated with the distribution of the oligolectic bee *Cebalurgus longipalpis*, its sole visitor and pollinator. *Cebalurgus* is the only bee genus endemic to the Caatinga region (Aguiar and Martins 1994, Rozen 1997, Zanella and Martins 2003) and its single species, *C. longipalpis* (Urban and Moure 1993), is restricted to the states of Bahia, Pernambuco, and Paraíba, Brazil (Silveira et al. 2002). The sub-family Rophitinae, in the family Halictidae, comprises bee species that are generally rare, non-social, and morphologically specialized. The bees have a long glossa and labial palps, and collect nutrients from a very restricted number of plant species (Silveira et al. 2002). *Cebalurgus longipalpis* has elongated mouthparts, apparently as an adaptation to take up nectar from tubular flowers (Zanella and Martins 2003). This matches well with the flower structure of *C. leucocephala*. Besides, both males and females of this bee have been reported to visit almost exclusively *C. leucocephala* in many populations (I.C. Machado unpublished data, C.F. Martins unpublished data, Urban and Moure 1993, Aguiar and Martins 1994, Machado and Lopes 2003, Zanella and Martins 2003, present study). This indicates narrow oligolecty (*sensu* Cane and Sipes 2006).

The foraging behavior of *Cebalurgus longipalpis* with repeated visits to flowers of the same inflorescence in *C. leucocephala* may induce geitonogamy, which could lead to pistil losses since the species is self- and intramorph-incompatible. This could also be one of the causes behind the very low percentage of natural fruit-set. In this way, vegetative reproduction in *C. leucocephala* (see Andrade-Lima 1989) may represent the major mode of reproduction in some patches. A similar situation was recorded for species growing in areas under severe environmental fluctuations (Herrera 1987), such as observed for the semi-arid Caatinga vegetation.

In spite of the existence of plant species with complex flowers and structures that restrict visitation by

lonia cornigera and *Tapinotaspis nordestina* (Machado et al. 2002), and *Cordia leucocephala* and *Cebalurgus longipalpis* (present study) – generalist pollination systems are the most common ones (Herrera 1996, Waser et al. 1996, Armbruster et al. 2000, Fenster et al. 2004, Machado and Lopes 2003, 2004, Machado and Sazima 2008).

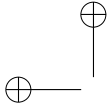
In fact, *Apis mellifera* and *Trigona spinipes*, which both display opportunistic and generalistic behaviors (Proctor et al. 1996, Sazima and Sazima 1989), were responsible for 38.5% and 46.2%, respectively, of the visits to melittophilous species in the main study area, Alagoinha (Machado and Lopes 2004). In the same study site, both bee species proved to be highly responsible for the strong connectance in the plant/bee pollination network (I.C. Machado unpublished data, Machado and Lopes 2003). The extremely aggressive foraging behavior of *A. mellifera* and, to a lesser extent, that of *T. spinipes* (Sazima and Sazima 1989), associated with their generalist foraging behavior, may lead them to experience high visitation rates. This could benefit heterostylic self-incompatible species occurring in the same area such as *Cordia globosa* (present study) and *Melochia tomentosa* (Machado and Sazima 2008).

ACKNOWLEDGMENTS

We thank the taxonomists of the Herbarium IPA for identifying plant species; João Amazonas (UFPE) and Severino Prazeres (*in memoriam*) for their help during field work. Bee identifications were kindly provided by João Camargo (Ribeirão Preto-USP) and Pe. Jesus Santiago Moure (UFPR). We also thank Maria Regina Barbosa and Zelma Quirino (UFPB/ Peld/CNPq Caatinga Project) who made possible field observations in the RPPN Fazenda Almas-PB; Marlene Barbosa (UFPE) for logistic help in the Herbarium UFP, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for essential financial support.

RESUMO

Neste estudo comparamos a biologia reprodutiva de *Cordia*



CONTRASTING BEE POLLINATION IN *CORDIA* (CORDIACEAE)

Embora elas compartilhem atributos melitófilos, o principal visitante e polinizador de *C. globosa* foi *Apis mellifera*, abelha generalista e exótica, enquanto o de *C. leucocephala* foi a abelha oligolética *Ceblurgus longipalpis*. Essas duas últimas espécies são restritas à Caatinga do Nordeste do Brasil, contrastando com a ampla distribuição de *C. globosa*. Enquanto a formação de frutos de *C. globosa* foi alta, independente se o doador ou receptor de pólen era um indivíduo brevi- ou longistilo, em *C. leucocephala* a formação de frutos foi baixa e ocorreu apenas quando o doador de pólen era brevistilo. Este fato levanta a possibilidade desta espécie estar se movendo em direção à dioécia. A alta formação natural de frutos de *C. globosa* confirma a abelha generalista como seu polinizador efetivo. A baixa formação de frutos após cruzamentos manuais em *C. leucocephala* pode ser devida à baixa viabilidade polínica. Adicionalmente, a baixa formação natural de frutos (duas vezes menor que a de cruzamentos) pode estar relacionada com o comportamento de forrageamento do polinizador especialista.

Palavras-chave: *Apis mellifera*, Caatinga, *Ceblurgus longipalpis*, *Cordia globosa*, *C. leucocephala*, floresta seca, heterostilia, oligoetia.

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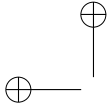
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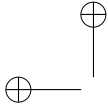
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