

Floral Traits and Pollination Systems in the Caatinga, a Brazilian Tropical Dry Forest

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- **Background and aims** Pollination is a critical stage in plant reproduction and thus in the maintenance and evolution of species and communities. The Caatinga is the fourth largest ecosystem in Brazil, but despite its great extent and its importance few studies providing ecological information are available, with a notable lack of work focusing on pollination biology. Here, general data are presented regarding the frequency of pollination systems within Caatinga communities, with the aim of characterizing patterns related to floral attributes in order to make possible comparisons with data for plant communities in other tropical areas, and to test ideas about the utility of syndromes. This paper also intends to provide a reference point for further studies on pollination ecology in this threatened ecosystem.
 - **Methods** The floral traits and the pollination systems of 147 species were analysed in three areas of Caatinga vegetation in northeastern Brazil, and compared with world-wide studies focusing on the same subject. For each species, floral attributes were recorded as form, size, colour, rewards and pollination units. The species were grouped into 12 guilds according to the main pollinator vector. Analyses of the frequencies of the floral traits and pollination systems were undertaken.
 - **Key Results** Nectar and pollen were the most common floral resources and insect pollination was the most frequent, occurring in 69.9 % of the studied species. Of the entomophilous species, 61.7 % were considered to be melittophilous (43.1 % of the total). Vertebrate pollination occurred in 28.1 % of the species (ornithophily in 15.0 % and chiropterophily in 13.1 %), and anemophily was recorded in only 2.0 %.
 - **Conclusions** The results indicated that the pollination systems in Caatinga, despite climatic restrictions, are diversified, with a low percentage of generalist flowers, and similar to other tropical dry and wet forest communities, including those with high rainfall levels.
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Key words: Floral traits, floral rewards, pollination syndromes, dry forests, Caatinga, northeast Brazil.

INTRODUCTION

Morphological, physiological and ecological floral traits are related to pollination vectors, and an analysis of these attributes can help in the prediction of the pollinator of a species (cf. Faegri and Pijl, 1979; Waser, 1983; Dafni and O'Toole, 1994; Endress, 1994; Proctor *et al.*, 1996). The relationships observed characterize pollination syndromes (*sensu* Vogel, 1954; Faegri and Pijl, 1979), and provide a valuable guide to studies on reproductive ecology. However, while some degree of variation is acceptable, it should be noted that floral traits are not infallible indicators of species' pollinators. In spite of the limits of studies based on floral syndromes, for example as mentioned by Herrera (1995) and Ollerton (1996), they contribute to the understanding of pollination biology at a community level (Rebello *et al.*, 1985; Ramirez *et al.*, 1990; Dafni and O'Toole, 1994; Tabla and Bullock, 2002; Muchhala and Jarrín-V, 2002), to comparisons of pollination system frequency among floras and vegetation types, and also towards directing more specific research. According to Cruden (1997) and Johnson and Steiner (2000), floral syndromes can be effectively tested by broad-scale comparisons between multiple floral traits and pollinators.

Floral morphology can exclude some floral visitors and attract potential pollinators, since the diversity of floral

types is also associated with the sensorial development of pollinators, particularly those related to the capacity to distinguish between and to memorize certain visual and olfactory patterns (Leppik, 1968; Faegri and Pijl, 1979; Ramirez *et al.*, 1990; Chittka *et al.*, 2001; Gegeer and Laverty, 2001). In addition, there are some interdependent relationships between flower and pollinator sizes (Feinsinger and Colwell, 1978; Frankie *et al.*, 1983). The occurrence of different floral resources indicates the presence of different kinds of pollinators, sometimes quite specialized as, for example, certain Anthophoridae and the Euglossini bees that pollinate flowers that offer oils, perfumes or resins as a reward (Vogel, 1966, 1974; Dressler 1968*a, b*; Armbruster, 1984).

Pollination is a critical stage in plant reproduction and thus in the maintenance and evolution of species and communities. Although most studies of pollination focus on one or a few species, a community perspective is important for pointing the way for specific studies, for comparing different ecosystems, for understanding sharing and competition for resources and their effects on community structure, and for guiding conservation programmes in threatened and fragmented ecosystems (*e.g.* Saunders *et al.*, 1991; Rathcke and Jules, 1993; Aizen and Feinsinger, 1994; Murcia, 1995, 2002; Kearns and Inouye, 1997; Ranta *et al.*, 1998; Renner, 1998).

The Caatinga is an ecological region of northeastern Brazil occupied by tropical dry forest and scrub vegetation,

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pastures and agricultural systems (Sampaio, 1995; MMA, 2002). It is an equatorial region of extreme drought, few wet months per year (3–5 months) with low annual rainfall levels (e.g. 500–750 mm year⁻¹), and extreme supra-annual variation in rainfall. Annual temperature averages 23–27 °C and the region suffers water deficit during most of the year (for details see Sampaio, 1995; Rodal and Melo, 1999).

The Caatinga is the fourth largest ecosystem in Brazil, after the Amazonian rain forest, the Cerrado, and the Atlantic forest (Aguiar *et al.*, 2002), covering 734 478 km² (MMA, 2002), which is almost 50 % of the northeastern region and 8.6 % of the country (Hueck, 1972). Recently the Caatinga was recognized as an 'Earth's last wild place', and included as one of the 37 'Wilderness Areas of the World' (Gil, 2002).

Despite its great extent and considering the importance of the Caatinga region for Brazil, few studies with ecological information are available, with a notable lack of publications focusing on the biology and the dynamics of its species (see Leal *et al.*, 2003 for review). Studies of pollination processes of Caatinga species are scarce (see Machado, 1996 and Machado and Lopes, 2002 for review), and these investigations focus mainly on individual species (Pinheiro *et al.*, 1991; Vogel and Machado, 1991; Machado and Sazima, 1995; Lewis and Gibbs, 1999; Locatelli and Machado, 1999; Kiill and Ranga, 2000; Piedade-Kiill and Ranga, 2000; Kiill and Drummond, 2001; Quirino and Machado, 2001; Machado *et al.*, 2002). Studies on pollination ecology of the Caatinga at a community level are even rarer (see Machado 1990, 1996; Machado and Lopes, 2002).

The Caatinga areas are, year by year, suffering increasing anthropic destruction, resulting in the loss of native fauna and flora (Sampaio, 1995; MMA, 2002). As a consequence, the plant species composition and vegetation structure are being significantly altered, with the habitat being reduced to small fragments. There are few previous biological and ecological studies relating to this. A broad knowledge of plant reproductive biology may be essential for the maintenance of the biodiversity of fragmented areas (Bawa, 1990) and for management projects in this ecosystem.

This work presents general data on the occurrence and the frequency of pollination systems in Caatinga communities. We aimed to characterize patterns related to the floral attributes of the taxa of this type of vegetation, to make possible comparisons with data for plant communities in other tropical areas, and to test ideas about the utility of syndromes and trends in specificity. This paper also intends to provide a reference point for further studies on pollination ecology in this threatened ecosystem.

MATERIALS AND METHODS

Study sites and species

The study was carried out on species referred in the literature as occurring in Caatinga vegetation (Andrade-Lima,

1989; Ferraz *et al.*, 1998; Rodal and Melo, 1999), and most of them were observed in three municipalities (Alagoinha, Buíque and Serra Talhada) located in the rural zone of Pernambuco State (PE), northeastern Brazil (Fig. 1). These areas have different physiognomies, and published floristic and phytosociological surveys are available (Ferraz *et al.*, 1998; Rodal *et al.*, 1998; Figueiredo *et al.*, 2000).

One of the areas, Sítio Riacho, is situated in the municipality of Alagoinha-PE (8°27'S, 36°46'W; 762 m a.s.l.), approx. 200 km from the coast, and comprises about 80 ha. The climate of this site is semiarid, of the Bs s'h' type according to the classification of Köppen. The number of dry months varies from 5–7, with mean annual temperature and precipitation approx. 22 °C and 550 mm, respectively (Griz and Machado, 2001). The vegetation is characterized by a shrubby, dense Caatinga (Egler, 1951), with a predominance of amply ramified and thorny shrubs.

The second area is the Vale do Catimbau (8°67'S, 37°11'W), a Brazilian National Park located in the municipality of Buíque-PE, and 285 km from the coast. The altitude in the area ranges between 800–1000 m a.s.l., and the mean annual precipitation is 1095.9 mm, with rain from January to June but mostly from April to June; the mean annual temperature is 25 °C (SUDENE, 1990). The vegetation of this valley is very unusual, with many plant species not found in other Caatinga areas, some of them normally found in other types of 'open' vegetation such as 'Campos Rupestres' (Rodal *et al.*, 1998).

The most inland area (approx. 700 km from the coast) is Fazenda Saco located in the municipality of Serra Talhada-PE (7°59'S, 38°19'W), and is an experimental station of the Agricultural Research Company of Pernambuco (IPA). The altitude in the area is approx. 600 m a.s.l. and the mean annual precipitation is 650 mm, with high variation from year to year. Generally, a pronounced dry period occurs from June to December, with rains from January to May. The mean annual temperature is 26 °C, with little monthly variation (Machado *et al.*, 1997a). The vegetation is dominated by shrubs, the majority around 3–4 m tall with stem diameter at breast height (DBH) of 3–6 cm, with a few trees reaching 15 m high and DBH of 60 cm (Ferraz *et al.*, 1998). As in the first area, the herbaceous stratum is not very dense, and is composed mainly of annual plants that grow only in the rainy period.

In addition to observations made on field trips, during which direct observations of floral biology and pollinators were made together with collections, some analyses were conducted using specimens deposited in local herbaria at Agricultural Research Company of Pernambuco and Federal University of Pernambuco (IPA and UFP, respectively).

A total of 147 species were studied (including 24 trees, 62 shrubs, 35 herbs, 21 vines and five epiphytes) distributed in 34 families, and 91 genera (see Appendix), which represents a small section of the number of species registered in the Caatinga (Sampaio *et al.*, 2002; Leal *et al.*, 2003).

Voucher specimens are deposited in the Herbarium UFP.

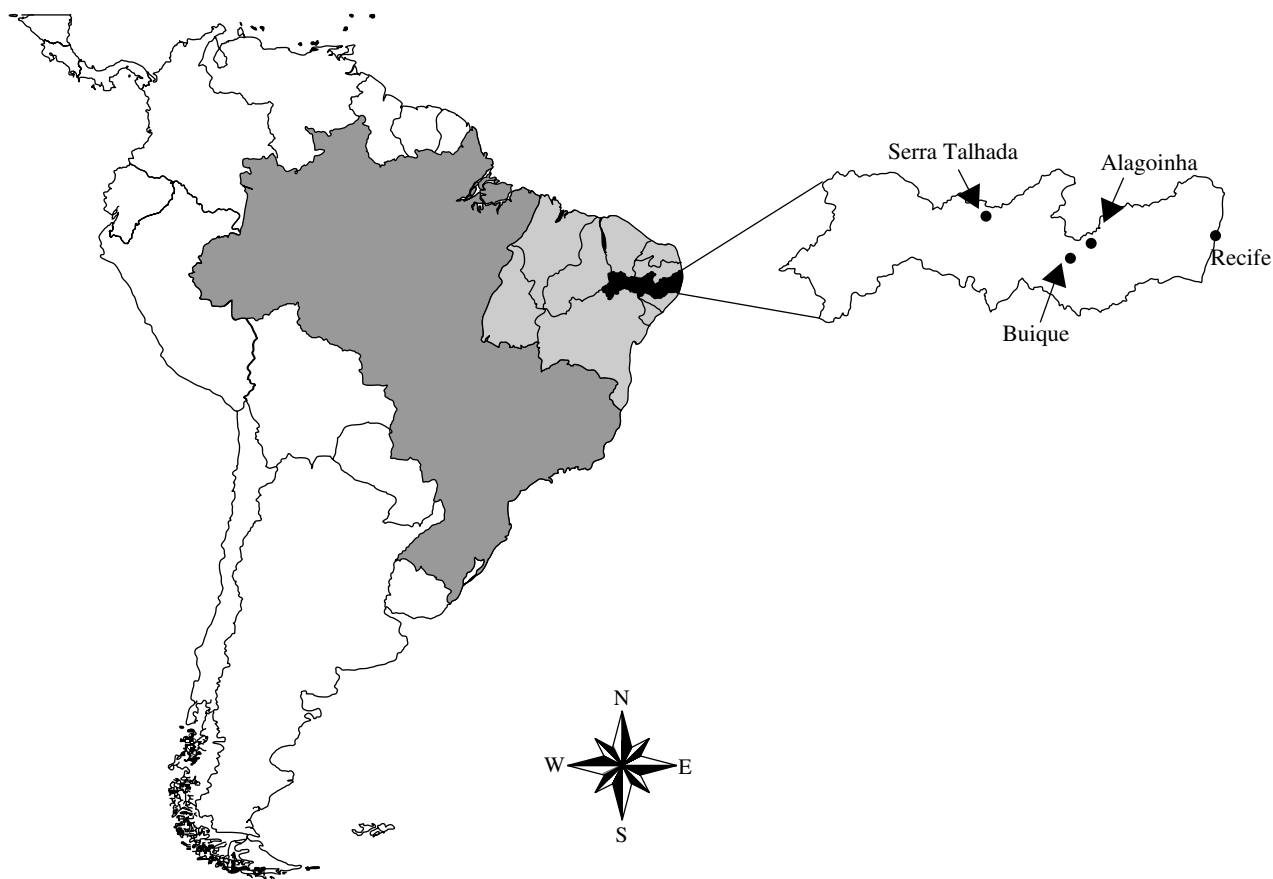


FIG. 1. Location of the studied sites (arrows) in Pernambuco state (detail), Northeast Region (light grey) of Brazil (dark grey).

Floral traits, rewards and pollination systems

The pollination system of 142 species (excluding five which do not fit in a specific pollination system) was first inferred by floral attributes and syndromes (*sensu* Faegri and Pijl, 1979), and for the majority of the species (99, or 69.7 %) it was confirmed by direct observations in the field. In these cases the time of observation for visitors/pollinators varied from 2–4 h up to more than 100 h. Independently of the number of hours, it was always at least the minimum time required in order to allow us to distinguish between the behaviour of a simple visitor and a pollinator. With regard to the remaining 43 species studied: (a) 12 (8.5 %), in spite of a lack of field observations, are without doubt pollinated by bees; they belong to genera largely known to be bee-pollinated whose species offer pollen in poricidal anthers (four *Solanum* spp. and four *Senna* spp.) or oil (four Malpighiaceae spp.; see Appendix); and (b) 31 species (21.8%) were studied from specimens deposited in herbaria, and literature sources (see Andrade-Lima, 1989; Machado, 1996; Machado and Lopes, 2002; and references therein). Field trips occurred five to six times per year, each one lasting 3–5 days, from January 1994 to September 2002.

For each species, floral attributes were recorded as form, size, colour and floral rewards. For some species,

observations were made related to the floral biology, including the behaviour of the visitors and pollinators. During the field studies, flowers and buds were fixed in ethanol (70 %) and/or FAA (50 %).

Flowers were classified according to floral types ('structural blossom classes') modified from Faegri and Pijl (1979). Eight floral types were considered: (1) tube; (2) gullet; (3) dish; (4) brush; (5) flag; (6) bell-funnel; (7) chamber; and (8) inconspicuous (<4 mm). The flower measurements (length and width) were taken from approx. 10–20 flowers per species. Flowers were classified as (1) small, ≤ 10 mm; (2) medium, $>10 \leq 20$ mm; (3) large, $>20 \leq 30$ mm; and (4) very large, >30 mm. Seven categories of flower colours were considered with regard to the main, most conspicuous, colour: (1) white; (2) red; (3) greenish (including beige, cream); (4) yellow; (5) orange; (6) lilac/violet (including blue); and (7) rose (light and pink).

Pollination units and the organization of the flowers and inflorescences were characterized according to Ramirez *et al.* (1990): (1) individual, when each flower is visited/explored individually; (2) collective, when the visitors explore and contact simultaneously with more than one flower; and (3) intermediate, when the visits are individual or collective according with the size and behaviour of the visitor/pollinator.

Five classes of floral resources were considered: (1) pollen; (2) nectar; (3) oil; (4) resin; and (5) pollen/nectar. In each class (excepting the last) only the main used resource was considered.

The species were also grouped into guilds according to the main pollinator vector: (1) wind; (2) medium-large bees (≥ 12 mm); (3) small bees (<12 mm); (4) wasps; (5) butterflies; (6) moths; (7) hawkmoths; (8) flies; (9) beetles; (10) diverse small insects; (11) hummingbirds; and (12) bats.

Statistical analysis

Analysis of the frequencies of the floral traits and pollination systems were tested by the *G*-test using the software BioEstat 2.0 (Ayres *et al.*, 2000).

RESULTS AND DISCUSSION

Floral traits, rewards and pollination systems

The floral attributes varied largely with respect to colour, types, symmetry and size.

Colour. A high proportion of species with colourful flowers were observed: 62.8 % (including red, yellow, orange, lilac/violet and rose) compared with 37.2 % of species with pale flowers (white and greenish, including cream and beige). Yellow flowers were the most frequent (25.0 %), followed by white (22.2 %) (Fig. 2A). In contrast to these results, flowers of pale colours have been reported to be prevalent for savanna communities in Brazil (Table 1), for Venezuelan shrubland (Table 1) and also for humid forests (Mantovani and Martins, 1988; Silva *et al.*, 1997).

Types and symmetry. A great variation of floral types was observed with a predominance of dish flowers (25.7 %), followed by tube (22.9 %) and flag types (15.3 %) (Fig. 2B). The high percentage of flag flowers was due to the high number of Leguminosae species.

The high frequency of tube and flag flowers contributed greatly to the high frequency of flowers whose floral reward is not easily available to visitors, which corresponded to

43.1 % of the species studied (represented by tube, gullet and flag flower types).

Actinomorphic flowers were found in the majority of the species (61.7 %), mainly due to tube and dish flowers (together with chamber, brush and inconspicuous types), with the remaining 38.3 % corresponding to zygomorphic species. Ramirez *et al.* (1990) also registered a high frequency of species with radial flowers (54.6 %), in comparison to 12.7 % with irregular and 32.7 % with bilateral flowers.

Sizes. Most of the species (54.1 %) had large (11.1 %) to very large flowers (43.0 %). Species with small and medium

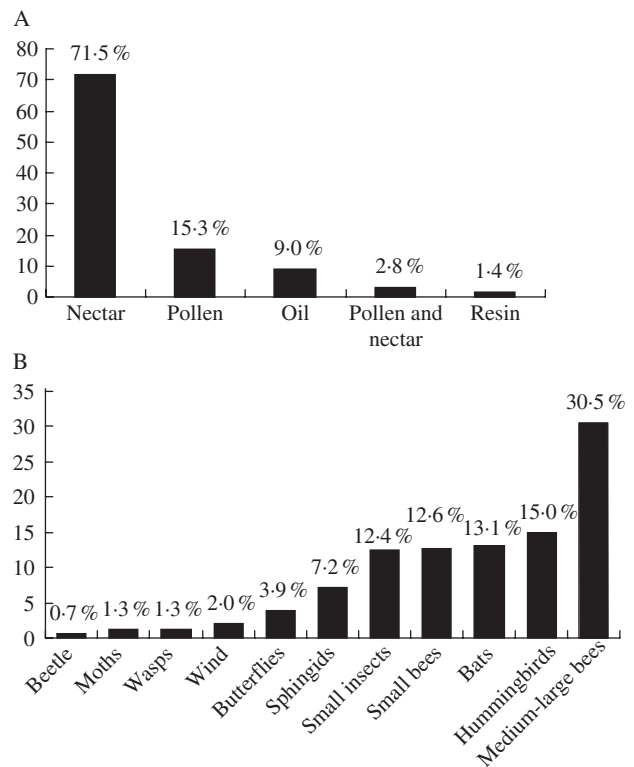


FIG. 2. Frequencies of (A) the floral colours and (B) types in Caatinga vegetation, northeastern Brazil.

TABLE 1. Frequency of colour categories in diverse neotropical ecosystems, as number of species (%)

Floral colours*	Dry forest – Caatinga (this study)	Dry forest – Cerrado (Silberbauer-Gottsberger and Gottsberger, 1988) ¹	Dry forest – Cerrado (Oliveira and Gibbs, 2000)	Shrubland (Ramirez <i>et al.</i> , 1990) ¹	Restinga (Ormond <i>et al.</i> , 1993) ²
Yellow	35 (25.0)	56 (23.2)	10 (17.0)	6 (10.9)	13 (9.6)
Orange	3 (2.1)	–	2 (3.4)	–	–
Greenish	21 (15.0)	63 (26.1)	11 (18.6)	9 (16.4)	37 (26.0)
Lilac/violet	25 (17.9)	46 (19.1)	4 (6.8)	10 (18.2)	25 (17.8)
Rose	9 (6.4)	–	3 (5.1)	–	–
Red	16 (11.4)	10 (4.2)	–	8 (14.5)	13 (8.9)
White	31 (22.2)	66 (27.4)	29 (49.1)	22 (40.0)	53 (37.7)

* Greenish including beige, cream; lilac/violet including blue and lilac-reddish; rose, including light rose and pink.

¹ Red including orange and rose.

² Data for nectariferous species only.

flowers were almost equally represented (23.7 and 22.2 %, respectively). *Pseudobombax marginatum* (Bombacaceae) and *Pilosocereus* spp. (Cactaceae) showed the largest flowers, whereas *Thiloua glaucocarpa* (Combretaceae) and *Maprounea* aff. *guianensis* (Euphorbiaceae) showed the smallest ones.

The size of the flowers is generally associated with the size of the respective pollinator (Opler, 1980). Some studies have shown correlations between the size of the floral tube and the size of the insects (Lindsey and Bell, 1985), the length of the proboscis (Real, 1983) or the length of the beak of the hummingbirds (Kodric-Brown *et al.*, 1984). With few exceptions, short-tube flowers, together with dish, brush and inconspicuous flowers, allow access to a great diversity of pollinators (Faegri and Pijl, 1979).

Bawa *et al.* (1985) reported that flowers with pale colours visited by small diverse insects were found to be smaller than 10 mm. Among the species we studied, small flowers were found to be pollinated by diverse small insects (*sensu* Bawa and Opler, 1975; Bawa *et al.*, 1985). However, when small flowers are organized in dense inflorescences it allows visits by medium-large bees, and also by bats and hummingbirds. For this reason, the generalist pollination system should not be inferred based only on the size of the flowers. Examples of species with small flowers which are, nonetheless, broadly attractive due to their organization in dense inflorescences are found in many Leguminosae, such as *Anadenanthera colubrina*, *Mimosa tenuiflora*, *Acacia farnesiana*, and *Parapiptadenia zehntneri*, as well as in other families such as Combretaceae (*Combretum hilarianum* and *C. pisonioides*), and Amaranthaceae (*Gomphrena vasa*).

Some relationships were observed between the size of the flowers and some colour classes. White and greenish flowers (including beige and cream) were generally smaller and tended to form collective units. This was also observed by Ramirez *et al.* (1990) in a tropical rain forest in Venezuela. In contrast, individually organized flowers were represented in practically all classes of colour and sizes, also corroborating what was found by Ramirez *et al.* (1990).

Pollination units. The individual pollination unit was the most representative, recorded in about 80.7 % of the species, compared with 14.5 % of collectivist and 4.8 % of intermediary types. Ramirez *et al.* (1990) also found the individual pollination unit as the most frequent in a tropical shrubby community in Venezuela. However, while the intermediate type was the least frequent in the present study, Ramirez *et al.* (1990) found a high percentage of species with this kind of pollination unit (27.3 %), with collectivists being the least common (9.1 %).

Floral resources. An interesting diversification of floral rewards was observed in the Caatinga vegetation, including very elaborate and unusual resources such as resin and oil. Nectar was the most frequent resource (Fig. 3A) at species (71.5 %), genus or family levels, similar to other studies in different ecosystems (Table 3; see also Percival, 1974; Silva *et al.*, 1997). This is related to the high percentage of species pollinated by nectar-seeking insects together with the ornithophilous and chiropterophilous species. Pollen flowers were registered in approx. 15.3 % of the species,

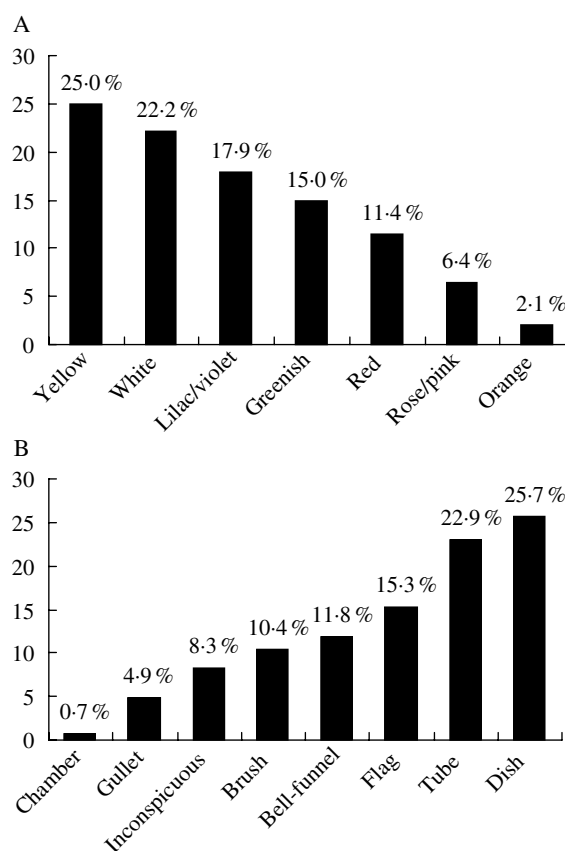


FIG. 3. Frequencies of (A) the floral rewards and (B) pollination systems in Caatinga vegetation, northeastern Brazil.

followed by oil (9.0 %), nectar and pollen (2.8 %) and resin (1.4 %) (Fig. 3A). Pollen flowers are mainly found in species of Leguminosae (*Senna*, *Chamaecrista*) and Solanaceae (*Solanum*). Pollen as a floral reward is offered mainly by species with poricidal anthers, pollinated by bees that vibrate during their visits (see Buchmann, 1983). This kind of anther dehiscence was found to occur in 11.0 % of all species investigated (the remaining 89 % of the species have longitudinal anther dehiscence), and all of them are pollinated by bees (Table 2). A higher frequency of species with poricidal anthers (30.9 %) was recorded by Ramirez *et al.* (1990), mainly due to the great number of species of Melastomataceae occurring at their study site, together with Ericaceae and Ochnaceae species.

In the present study, the percentage of flowers offering both pollen and nectar as a floral reward (pollen in this category being intentionally collected) was lower (2.8 %) than that recorded in other tropical shrubby communities (17.6 %, Silberbauer-Gottsberger and Gottsberger, 1988; 28.6 %, Ramirez *et al.*, 1990; Table 3).

Floral oils were mainly restricted to plant species of the herbaceous and shrubby strata, such as *Angelonia* spp. (Scrophulariaceae) (Vogel and Machado, 1991; Machado *et al.*, 2002), *Byrsonima* spp. (Malpighiaceae) and *Krameria tomentosa* (Krameriaceae) (Machado *et al.* 1997b). These species constitute an important food source for the larvae of

TABLE 2. Number of species of each pollination system with respect to floral traits

Floral traits	Pollination systems										
	Wind	Beetles	Wasps	Moths	Butterflies	Hawkmoths (Sphingids)	Hummingbirds	Diverse small insects	Bats	Medium-large bees	Small bees
Floral Symmetry											
Actinomorphic	3	1	1	2	4	10	13	18	13	22	17
Zygomorphic	–	–	1	–	2	1	10	–	5	31	5
Floral reward											
Nectar	–	–	2	2	6	11	23	17	20	19	8
Resin	–	–	–	–	–	–	–	–	–	2	1
Oil	–	–	–	–	–	–	–	–	–	12	1
Pollen	–	1	–	–	–	–	–	–	–	18	9
Nectar/pollen	–	–	–	–	–	–	–	2	–	–	2
Floral shape											
Bell-funnel	–	–	–	–	–	2	–	–	7	7	2
Tube	–	–	–	1	5	3	19	–	1	2	2
Dish	3	–	2	–	–	1	1	6	2	20	10
Pseudanthus	–	–	–	–	–	–	–	–	–	1	1
Flag	–	–	–	–	–	–	2	–	2	17	2
Gullet	–	–	–	–	–	–	–	–	1	4	2
Brush	–	–	–	1	1	5	–	3	7	1	2
Inconspicuous Chamber	–	1	–	–	–	–	–	10	–	–	1
Anther dehisc.											
Longitudinal	3	1	2	2	6	11	23	18	20	37	16
Poricide	–	–	–	–	–	–	–	–	–	16	6
Floral size											
≤10 mm	3	–	1	1	4	–	1	17	1	2	5
>10 x ≤20 mm	–	1	–	1	2	–	6	1	1	12	4
>20 x ≤30 mm	–	–	–	–	–	2	4	–	2	7	1
>30 mm	–	–	1	–	–	8	11	1	13	25	10
Floral colour											
Lilac	–	–	–	–	1	–	2	1	–	15	8
Yellow	–	–	–	–	1	1	1	5	3	21	5
White	–	–	1	1	1	7	–	2	13	6	8
Greenish-cream	3	–	1	–	–	3	1	9	4	3	–
Red	–	–	–	1	–	–	14	1	–	1	–
Rose	–	–	–	–	2	–	4	1	–	1	1
Orange	–	1	–	–	1	–	1	–	–	–	–
Sexual systems											
Hermaphrodite – homostylous	–	1	1	2	5	11	21	7	20	41	12
Hermaphrodite – heterostylous	–	–	–	–	–	–	1	1	–	1	3
Dioecious	–	–	–	–	–	–	–	2	–	1	–
Monoecious	3	–	1	–	1	–	1	7	–	2	1
Andromonoecious	–	–	–	–	–	–	–	1	–	6	6
Poll. Unit											
Flower	–	1	1	1	2	11	23	3	19	49	18
Inflorescence (collectivist)	–	–	1	–	4	–	–	11	1	2	4
Flower/Inflorescence (intermediate)	3	–	–	1	–	–	–	4	–	1	–
Species of each pollination system*	3	1	2	2	6	11	23	19	20	66	

n = 142 species (99 with direct observation in the field for pollinators); 5 species which do not fit in a specific pollination system were excluded; 7 species pollinated by hawkmoths and bats, were included in both pollination systems; 3 species pollinated by wind and diverse small insects were included in both systems; 1 species, pollinated by bees and hummingbirds, was included in both systems; 9 species pollinated by small and medium-large bees were included in both.

anthophorid bees (Vogel, 1974) and are thus essential for the maintenance of this bee guild in the community.

In this study, floral resin was found to be offered by flowers of *Clusia nemorosa* and *Dalechampia* sp. Among angiosperms, resin is reported as a floral reward only in these two genera plus *Clusiella*, which are mostly distributed in humid areas (cf. Armbruster, 1984; Bittrich and

Amaral, 1997; Lopes and Machado, 1998). Thus, the presence of any species with resin flowers was surprising, due to their rarity and distribution.

Pollination systems. Insect pollination was the most frequent, occurring in approx. 69.9 % of the studied species, followed by hummingbird (15.0 %) and bat pollination

TABLE 3. Frequency of floral reward categories in diverse neotropical ecosystems, as number of species (%)

Floral rewards	Dry forest – Caatinga (this study)	Dry forest – Cerrado (Silberbauer- Gottsberger and Gottsberger, 1988)	Dry forest – Cerrado (Oliveira and Gibbs, 2000)	Shrubland (Ramirez <i>et al.</i> , 1990)	Restinga (Ormond <i>et al.</i> , 1993)*
Nectar	103 (71.5)	128 (45.9)	40 (70.2)	20 (40.8)	141 (62.0)
Pollen	22 (15.3)	46 (16.5)	11 (19.3)	13 (26.5)	–
Nectar + pollen	4 (2.8)	49 (17.6)	3 (5.3)	14 (28.6)	–
Oil	13 (9.0)	10 (3.6)	2 (3.5)	–	–
Resin	2 (1.4)	–	–	2 (4.1)	–
Floral parts	0	6 (2.2)	–	–	–
Without reward	0	40 (14.3)	–	–	–
Pollen + Petals	0	–	1 (1.7)	–	–
Total species	144	269	57	49	228

* Data for nectariferous species only.

TABLE 4. Percentage of pollination systems in this study and in other tropical communities

Pollination system	Dry forest – Caatinga (this study)	Dry forest – Cerrado (Silberbauer- Gottsberger and Gottsberger, 1988)	Dry forest – Cerrado (Oliveira and Gibbs, 2000)	Coastal vegetation – Restinga (Ormond <i>et al.</i> , 1993) ¹	Shrubland (Ramirez, 1989)	Rain forest (Bawa <i>et al.</i> , 1985)	Rain forest (Kress and Beach, 1994)	Dipterocarpaceae forest (Kato, 1996)
Wind	2.0	13.6	0.0	–	8.2	2.5	2.5	0.0
Beetles	0.7	2.8	2.0	–	2.7	7.3	12.7	2.4
Wasps	1.3	–	–	–	–	4.3	2.5	2.4
Moths	1.3	2.2 ²	12.0	29.8 ²	10.9 ²	7.9	8.0	2.4
Butterflies	3.9	–	0.0	–	–	4.9	4.3	2.4
Sphingids	7.2	2.2	–	4.5	–	8.0	–	–
Hummingbirds	15.0	1.8	2.0	5.4	12.3	4.3	14.9	–
Sunbird	0.0	–	–	–	–	–	–	9.8
Diverse small insects	12.4	–	49.0	–	–	15.8	11.2	2.4
Bats	13.1	1.8	3.0	2.1	–	3.0	3.6	0.0
Medium-large bees	30.5	65.2 ³	32.0	40.8 ³	56.2 ³	27.5	24.3	26.7
Small bees	12.6	–	–	–	–	14.0	14.1	44.0
Flies	0.0	10.4	–	17.8	9.6	–	1.8	7.3
Thrips	0.0	–	–	–	–	0.6	–	–

¹ Data for nectariferous species only; ² sum of percentages of moth and butterfly pollination systems; ³ sum of percentages of medium-large bees and small bees pollination systems.

(13.1 %) (Fig. 3B; Table 4). Among the entomophilous species, 61.7 % were considered to be melittophilous, with the remaining 38.3 % pollinated by diverse other groups of insects. Of the 34 families investigated, the only one lacking any entomophilous species was Tiliaceae (here represented only by one chiropterophilous species of *Luehea*). At the community level, the proportion of species pollinated by bees is the largest (43.1 %), similar to other tropical forest ecosystems (Table 4). The frequency of species pollinated by medium-large and small bees also agreed with those observed in other tropical ecosystems, where pollination by medium-large bees is the most representative (Table 4).

With respect to pollination systems other than entomophilous, we found a high percentage of ornithophilous and chiropterophilous species in comparison with Bawa *et al.* (1985), Silberbauer-Gottsberger and Gottsberger (1988) and Oliveira and Gibbs (2000) (Table 4). The level of ornithophily was, however, similar to some studies (Feinsinger, 1983; Linhart *et al.*, 1987; Ramirez, 1989;

Kress and Beach, 1994; Table 4). In humid tropical forests at least, ornithophily has been mentioned in the literature as occurring in approx. 10–15 % of the species of a local flora (Feinsinger, 1983; Linhart *et al.*, 1987; Kress and Beach, 1994; Buzato *et al.*, 2000). The percentage of bat-pollinated flowers was greater than in other studies (Table 4).

The most representative families with ornithophilous species at our sites were: Acanthaceae, Bromeliaceae, Cactaceae, Leguminosae, Passifloraceae, and Sterculiaceae. Eight species of hummingbird were recorded: *Amazilia fimbriata*, *A. lactea*, *A. versicolor*, *Chlorostilbon aureoventris*, *Chrysolampis mosquitus*, *Eupetomena macroura*, *Hylacharis sapphirina* and *Phaethornis gounellei*. These birds forage on different plant species, some of them visiting flowers that do not have typical attributes of the ornithophilous syndrome, such as the melittophilous flowers of *Melochia tomentosa* (Sterculiaceae) and *Lonchocarpus aff. campestris* (Leguminosae). Except for *Phaethornis gounellei*, the other hummingbird species are of the subfamily Trochilinae,

which is normally associated with opportunistic behaviour (Des Granges, 1978; Sick, 1997; Buzato *et al.*, 2000).

In contrast to generalist behaviour, hummingbirds were observed in the field to act as effective and exclusive pollinators in *Ruellia asperula* (Acanthaceae), species of Cactaceae (*Opuntia* spp. and *Melocactus* spp.) and Bromeliaceae (*Portea leptantha*, *Billbergia porteana* and others), *Passiflora luetzelburgii* (Passifloraceae), *Periandra coccinea* (Leguminosae), *Helicteres* spp. (Sterculiaceae).

Chiropterophilous species were found in Acanthaceae, Bombacaceae, Bromeliaceae, Cactaceae, Capparaceae, Convolvulaceae, Leguminosae, Passifloraceae and Tiliaceae (Machado *et al.*, unpubl.). These same families have other chiropterophilous species in many different ecosystems (e.g. Vogel, 1968; Dobat and Peikert-Holle, 1985; Sazima *et al.*, 1999).

Only one species (0.7%), belonging to the Annonaceae family, was found to be cantharophilous. Percentages of beetle pollination in the literature vary from 2% (Oliveira and Gibbs, 2000) to 12.7% (Kress and Beach, 1994) (Table 4).

Anemophilous species were also not numerous (Table 4), corresponding to 2% of the studied species. Wind pollination has been cited by Kress and Beach (1994) as including 2.5% of the flora of tropical forests. Bawa *et al.* (1985) also recorded 2.5% of wind-pollinated species among tropical lowland rain forest trees. Oliveira and Gibbs (2000) did not record any species pollinated by wind among woody plants in a Brazilian savanna. However, Silberbauer-Gottsberger and Gottsberger (1988), studying a different Brazilian savanna community, found wind pollination to occur in 13.6% of the species (Table 4).

Pollination systems × floral traits

Zygomorphic flowers were mostly found among hummingbird- and medium-large bee-pollinated species (Table 2) and, in fact, zygomorphy is largely known as a visual attractant for some groups of pollinators such as bees and hummingbirds (Faegri and Pijl, 1979; Endress, 1994; Proctor *et al.*, 1996). Conversely, flowers pollinated by wind and diverse small insects, for example, were 100% actinomorphic. Nocturnal flowers, pollinated by bats and hawkmoths mainly orientated by sonar (von Helversen, 1993) and olfactory cues, respectively were mostly actinomorphic, too.

With respect to floral rewards, resin and oil were always related to bee-flowers, as well as pollen-flowers; the latter, with the exception of one beetle-pollinated species, were also associated with bee pollination. In fact resin and oil are strictly related to bee-flowers (Vogel, 1974; Armbruster, 1984). Flowers offering both nectar and pollen were, as expected, pollinated by diverse small insects, including small bees. Nectar, known as the most widespread floral resource (e.g. Faegri and Pijl, 1979; Endress, 1994; Proctor *et al.*, 1996), was recorded in all classes of pollination systems. In most of the cases it was the only offered reward, as for hawkmoth-, bat- and hummingbird-pollinated species.

Associations were observed between floral shape and the pollination system. The great majority of hummingbird- and

butterfly-pollinated flowers were of the tube type; most of the diverse small insect-pollinated flowers were inconspicuous; bat-pollinated species had mainly bell-funnel or brush flowers, and bee-pollinated flowers were mainly of the dish or flag type.

Regarding floral size and colour, the frequency of small flowers visited by diverse small insects was significantly different from the frequencies of medium and large flowers visited by this group of pollinators ($G = 26.19$; $P < 0.001$, $DF = 2$; Table 2). Significant differences were also observed in the frequency of greenish-cream and yellow flowers visited by diverse small insects compared with those of other colour categories ($G = 14.61$; $P = 0.012$; $DF = 5$; Table 2). These small insects showed a preference for grouped flowers, forming collectivist pollination units, when compared with the other kinds of pollination units ($G = 5.93$; $P < 0.05$; $DF = 2$; Table 2).

Studies in lowland tropical forests show that the frequencies of flower colours by themselves are not significantly related to the pollination systems (Momose *et al.*, 1998; see also Johnson and Steiner, 2000 for a review). In fact if the frequency of any single floral attribute is used to study the frequencies of pollination systems, then the influence of other attributes is neglected. Nonetheless, it is apparent that some pollinators preferentially visit flowers of some colours (or have preference for some other attribute as mentioned above). For example, our results show that among the species visited by hawkmoths and bats, white flowers predominated, a result also found in other studies (Muchhala and Jarrín-V, 2002). Similar relationships are observed for hummingbirds and red flowers, and medium-large bees and yellow flowers, although these colours are visited by other animals, too (Table 2).

CONCLUDING REMARKS

The range of pollination characters in Caatinga species is similar to other tropical forests. Specialized pollination mechanisms were found to be common in the Caatinga, although more generalization might have been expected for an open vegetation with extreme climatic conditions (low and irregular precipitation). Examples are the existence of a relatively high percentage (9.0%) of oil flower species; the high percentage of vertebrate pollination (28.1%) and the also great number of species (43.1%) with hidden floral rewards (represented by the types tube, gullet and flag).

To avoid misinterpretation and to check if our values for pollination systems really reflect a typical Caatinga community, 19 species occurring only in Buíque, a special type of Caatinga (Rodal *et al.*, 1998) were removed from the analyses. The differences in the results were not found to be significant (pollination systems $G = 0.42$, NS; floral colours $G = 7.57$, NS; floral rewards $G = 4.2$, NS), showing the similarity of the floral traits and pollination systems between the different physiognomies of the Caatinga. The observed floral features obviously reflect the characteristic plant families and their adaptations, and are not a product of selective forces.

Some preconceptions about Caatinga biodiversity, such as ‘the Caatinga biome is homogeneous and poor in species and endemisms’, are proving to be false on closer study (MMA, 2002). Our results show the diversity and uniqueness of this vegetation type in the reproductive biology of its plants, a subject of critical importance in the urgent task of conservation.

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APPENDIX

Families and genera of the species studied. Species followed by an asterisk were observed in the field for pollinators.

Acanthaceae (2 genera/4 species)

Harpochilus nessianus Mart.*
Ruellia asperula (Nees) Lindau*
Ruellia aff. *paniculata* L.*
Ruellia sp.*

Amaranthaceae (1/1)

Gomphrena vaga Mart.

Anacardiaceae (3/3)

Myracrodruon urundeuva Allemão*
Schinopsis brasiliensis Engl.
Spondias tuberosa Arruda*

Annonaceae (1/1)

Rollinia leptopetala R.E. Fries*

Apocynaceae (3/4)

Aspidosperma pyrifolium Mart.*
Allamanda blanchetii A. DC.
Allamanda sp.
Mandevilla tenuifolia (Mikan) Woodson

Bignoniaceae (2/2)

Tabebuia impetiginosa (Mart. ex DC.) Standl.
Anemopaegma sp.

Bombacaceae (2/2)

Pseudobombax marginatum (A. St.-Hil.) A. Robyns*
Ceiba glaziovii (Kuntze) K. Schum.*

Boraginaceae (1/2)

Cordia globosa (Jacq.) Kunth*
C. leucocephala Moric.*

Bromeliaceae (6/8)

Dyckia pernambucana L.B.Sm.*
Billbergia porteana Brongn.*
Encholirium spectabile Mart. ex Schult.f.*
Neoglaziovia variegata (Arr.Cam.) Mez.*
Portea leptantha Harms*
Tillandsia gardneri Lindl.*
T. loliacea Mart. ex Schult.
T. streptocarpa Baker

Burseraceae (1/1)

Commiphora leptophloeos (Mart.) J.B. Gillett

Cactaceae (5/11)

Cereus jamacaru DC.*
Harrisia adscendens (Gürke) Britton & Rose
Melocactus bahiensis (Br. Et Rose) Werderm.*
M. zehntneri (Britton & Rose) Luetzelburg*
Opuntia inamoena K. Schum.*
O. palmadora Britton & Rose*
Pilosocereus catingicola (Gürke) Byles & G.D. Rowley*
P. chrysostele (Vaupel) Byles & G.D. Rowley*
P. gounellei (F.A.C.Weber) Byles & G.D. Rowley*
P. pachycladus (Werderm.) Byles & G.D. Rowley*
P. tuberculatus (Werderm.) Byles & G.D. Rowley*

Capparaceae (1/4)

Capparis hastata Jacq.*
C. flexuosa (L.) L.*
C. jacobinae Moric. ex Eichler*
C. yco (Mart.) Eichler

Clusiaceae (1/1)

Clusia nemorosa G. Mey.*

Combretaceae (2/4)

Combretum hilarianum D. Dietr.
C. leprosum Mart.*
C. pisonioides Taub.*
Thiloa glaucocarpa (Mart.) Eichler

Convolvulaceae (4/7)

Evolvulus sp.
Ipomoea acuminata (Vahl) Roem. & Schult.
Ipomoea sp.1
Ipomoea sp.2
Jacquemontia densiflora (Meissn.) Hall.
Merremia aegyptia L. Urban*
Merremia sp.

Euphorbiaceae (8/12)

Acalypha multicaulis Müll. Arg.
Cnidocolus urens (L.) Arthur*
Croton argyrophyloides Müll. Arg.*
C. sonderianus Müll. Arg.*
Croton sp.
Dalechampia sp.*
Euphorbia comosa Vell.
Jatropha mollissima (Pohl.) Baill.*
J. mutabilis (Pohl.) Baill.*
J. ribifolia (Pohl.) Baill.*
Manihot cf. *pseudoglaziovii* Pax & K. Hoffm.
Maprounea aff. *guianensis* Aubl.

Krameriaceae (1/1)

Krameria tomentosa A. St.-Hil.*

Lamiaceae (1/1)*Hyptis martiusii* Benth.**Leguminosae* (15/29)

Acacia farnesiana (L.) Willd.*
Amburana cearensis (Allemão) A.C. Sm.
Anadenanthera colubrina var. *cebil* (Griseb.) Altschul.
Bauhinia acuruana Moric.*
B. cheilantha (Bong.) Vogel ex Steud.*
B. pentandra (Bong.) Vogel ex Steud.*
Caesalpinia ferrea Mart. ex Tul.*
C. pyramidalis Tul.*
Calliandra aescynomenoides Benth.*
Chamaecrista cytisoides (Collad.) Irwin & Barneby*
Chamaecrista ramosa (Vogel) Irwin & Barneby*
Chamaecrista sp.1*
Cratylia mollis Mart. ex Benth.*
Erythrina velutina Willd.*
Lonchocarpus aff. *campestris* Benth.*
Mimosa lewisii Barneby*
M. tenuiflora (Willd.) Poir.
Parapiptadenia zehntneri (Harms) M.P. Lima & H.C. Lima*
Periandra coccinea (Schrad.) Benth.*
Senna acuruensis (Benth.) Irwin & Barneby*
S. angulata (Vogel) Irwin & Barneby*
S. chrysocarpa (Desv.) Irwin & Barneby*
S. macranthera (Collad.) Irwin & Barneby*
S. martiana (Benth.) Irwin & Barneby*
S. rizzini Irwin & Barneby*
S. spectabilis (DC.) var. *excelsa* (Schrad.) Irwin & Barneby*
S. splendida (Vogel) Irwin & Barneby*
S. trachypus (Benth.) Irwin & Barneby*
Zornia sericea Moric.

Malpighiaceae (5/7)

Banisteriopsis schizoptera (A. Juss.) B. Gates
Byrsonima gardneriana A. Juss.*
Byrsonima vacciniaefolia A. Juss.*
Byrsonima sp.
Janusia anisandra (Juss.) Griseb.
Heteropteris sp.
Stigmaphyllon paralias A. Juss.*

Malvaceae (4/5)

Bakeridesia pickelii Monteiro*
Herissantia tiubae (K.Sch.) Briz.*
Pavonia humifusa A. St.-Hil.
P. martii Mart. ex Colla*
Sida sp.*

Orchidaceae (2/2)

Cyrtopodium intermedium Brade*
 Indet. sp. 1*

Passifloraceae (1/4)

Passiflora foetida L.*
P. luetzelburgii Harms*

Passiflora sp.1**Passiflora* sp.2*Rhamnaceae* (1/1)*Ziziphus joazeiro* Mart.**Rubiaceae* (2/2)

Coutarea hexandra (Jacq.) K. Schum.
Tocoyena formosa (Cham. & Schltdl.) K. Schum.*

Sapindaceae (2/2)

Allophylus quercifolius (Mart.) Radlk.
Serjania comata Radlk.*

Sapotaceae (1/1)*Bumelia sartorum* Mart.**Scrophulariaceae* (3/7)

Angelonia bisaccata Benth.*
A. cornigera Hook.*
A. hirta Cham.*
A. hookeriana Gardn.*
A. pubescens Benth.*
Bacopa sp.*
Stemodia sp.*

Solanaceae (2/7)

Nicotiana tabacum L.
Solanum asperum Rich.
S. baturitense Huber*
S. crinitum Lam.
S. gardneri Sendtn.
S. paludosum Moric.*
S. variabile Mart.

Sterculiaceae (3/4)

Helicteres mollis K. Schum.*
H. velutina K. Schum.*
Melochia tomentosa L.*
Waltheria rotundifolia Schrank*

Tiliaceae (1/1)*Luehea* sp.**Turneraceae* (1/2)

Turnera diffusa Willd. ex Schult.*
Turnera sp.

Verbenaceae (2/3)

Lantana camara L.*
Lippia gracilis Schau.*
L. schomburgkiana Schau.

Violaceae (1/1)*Hybanthus calceolaria* (L.) G.K. Schulze.*