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# Phenology and dispersal modes of wood species in the Carrasco, a tropical deciduous shrubland in the Brazilian semiarid

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**Abstract**   We provide, for the first time, data on phenology and dispersal modes for the Carrasco, a tropical deciduous shrubland in the Brazilian semiarid. The study was conducted in the Serra das Almas Reserve (5°8′45″S, 40°55′43″W), northeastern Brazil. We sampled 2,790 individuals from 39 species, 30 genera, and 17 families. Fabaceae, Euphorbiaceae, and Myrtaceae were the most representative. All species lose leaves, fully or partially, during the dry season. Leaf flush was observed to increase at the end of the dry season with a peak during the rainy season. Similarly, the peak of flowering/fruiting occurred at the end of the dry and the beginning of the rainy season. Air humidity and maximum temperature were the only variables correlated with leaf flush. Most species showed annual flowering/fruiting. Flowering lasted 2–5 months, but even longer fruiting periods were observed. Zoochory was the most frequent dispersal mode, followed by autochory. Zoochoric, barochoric, and autochoric species fruited throughout the year, while for anemochorics fruiting occurred at the end of the rainy and/or during dry season. Despite both, the Carrasco and the Caatinga are deciduous, the Carrasco has a greater intensity and duration of phenological events and a higher frequency of zoochory, thus being more similar to less arid ecosystems. We discuss the local implications of these patterns, as well as how our results are in accordance with other regional and global studies with similar approaches.

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## Introduction

The timing, length, and synchrony of phenophases have major implications for plant
community structure, functioning, and regeneration, as well as, for the quantity and quality
of resources available for consumers (Williams et al. 1999). Although vegetative and
reproductive phenological cycles may be determined by specific genetic factors, the
physical environment controls the possibility of their expression (Seghieri et al. 2009). The
abiotic factors that trigger and regulate the duration and intensity of plant phenophases are
primarily temperature, photoperiod, and water availability (e.g., Smythe 1970; Frankie
et al. 1974; Opler et al. 1976; Borchert 1983; Van Schaik et al. 1993; Ferraz et al. 1999).
Thus, to reasonable describe plant phenological patterns and correlate them with the
regulatory factors it is crucial to understand the temporal dynamics of biological
communities.

In the tropics and subtropics, phenological events are mainly related to the distribution
of annual rainfall (Van Schaik et al. 1993) and soil moisture conditions (Sing and
Kushwaha 2005), whereas, in temperate zones, in general, the alternation of the pheno-
phases occurs when certain limits of temperature and photoperiod are exceeded (e.g.,
Larcher 2000; Sakai 2001). Although in some ecosystems as rainforests the phenological
patterns are not very seasonal due to the constant warm and humid climate (Rathcke and
Lacey 1985; Reich 1995; Morellato 2003), in seasonal tropical climates there is a greater
synchrony between phenological events and the rainy season, especially regarding leaf and
flower production, and the greater the seasonality, the greater is this synchrony (e.g.,
Frankie et al. 1974; Janzen 1976; Bullock and Solis-Magallanes 1990; Williams et al.
1997; Eamus 1999; Silberbauer-Gottsberger 2001; Batalha and Martins 2004). Actually,
the structure and ecophysiological properties of seasonal tropical ecosystems are closely
determined by the duration and seasonality of the dry period, which selects adaptations
associated with avoidance, resistance, or tolerance to water stress (Sing and Kushwaha
2005).

Indeed, hydric stress seems to be relevant for plant growing in savannas of the West
Africa, but this is not the only factor responsible for the triggering of vegetative and
reproductive phenophases (Seghieri et al. 1995). Instead, in these ecosystems just a small
proportion of the phenological variability of woody species is explained by rainfall and soil
moisture, other variables, as air humidity, influencing reproduction in dry areas (Seghieri
et al. 2009).

Studies on dispersal mechanisms have also shown that these can be associated with
climatic factors (e.g., Frankie et al. 1974; Fleming 1979; Gentry 1982; Wikander 1984;
Griz and Machado 2001), and probably the temporal patterns of water availability have the
greatest impact on plant propagation in tropical regions (Griz and Machado 2001).
Zoochory has been described as being the predominant mechanism (more than 80%) in
humid tropical forests (e.g., Fleming 1979; Gentry 1982), with a decrease in ecosystems
with dryer tropical climates (Gentry 1982).

In the Brazilian semiarid zone, the main limiting factor is water availability; the annual
rainfall is concentrated in just three or four consecutive months (Sampaio 1995; Barbosa
et al. 2006). The vegetation is a mosaic of physiognomic types occurring associated with
varying degrees of topoclimatic and edaphoclimatic aridity, thus differing with regard to

rainfall periodicity and soil moisture conditions (Araújo et al. 2005). This suggests that the phenological behavior and the dispersal modes in the vegetation types of this zone should also diverge. Phenological studies at community level will assist in the functional classification of the vegetation of this domain.

The vegetation that dominates the lowland areas of the crystalline basement complex in this zone is the Caatinga, a deciduous thorny savanna, well adapted to seasonal hydric shortage, occurring in shallow soils (see Cole 1960; Leal et al. 2003). The few studies on phenology (Oliveira et al. 1988; Pereira et al. 1989; Machado et al. 1997; Barbosa et al. 2003) and dispersal modes (Griz and Machado 2001; Barbosa et al. 2003; Tabarelli et al. 2003) carried out in the Caatinga show, as expected, that vegetative and reproductive phenological patterns are similar to those recorded in other dry and seasonal environments (see Frankie et al. 1974; Fleming 1979; Gentry 1982).

In addition to the Caatinga, in the Brazilian semiarid it is also found a dense, deciduous, spineless shrubland vegetation called Carrasco. It occurs at higher altitudes, around 700–900 m a.s.l., in arenosols chemically poor and deep, specifically in the Araripe highlands and Ibiapaba plateau (Araújo et al. 1998; Araújo and Martins 1999; Araújo et al. 1999, 2005). It differs also physiognomically and floristically from the Caatinga. In the Carrasco there is a higher density of woody individuals, and cacti and bromeliads are almost absent.

Accordingly, despite both of these vegetation types are deciduous, we expect that more humid areas, with higher altitudes, and deeper soils, as the Carrasco, will show a greater intensity and duration of phenological events and a higher frequency of zoochory, than Caatinga areas, thus being more similar to seasonal tropical vegetation in less arid climates. Thus, abiotic factors other than annual rainfall will probably be associated with phenological events.

To address this assumption we examined in this study the annual phenological behavior, both at species and community levels, and the dispersal spectrum in an area of Carrasco in the Brazilian semiarid. To our knowledge, beyond the analysis whether abiotic factors act as drivers of phenological events, this is the first study to describe the phenological patterns of this ecosystem. We use our results to discuss the local implications of these patterns, as well as to discuss how these results are in accordance with other regional and global studies with similar approaches.

## Methods

### Study site

The study was conducted from April 2004 to March 2005 in an area of Carrasco vegetation with an altitude of 700 m (5°8′45″S, 40°55′43″W – 5° 8′44.9″S, 40°55′40.5″W and 5°8′48.1″S, 40°55′40.5″W – 5°8′48.4″S, 40°55′42″W) in the Serra das Almas Natural Reserve, northeast Brazilian semiarid (Fig. 1). The average temperature at the study site in 2004 was 24.84°C and the annual rainfall was 1,173 mm. The mean annual minimum and maximum temperatures were $19.14 \pm 1.78$ and $33.6 \pm 3.85$°C, respectively. With the total precipitation and average monthly temperatures of 2004, an ombrothermic diagram was built according to Walter (1986) for determining the extent of the dry and wet periods (dry season—June to December, rainy season—January to May) (Fig. 2). The mean annual rainfall between 1978 and 2008 was 636.61 mm, the historical rainfall, and the air humidity in the area are represented in Figs. 3, 4, and 5.
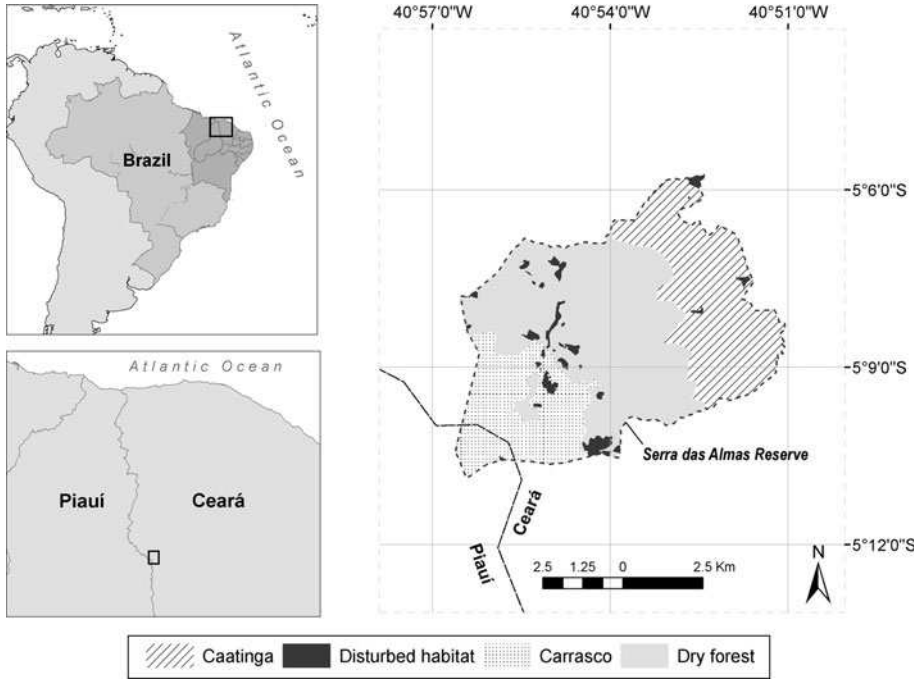
**Fig. 1** Map of Brazil (*up left*) showing the localization of the Study Site (*down left*), Serra das Almas Reserve (*right*), at the States of Ceará and Piauí. *Right figure* illustrates also the distribution of the vegetation types in the Reserve. The study was developed in the Carrasco vegetation (*dotted area*) in the municipality of Crateús, Ceará, Brazil
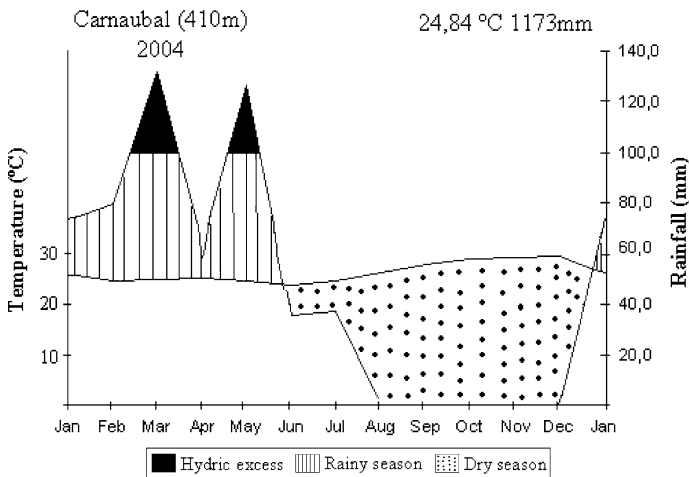


**Fig. 2** Ombrotermic graphic with data on temperature and rainfall in 2004 of the locality Carnaubal at the Ibiapaba plateau, Crateús municipality, Ceará State, Brazil
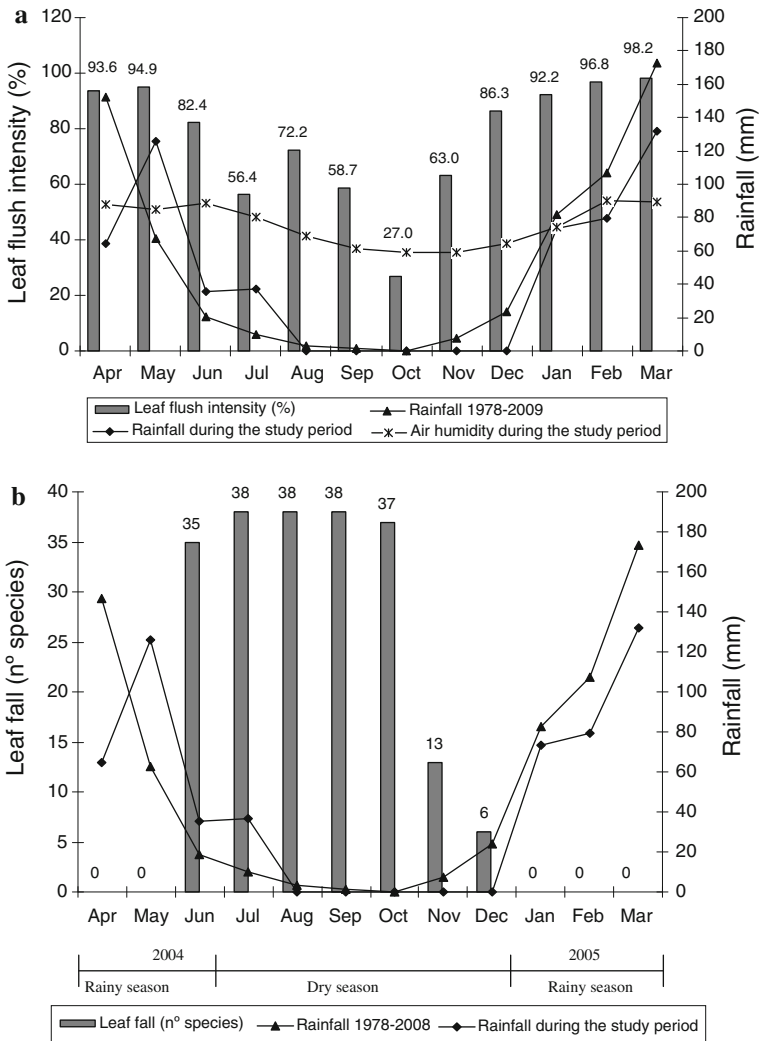
**Fig. 3** Leaf flush intensity by individuals/month (**a**) and number of species loosing leaves/month (**b**) during the period of April/2004–March/2005. Observe in (**a**) and (**b**) mean rainfall during 1978–2008 and during the study period in the Carrasco vegetation of the Ibiapaba plateau, Crateús municipality, Ceará State, Brazil. Air humidity during the study period is also represented in (**a**)

Phenology

To study the vegetative and reproductive phenophases, fruit attributes, and dispersal modes in the shrubby and tree community, we sampled and marked all individuals with perimeter at the ground level ≥9 cm, occurring within an area of 0.5 ha. The species were classified into families according to the APG II (2003).

Observations for registration of phenophases as leaf flush and fall, flowering, and fruiting were made monthly. For each individual we estimated the intensity of each phenophase using the semiquantitative scale interval proposed by Fournier (1974), which
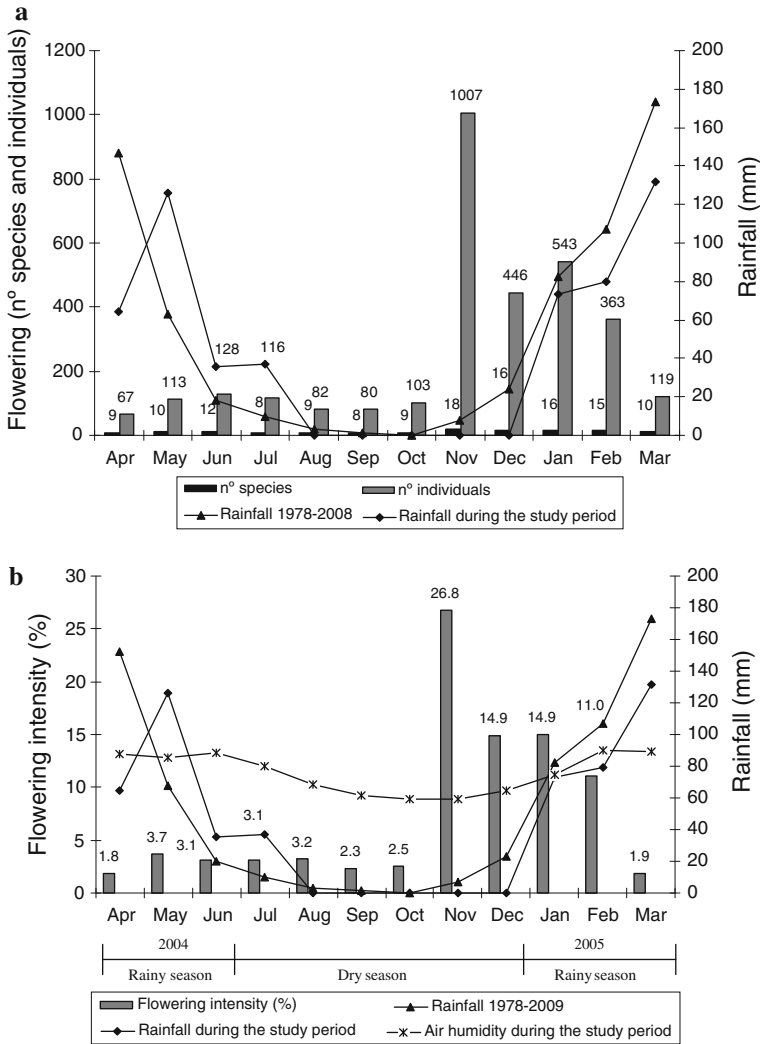
**Fig. 4** Number of flowering species and individuals/month (**a**) and flowering intensity of the individuals/month (**b**) during the period of April/2004–March/2005. Note also in (**a**) and (**b**) mean rainfall during 1978–2008 and during the study period in the Carrasco vegetation of the Ibiapaba plateau, Crateús municipality, Ceará State, Brazil. Air humidity during the study period is also represented in (**b**)

considered five categories (0–4) at intervals of 25% between each category. To verify the frequency and duration patterns of flowering and fruiting in both the species and community levels we used the classification of Newstrom et al. (1994) and considered the following categories: (1) annual (one cycle per year), (2) sub-annual (more than one cycle per year), and (3) continuous (with short interval periods in 1 year).

Proposals of Newstrom et al. (1994) were also used for the phenophase length criterion, which refers to the amplitude of time (months) of each phenophase, and recognizes three classes: (1) brief (<1 month), (2) intermediate (2–5 months), and (3) extended (>5 months). The length of flowering or fruiting was determined as the period beginning
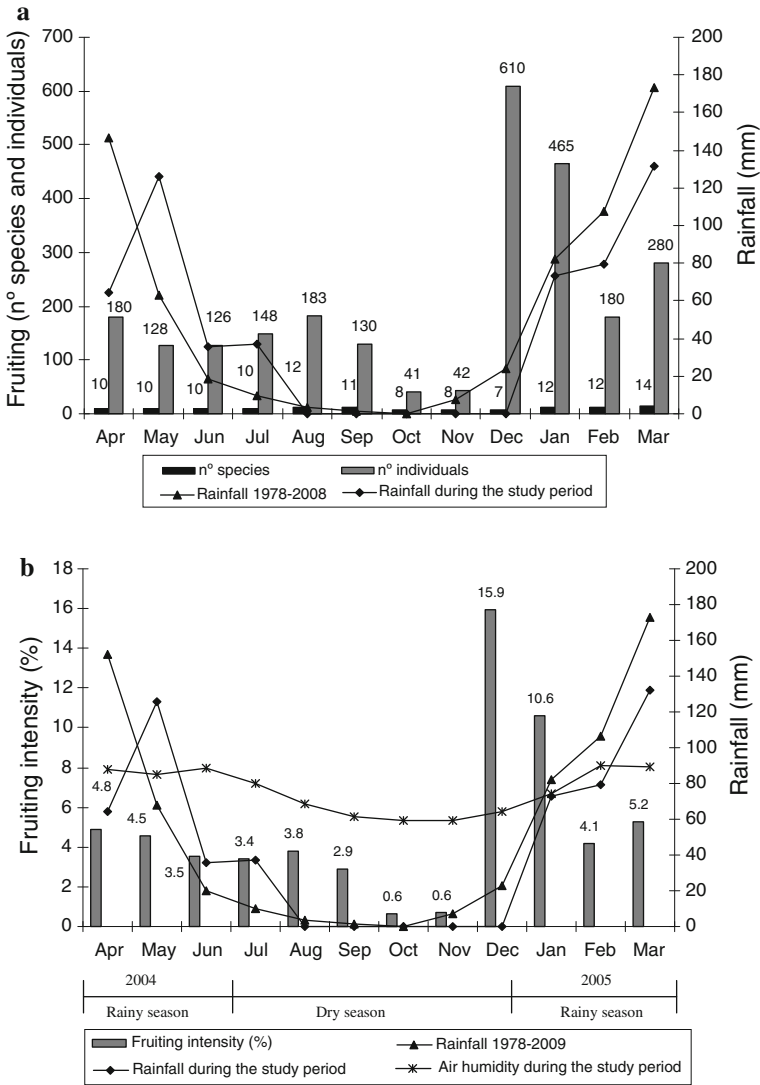
**Fig. 5** Number of fruiting species and individuals/month (**a**) and fruiting intensity of the individuals/month (**b**) during the period of April/2004–March/2005. Observe also in (**a**) and (**b**) mean rainfall during 1978–2008 and during the study period in the Carrasco vegetation of the Ibiapaba plateau, Crateús municipality, Ceará State, Brazil. Air humidity during the study period is also represented in (**b**)

when the first individual entered the phenophase and ending when the last individual left it (Silberbauer-Gottsberger 2001).

To verify the relationship between leaf flush, flowering, and fruiting phenophases with mean annual rainfall, temperature (mean, maximum, and minimum), and air humidity, Spearman or Pearson correlations were carried out depending on data normality. Data normality was checked using a Lilliefors' test.

Types of fruit and dispersal modes

Fruits were classified using the categories proposed by Spjut (1994). Fruit and seed size categories followed Tabarelli and Peres (2002): (1) small fruits/seeds (<0.6. cm in length), (2) medium sized (0.6–1.5 cm), (3) large (1.6–3.0 cm), and very large (>3.0 cm). The dispersal modes were classified based on attributes according to Pijl (1982) as fruit type, texture, and color, and were grouped as biotic (zoochory: ornithochory, mammaliochory, and myrmecochory) or abiotic (anemochory, barochory, and autochory, the latter being also called ballistic dispersal by the author). In addition to field observations, information from the literature (only published and referenced) and from specimens deposited in the Herbarium EAC of the Federal University of Ceará were also compiled to verify fruit attributes (color, type, dehiscence, size), dispersal modes, and dispersal units (fruit or seed) of the species.

## Results

We marked 2,790 individuals belonging to 39 species, 30 genera, and 17 families (Table 1). The families with highest species richness were: (1) Fabaceae [12 spp. or 30.7%: Caesalpinioideae with 8 spp. (20.5%), Faboideae with 1 spp. (2.5%), and Mimosoideae with 3 spp. (7.7%)], (2) Euphorbiaceae (6 spp.), (3) Myrtaceae (6 spp.), 15.3% each, and (4) Malvaceae (2 spp., 5.1%). The remaining families were only represented by a single species (Table 1). The most abundant species were: *Eugenia* sp. n. (*E.* aff. *dysenterica*) (959 individuals), *Bauhinia acuarana* (334), *Acacia langsdorfii* (263), *Eugenia* sp. (242) (Table 1).

Leaf flush and fall

Leaf buds were observed to increase at the end of the dry season with a peak in the first months of the rainy season. The presence of leaves was most intense in February and March (sensu Fournier 1974), and the community had more than 90% intensity from January to May, reaching almost 100% in March (Fig. 3a). Leaf flush was positively correlated with air humidity ($r = 0.7098$; $P = 0.0097$) and negatively correlated with maximum temperature ($\rho = -0.6783$; $P = 0.0153$). However, there was no correlation between this phenophase and rainfall ($r = -0.0825$; $P = 0.7986$), mean temperature ($r = -0.5462$; $P = 0.0661$), or minimum temperature ($r = 0.15$; $P = 0.6406$) during the study period. As to leaf flush, the community proved to be very seasonal with respect to leaf fall, and this phenophase was concentrated during the dry season, when all species lost leaves fully or partially (Fig. 3b). The lowest percentage of leaf coverage (27.0%) occurred near the end of this season, in October (Fig. 3a). Most species, 25 (64.1%) were deciduous, losing all its leaves from June to December. The remaining species were semi-deciduous, partially losing their leaves during the same period. The two most abundant species *Bauhinia acuarana* (334 stems, 12% of the community) and *Eugenia* sp. n. (*E.* aff. *dysenterica*) (959, 34.3%) lost their leaves mainly in September and October, respectively. However, after losing all leaves, *Eugenia* aff. *dysenterica* produced small leaf buds that developed during the first rainfall.

Flowering

During the study period 36 species (92.3%) produced flowers, but flowering was not observed in three species, *Copaifera martti* (4 individuals) *Maytenus* sp. (1) and *Alibertia* sp. (2; Table 1).

**Table 1** Studied species with total number of individuals (NI), number of flowering (Fl), and fruiting (Fr) individuals/month and duration of each phenophase in months in the Carrasco of the Ibiapaba plateau, Ceará State, Brazil

| Species | NI | | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Duration |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Annonaceae | 57 | Fl | | | | | 1 | | | 1 | | 23 | 3 | | 4 |
| *Rollinia leptopetala* R. E. Fr. | | Fr | | | | | | | | | | | | 4 | 1 |
| Apocynaceae | 12 | Fl | | | | | | 1 | | 11 | | | | | 2 |
| *Aspidosperma subincanum* Mart. | | Fr | | | | | | 1 | | | | | | 7 | 2 |
| Boraginaceae | 1 | Fl | | | | | | | | 1 | | | | | 1 |
| *Cordia rufescens* A. DC. | | Fr | | | | | | | | 1 | | | | | 2 |
| Burseraceae | 3 | Fl | | | | | | | | | 1 | | | | 1 |
| *Commiphora leptophloeos* (Mart.) J. B. Gillett | | Fr | | | | | | | | | | | | | – |
| Celastraceae | 1 | Fl | | | | | | | | | | | | | – |
| *Maytenus* sp. | | Fr | | | | | | | | | | | | | – |
| Eryrthroxylaceae | 53 | Fl | | | | | | | | 29 | 27 | 3 | | | 3 |
| *Erythroxylum* sp. nova | | Fr | 1 | | | | | | | | | 17 | 22 | 1 | 4 |
| Euphorbiaceae | 9 | Fl | 1 | | | | | | 6 | 1 | 4 | 5 | 4 | 6 | 7 |
| *Cnidoscolus vitifolius* (Mill.) Pohl | | Fr | 2 | | | | | | | 1 | | | | 1 | 3 |
| *Croton argyrophylloides* Müll. Arg. | 17 | Fl | | | | | | | | | | 15 | 7 | | 2 |
| | | Fr | | | | | | | | | | | | 7 | 1 |
| *Croton betaceus* Baill. | 3 | Fl | | | | | | 1 | | | | 1 | 1 | | 3 |
| | | Fr | | | | | | | | | | | | | – |
| *Croton zehntneri* Pax & H. Hoffm. | 35 | Fl | | | | | | | | | 8 | 31 | | | 2 |
| | | Fr | | | | | | 1 | | | | 12 | 9 | | 3 |
| *Sapium lanceolatum* (Müll. Arg.) Huber | 18 | Fl | | 2 | | | | | | | | 6 | 2 | | 3 |
| | | Fr | 9 | 1 | | | | | | | | | | | 2 |
| *Sebastiania brasiliensis* Spreng. | 2 | Fl | | | | | | | | | 1 | | | | 1 |
| | | Fr | 2 | 3 | | | | | | | | | 1 | | 3 |

**Table 1** continued

| Species | NI | | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Duration |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fabaceae (Caesalpinioideae) | 334 | Fl | 26 | 12 | 11 | 3 | 1 | | | 1 | | 106 | 146 | 70 | 9 |
| *Bauhinia acuruana* Moric. | | Fr | 96 | 94 | 82 | 106 | 54 | 27 | 1 | 1 | | 19 | 24 | 97 | 11 |
| *Copaifera martii* Hayne | 4 | Fl | | | | | | | | | | | | | – |
| | | Fr | | | | | | | | | | | | | – |
| *Hymenaea eriogyne* Benth. | 71 | Fl | 12 | | 9 | | | 6 | 7 | 43 | 45 | 34 | 33 | 19 | 9 |
| | | Fr | 42 | | 6 | 4 | 28 | 18 | 14 | 5 | 8 | 5 | 5 | 23 | 11 |
| *Hymenaea velutina* Ducke | 99 | Fl | | | | | 18 | 49 | 56 | 8 | 3 | | 2 | | 6 |
| | | Fr | 23 | 12 | 17 | 16 | 16 | 9 | 18 | 28 | 29 | 26 | 27 | 42 | 12 |
| *Senna cearensis* Afr. Fern. | 15 | Fl | 14 | 11 | 4 | 1 | | | | | | | 2 | 8 | 6 |
| | | Fr | | 8 | 10 | 11 | 11 | 3 | 1 | | | | | | 6 |
| *Senna gardneri* (Benth.) H. S. Irwin & Barneby | 25 | Fl | | 1 | 11 | 14 | 18 | 5 | | | | | | | 5 |
| | | Fr | | | 2 | | 6 | 2 | | | | | | | 3 |
| *Senna trachypus* (Benth.) H. S. Irwin & Barneby | 8 | Fl | | 3 | 4 | 2 | | | | | | | | | 3 |
| | | Fr | | 1 | 1 | 1 | 1 | 2 | | | | | | | 5 |
| *Swartzia flaemingii* Raddi | 9 | Fl | | | | | | | | | 1 | | | | 1 |
| | | Fr | | | | | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | 7 |
| Fabaceae (Faboideae) | 5 | Fl | | | 1 | | | | | | | | | | 1 |
| *Cratylia mollis* Mart. ex Benth. | | Fr | | | | | | | | | | | | | – |
| Fabaceae (Mimosoideae) | 263 | Fl | | | | 1 | | | 27 | 171 | 206 | 222 | 69 | 1 | 7 |
| *Acacia langsdorfii* Benth. | | Fr | | | | | | | | | 3 | 2 | 29 | 70 | 4 |
| *Mimosa verrucosa* Benth. | 105 | Fl | 1 | 71 | 75 | 84 | 37 | 13 | | 1 | | | | 1 | 8 |
| | | Fr | | 1 | 1 | | 57 | 63 | | | | | | | 4 |
| *Piptadenia moniliformis* Benth. | 110 | Fl | | | | | | | | 2 | | 54 | 87 | 5 | 4 |
| | | Fr | | | | | | | | | | | | 1 | 1 |
| Malpighiaceae | 99 | Fl | | | | | 1 | | 1 | 2 | 21 | 19 | 1 | | 6 |
| *Byrsonima gardnerana* A. Juss. | | Fr | | | | | | | 1 | | | 1 | 10 | 15 | 4 |

**Table 1** continued

| Species | NI | | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Duration |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Malvaceae | 1 | Fl | 1 | 2 | 1 | | 1 | | | | | | | | 4 |
| Helicteres muscosa Mart. | | Fr | | | | 1 | | | | | | | | | 1 |
| Waltheria brachypetala Turzc. | 6 | Fl | | 4 | 4 | 4 | 4 | 4 | | | | | | 2 | 6 |
| | | Fr | | | | | | | | | | | | | – |
| Myrtaceae | 24 | Fl | | | | | | | | 1 | 38 | | | | 2 |
| Campomanesia aromatica (Aubl.) Griseb. | 959 | Fr | | | | | | | | | | 1 | | 1 |
| Eugenia aff. dysenterica DC. | | Fl | | | | | 1 | | 1 | 684 | 54 | 8 | 1 | | 6 |
| | | Fr | | | | | 1 | | | | 517 | 344 | 31 | 1 | 5 |
| Eugenia punicifolia (Kunth) DC. | 1 | Fl | | | | | 1 | | 1 | 684 | 54 | 8 | 1 | | 6 |
| | | Fr | 1 | | 1 | 1 | | | | | | | | | 3 |
| Eugenia flavescens DC. | 30 | Fl | | | | | | | | | 1 | 13 | | | 2 |
| | | Fr | 3 | 3 | | | 1 | | | 2 | | 2 | 1 | 10 | 7 |
| Eugenia cf. vauthiereana O. Berg. | 3 | Fl | | | 1 | | | | | | | | | | 1 |
| | | Fr | | | | 1 | | | | | | | | | 1 |
| Eugenia sp. | 242 | Fl | | | | | | | | 33 | 24 | | 1 | | 3 |
| | | Fr | | | | | | | | | 31 | 33 | 20 | | 3 |
| Nictaginaceae | 42 | Fl | | | | | | | | 26 | | 2 | | | 2 |
| Guapira graciliflora (Schmidt) Lundell | | Fr | | 1 | | | | | | | 21 | 3 | | | 3 |
| Olacaceae | 1 | Fl | | | | | | | 1 | 1 | | | | | 2 |
| Ximenia americana L. | | Fr | | | | | | | | | | | | | – |
| Opiliaceae | 93 | Fl | | | | | | | 3 | 1 | | | | | 2 |
| Agonandra brasiliensis Miers ex Benth. & Hook. f. | | Fr | | | | | | | 3 | 1 | | | | | 2 |
| Rhamnaceae | 13 | Fl | 2 | 1 | 1 | | | | | | 1 | 1 | 4 | 1 | 7 |
| Colubrina cordifolia Reissek | | Fr | | 4 | 2 | 4 | 4 | | | | | | | | 4 |
| Rubiaceae | 2 | Fl | | | | | | | | | | | | | – |
| Alibertia sp. | | Fr | | | | | | | | | | | | | – |

**Table 1** continued

| Species | NI | | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Duration |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Rutaceae | 15 | Fl | 9 | 6 | 6 | 7 | | 1 | 1 | 1 | | | | 6 | 8 |
| *Zanthoxylun stelligerum* Turcz. | | Fr | 1 | | 4 | 3 | 3 | 3 | 2 | 2 | | | | | 7 |
| Total | 2,790 | Fl | 67 | 113 | 128 | 116 | 82 | 80 | 103 | 1,007 | 446 | 543 | 363 | 119 | _ |
| | | Fr | 180 | 128 | 126 | 148 | 183 | 130 | 41 | 42 | 610 | 465 | 180 | 286 | _ |

The period with the largest number of species and individuals flowering occurred from November to February, which is the end of the dry season and beginning of the rainy season (Fig. 4a; Table 1). November was the month with the highest number of species and individuals flowering (18 spp.; 1,007 stems; Fig. 4a) and with greatest intensity of flowering (26.8%; Fig. 4b) as well. Despite these variations, there was no significant correlation between the production of flowers and rainfall during the study period ($\rho = -0.3698$; $P = 0.2367$). The same was observed for this phenophase and air humidity ($\rho = -0.27$ $P = 0.39$), mean temperature ($\rho = 0.2268$; $P = 0.4844$), minimum temperature ($\rho = 0.2378$; $P = 0.4568$), and maximum temperature ($\rho = 0.1329$; $P = 0.6806$). The lowest number of individuals flowering occurred in April (67 or 2.4%), corresponding to nine species (23.1%; Fig. 4a).

Most species (21 or 53.8% of all species studied) showed the annual type of flowering (sensu Newstrom et al. 1994), while 13 (33.3%) were sub-annual, and two (5, 1%) had the continuous pattern (7.6%; Table 1). With regard to flowering duration, the majority (17 or 43.5%) had intermediate flowering, seven (17.9%) had brief flowering, and 12 (30.7%) had extended flowering (Table 1). The minimum duration of flowering was 1 month (*Cordia rufescens*, *Cratyllia mollis*, *Eugenia punicifolia*, *Eugenia* cf. *vauthiereana*, *Sebastiania brasiliensis*, *Commiphora leptophloeos*, and *Swartzia flaemingii*) and the maximum was 9 months (*Bauhinia acuarana* and *Hymenaea eryogine*) and intraspecific synchrony was recorded with respect to flowering (Table 1).

For some species the majority of the individuals flowered in the month subsequent to the loss of leaves, which were: *Mimosa verrucosa*, most individuals lost their leaves in June and flowered in July; *Eugenia punicifolia* lost their leaves in October and flowered in November; *Senna gardneri*, most individuals losing leaves in June and flowering in August and *Zanthoxylum stelligerum*, most individuals losing leaves in June and flowering in July.

Fruiting

The period with greatest amount of fruit (both immature and ripe fruits) occurred from December to March which, as with flowering, corresponds to the end of the dry season and beginning of the rainy season. Some species, however, had fruits throughout the year (Table 2; Fig. 5a). The peak of fruiting individuals (15.96%) occurred in December (Fig. 5b) subsequent to the flowering peak. Similar to flowering, there was no correlation between rainfall and fruiting ($\rho = -0.2682$; $P = 0.3991$) nor between this phenophase and air humidity ($\rho = 0.47$ $P = 0.12$), mean temperature ($\rho = -0.0839$; $P = 0.7954$), maximum temperature ($\rho = 0.1608$; $P = 0.6175$), or minimum temperature ($\rho = -0.4336$; $P = 0.159$). The lowest number of individuals bearing fruit per month was 41, belonging to eight species, in October, and the maximum was 610 individuals (7 spp.) in December (Fig. 5a). The largest number of fruiting individuals occurred in March and it did not coincide with the largest number of fruiting species. There were 14 species in the fruiting and only 286 individuals (Fig. 5a).

Most species (61.5%, representing 24 species) showed the annual type of fruiting, while five species (12.8%) were sub-annual, two (5.1%) had the continuous pattern and eight (20.5%) species had no fruit during the observation period, including the three that did not flower (Table 2). Regarding fruiting duration, six species (19.3%) had brief fruiting, most (18 or 58%) had intermediate, and seven (22.6%) had extended fruiting (Table 1). The minimum extension of fruiting was 1 month (*Rollinia leptopetala*, *Croton argyrophylloides*, *Piptadenia moniliformis*, *Campomanesia aromatica*, *Helicteres muscosa*, and *Eugenia* cf. *vauthiereana*), while the species *Bauhinia acuarana* and *Hymenaea eryogine* bore fruit

**Table 2** Studied species in the Carrasco of the Ibiapaba plateau, Ceará State, Brazil with fruit attributes as color, type (modified from Spjut 1994), dehiscence, fruit and seed sizes, dispersal mode (sensu Pijl 1982), dispersal unit, and references

| Species | Color | Type | Dehiscence | Fruit size[a] | Dispersal mode | Dispersal unit | Seed size[a] | References |
|---|---|---|---|---|---|---|---|---|
| **Annonaceae** | | | | | | | | |
| *Rollinia leptopetala* | Yellow[1] | Multiple fruit (follicle)[1] | No[1] | Large (1.9 cm length/ 0.6 cm width) [1] | Zoochory (ornitochory)[1] | Fruit[1] | Medium (0.7 cm length/0.5 cm width)[2] | 1—This study, 2—Pontes et al. (2004) |
| **Apocynaceae** | | | | | | | | |
| *Aspidosperma subincanum* | Brown[1] | Follicle[1] | Yes[1] | Very large (8 cm length/4 cm width)[2] | Anemochory[1] | Seed[1] | Very large (4.3 cm length/3 cm width)[2] | 1—This study, 2—Lorenzi (2002) |
| **Boraginaceae** | | | | | | | | |
| *Cordia rufescens* | Yellow | Drupe | No | Medium (0.9 cm diameter) | Zoochory (ornitochory) | Fruit | Medium | This study |
| **Burseraceae** | | | | | | | | |
| *Commiphora leptophloeos* | Greenish[1] | Septicidal capsule[2] | Yes[3] | Large (2 cm length/ 1 cm width)[3] | Zoochory (ornitochory)[1] | Seed[1] | Medium (1.0 cm length/0.7 cm width)[3] | 1—This study, 2—Griz and Machado (2001), 3—Lorenzi (2002) |
| **Celastraceae** | | | | | | | | |
| *Maytenus* sp. | Green[1] | Capsule[2] | Yes[2] | – | Zoochory (ornitochory)[1] | Seed[1] | Medium[1] | 1—This study, 2—Lorenzi (2002) |
| **Eryrthroxylaceae** | | | | | | | | |
| *Erythroxylum* sp. nova | Red | Drupe | No | Medium (1 cm length/0.5 cm width) | Zoochory (ornitochory) | Fruit | Medium | This study |
| **Euphorbiaceae** | | | | | | | | |
| *Cnidoscolus vitifolius* | Green | Schizocarp | Yes | Large (2 cm length/ 1.5 cm width) | Autochory (ballistic)/ myrmecochory | Seed | Large | This study |

**Table 2** continued

| Species | Color | Type | Dehiscence | Fruit size[a] | Dispersal mode | Dispersal unit | Seed size[a] | References |
|---|---|---|---|---|---|---|---|---|
| *Croton argyrophylloides* | Brown[1] | Schizocarp[2] | Yes[2] | Small (0.5 cm length/ 0.8 cm width)[1] | Autochory (ballistic)[2] | Seed[2] | Small[1] | 1—This study, 2—Griz and Machado (2001) |
| *Croton betaceus* | Brown | Schizocarp | Yes | Medium (0.9 cm length/0.7 cm width) | Autochory (ballistic) | Seed | Medium | This study |
| *Croton zehntneri* | Brown | Schizocarp | Yes | Small (0.5 cm length/ 0.4 cm width) | Autochory (ballistic) | Seed | Small | This study |
| *Sapium lanceolatum* | Brown | Schizocarp | Yes | Medium (1 cm length/1 cm width) | – | Seed | Medium | This study |
| *Sebastiania brasiliensis* | Brown[1] | Schizocarp[2] | Yes[3] | Medium (1.5 cm length/1 cm width)[3] | Autochory[2] | Seed[2] | Medium (0,6 cm length/0.5 cm width)[3] | 1—Backes and Irgang (2004), 2—This study, 3—Lorenzi (2002) |
| Fabaceae (Caesalpinioideae) | | | | | | | | |
| *Bauhinia acuruana* | Brown | Legume | Yes | Very large (15–20 cm length) | Autochory | Seed | Medium | This study |
| *Copaifera martii* | Brown[1] | Capsule[1] | Yes[1] | Large (2 cm length/ 2 cm width)[2] | Zoochory (ornitochory)[2] | Seed[3] | Medium (0.9 cm length/0.7 cm width)[2] | 1—This study, 2—Lorenzi (2002), 3—Backes and Irgang (2004) |
| *Hymenaea eriogyne* | Brown | Camara | No | Very large (17 cm length/7 cm width) | Barochory/ zoochory | Fruit | Very large | This study |
| *Hymenaea velutina* | Brown | Camara | No | Very large (17 cm length/7 cm width) | Barochory/ zoochory | Fruit | Very large | This study |
| *Senna cearensis* | Brown | Camara | No | Small (0.5 cm length/ 13 cm width) | Barochory/ zoochory | Fruit | Small | This study |
| *Senna gardneri* | Brown | Camara | No | Very large (11 cm length/1.2 cm width) | Barochory/ zoochory | Fruit | Medium | This study |

**Table 2** continued

| Species | Color | Type | Dehiscence | Fruit size[a] | Dispersal mode | Dispersal unit | Seed size[a] | References |
|---|---|---|---|---|---|---|---|---|
| *Senna trachypus* | Brown | Camara | No | Very large (13.5 cm length/1.6 cm width) | Anemochory | Fruit | Medium | This study |
| *Swartzia flaemingii* | Brown | Berry | No | Very large (9 cm length/6.5 cm width) | Barochory/ zoochory | Fruit | Very large | This study |
| Fabaceae (Faboideae) | | | | | | | | |
| *Cratylia mollis* | – | – | – | – | – | – | Medium | – |
| Fabaceae (mimosoideae) | | | | | | | | |
| *Acacia langsdorfii* | Brown | Legume | – | Very large (11 cm length/1.5 cm width) | – | Seed | Small | This study |
| *Mimosa verrucosa* | Brown[1] | Craspedium[2] | No[3] | Very large (2–5 cm length)[3] | Autochory (ballistic)[3] | Seed[3] | Small (0.5 cm length/0.3 cm width)[1] | 1—Lorenzi (2002), 2—Andrade-Lima (1989), 3—This study |
| *Piptadenia moniliformis* | Brown[1] | Legume[1] | Yes[1] | Very large (7–12 cm length)[2] | – | Seed[2] | Medium | 1—Backes and Irgang (2004), 2—This study |
| Malpighiaceae | | | | | | | | |
| *Byrsonima gardnerana* | Yellow | Drupe | No | Medium (0.6 cm length/0.6 cm width) | Zoochory (ornitochory) | – | Medium | This study |
| Malvaceae | | | | | | | | |
| *Helicteres muscosa* | Brown[1] | Septicidal capsule[1] | Yes[1] | – | Autochory (ballistic)[1] | Seed[2] | Medium[2] | 1—Griz and Machado (2001), 2— This study |
| *Waltheria brachypetala* | Brown | – | – | – | – | – | Small | This study |
| Myrtaceae | | | | | | | | |

**Table 2** continued

| Species | Color | Type | Dehiscence | Fruit size[a] | Dispersal mode | Dispersal unit | Seed size[a] | References |
|---|---|---|---|---|---|---|---|---|
| *Campomanesia aromatica* | Yellow | Berry | No | Small (0.5 cm length/ 0.4 cm width) | Zoochory (ornitochory) | Fruit | Small | This study |
| *Eugenia* aff. *dysenterica* | Yellow | Berry | No | Large (2.5 cm length/ 2 cm width) | Zoochory (ornito/mam) | Fruit | Large (1.8 cm length) | This study |
| *Eugenia punicifolia* | Red | Berry | No | Medium (1 cm length/0.6 cm width) | Zoochory (ornito/mam) | Fruit | Medium | This study |
| *Eugenia flavescens* | Yellow | Berry | No | Medium (0.6 cm length/0.9 cm width) | Zoochory (ornito/mam) | Fruit | Medium | This study |
| *Eugenia* cf. *vauthiereana* | Purple | – | – | – | – | – | – | This study |
| *Eugenia* sp. | Yellow | Berry | No | Very large (>3.0 cm length) | Zoochory (ornito/mam) | Fruit | Very large | This study |
| Nictaginaceae | | | | | | | | |
| *Guapira graciliflora* | Red[1] | Drupe[2] | No[2] | Medium (1.5 cm length/0.8 cm width)[2] | Zoochory (ornitochory)[2] | Fruit[2] | Small (1.2 cm length/0.5 cm width)[1] | 1—Lorenzi (2002), 2—This study |
| Olacaceae | | | | | | | | |
| *Ximenia americana* | Yellow | Drupe | No | Medium (1 cm length/0.8 cm width) | Zoochory | Fruit | Medium | This study |
| Opiliaceae | | | | | | | | |
| *Agonandra brasiliensis* | Green | Drupe | No | Large (2 cm length/ 1 cm width) | Zoochory (ornitochory) | Fruit | Large | This study |
| Rhamnaceae | | | | | | | | |

**Table 2** continued

| Species | Color | Type | Dehiscence | Fruit size[a] | Dispersal mode | Dispersal unit | Seed size[a] | References |
|---|---|---|---|---|---|---|---|---|
| *Colubrina cordifolia* | – | Septicidal capsule | Yes | Medium (1 cm length/0.9 cm width) | – | – | Medium | This study |
| Rubiaceae | | | | | | | | |
| *Alibertia* sp. | – | – | – | – | – | – | Medium | This study |
| Rutaceae | | | | | | | | |
| *Zanthoxylum stelligerum* | Brown[1] | Multiple fruit[2] | | Very large (5 cm diameter)[3] | Zoochory[1] | | Medium | 1—This study, 2—Barroso et al. (1999), 3—Lorenzi (2002) |

[a] Sensu Tabarelli and Peres (2002); small sized seed/fruit: <0.6 cm in length, medium sized: 0.6–1.5 cm, large: 1.6–3.0 cm, and very large: >3.0 cm

for 11 months and *Hymenaea velutina* for the whole study period. Intraspecific synchrony was also recorded for fruiting (Table 1).

Fruit types and dispersal modes

Most species had brown fruits (56%), followed by yellow (25%), green (11%), and red (8%) fruits (Table 2). Among the most abundant families, all species of Leguminosae and five out of the six species of Euphorbiaceae had brown fruits. Of the six species of Myrtaceae, five had yellow fruits and one had red fruits (Table 2).

We observed nine types of fruits in the studied community, but species bearing berries, drupes, and schizocarps were the most common, with 17.14% each, followed by species with capsule and chamber fruits (14.29% each), legume pods (8, 57%), multiple fruits (5.71%), craspedium, and follicle (2.86% each; Table 3). Schizocarps were the only type found in Euphorbiaceae and berries were the only observed in Myrtaceae (Table 2). Chamber fruits were the most representative in Fabaceae (45.4%) followed by legume pods (27.2%; Table 2). Excluding Fabaceae, Euphorbiaceae, and Myrtaceae, drupes represented 54.5% of the species, followed by capsules (36.3%). Most species (57.6%) showed indehiscent fruits (Table 2) and 65.7% of the species had fleshy fruits. Of these, most (78%) fruited during the rainy season.

With respect to fruit size, a greater percentage of species had very large and medium-sized fruits (34.4% each), followed by large (18.7%), and small (12.5%) fruits. Of the large or very large fruits, the majority (60%) were fleshy. Fruits were the most frequent dispersal units (diaspores), occurring in 56.7% of the species, the remaining species with seeds as diaspores (Table 2). Most of the 39 species had medium-sized seeds (22 spp. or 56.41%), followed by species with small (9 spp./23.1%), very large (5 spp./12.8%), and large (3 spp./7.7%) seeds.

Among the species studied, zoochory was the most frequent dispersal mode, represented by 51.6%, followed by autochory (25.8%), barochory with secondary zoochory (16.1%), and anemochory (6, 5%; Table 2). Analyzing the dispersal modes per family, Fabaceae was the only family with representatives of the four types (barochory 55.5%, autochory 22.3%, zoochory 11.1%, and anemochory 11.1%; Table 2). Barochory was not observed in any other family. Autochory was the only dispersal mode observed in Euphorbiaceae and zoochory was the only one observed in Myrtaceae (Table 2). Among other families, excluding Fabaceae, Euphorbiaceae, and Myrtaceae, zoochory was represented in 88.2% of the species.

| Type | Number of species | % |
|---|---|---|
| Berry | 6 | 17.14 |
| Drupe | 6 | 17.14 |
| Schizocarp | 6 | 17.14 |
| Camara | 5 | 14.29 |
| Capsula | 5 | 14.29 |
| Legume | 3 | 8.57 |
| Multiple fruit | 2 | 5.71 |
| Craspedium | 1 | 2.86 |
| Follicle | 1 | 2.86 |
| Total | 35 | 100 |

**Table 3** Fruit types of 35 studied species at the Carrasco vegetation of the Ibiapaba plateau, Ceará state, Brazil, according with the Classification of Spjut (1994)

Most zoochoric species bore fruit during the months of January, February, and March (months with most of the rainfall). However, the production of zoochoric fruits occurred throughout the year. The autochoric and barochoric species fruited practically the whole year round (Fig. 6). The only two anemochoric species were *Aspidosperma subincanum* and *Senna trachypus* and most individuals of *A. subincanum* bore fruit in March, the second half of the rainy season, dispersing their fruits in the dry season. *Senna trachypus* fruited at the end of the rainy season and during the dry season, dispersing its fruits in the middle of the dry season (Table 1).

## Discussion

### Phenology

Tropical forests exhibit a wide range of vegetative and reproductive phenological patterns, both at large and small geographical scales (Morellato et al. 2000). This phenological diversity can be explained by the seasonality and species composition in these ecosystems (Frankie et al. 1974).

The synchrony of vegetative and reproductive phenological events with the rainy season observed in the studied community is consistent with the pattern observed by Frankie et al. (1974) and Morellato et al. (1990, 2000) for seasonal ecosystems, where the occurrence of phenological events is associated with water availability. However, despite this synchrony, no significant correlation was observed between rainfall and the studied phenophases as discussed below.

The pattern of leaf production and fall, with all species loosing their leaves during the dry period and leaf flush taking place at the end of the dry season with a peak during the rainy, is expected for semiarid climates (Bullock and Solis-Magallanes 1990). This pattern was also observed in the Caatinga (Machado et al. 1997). The period of greatest leaf intensity occurring during the rainy season was also similar to the Caatinga (Machado et al. 1997). Despite leaf flush peak had occurred during the rainy season, there was no significant correlation between rainfall and this phenophase at the study site. However, this phenophase was positively correlated with air humidity and negatively correlated with maximum temperature. Similarly, in less dryer savannas of the West Africa, temperature decrease was significantly correlated with an increase in leafing (Seghieri et al. 2009). Also, analysis of the relationship of plant phenology and three climate variables (rainfall, minimum and maximum temperatures) at 17 savannas sites in southern Africa revealed that the most important determinant of the phenological patterns at these savannas was the interaction between minimum and maximum temperatures (Chidumayo 2001). In the Caatinga, some species maintain their leaves during the dry period, and stand out among the dry vegetation (Ferraz 1994; Machado et al. 1997), a pattern also observed in other dry forests (Frankie et al. 1974; Bullock and Solis-Magallanes 1990). In the studied community, the occurrence of evergreen species was not observed, but some species lose their leaves and then re-grow them, even during the dry period, while most Caatinga species remain without leaves until the next rainfall (see Machado et al. 1997).

Although the Carrasco also shows synchrony between phenological events and the rainy season, compared with the Caatinga, there is a proportionately larger number of species flowering and fruiting in the dry season. This is an expected pattern because in the studied Carrasco the annual rainfall is around 1,000 mm, which is the maximum isoyeta for
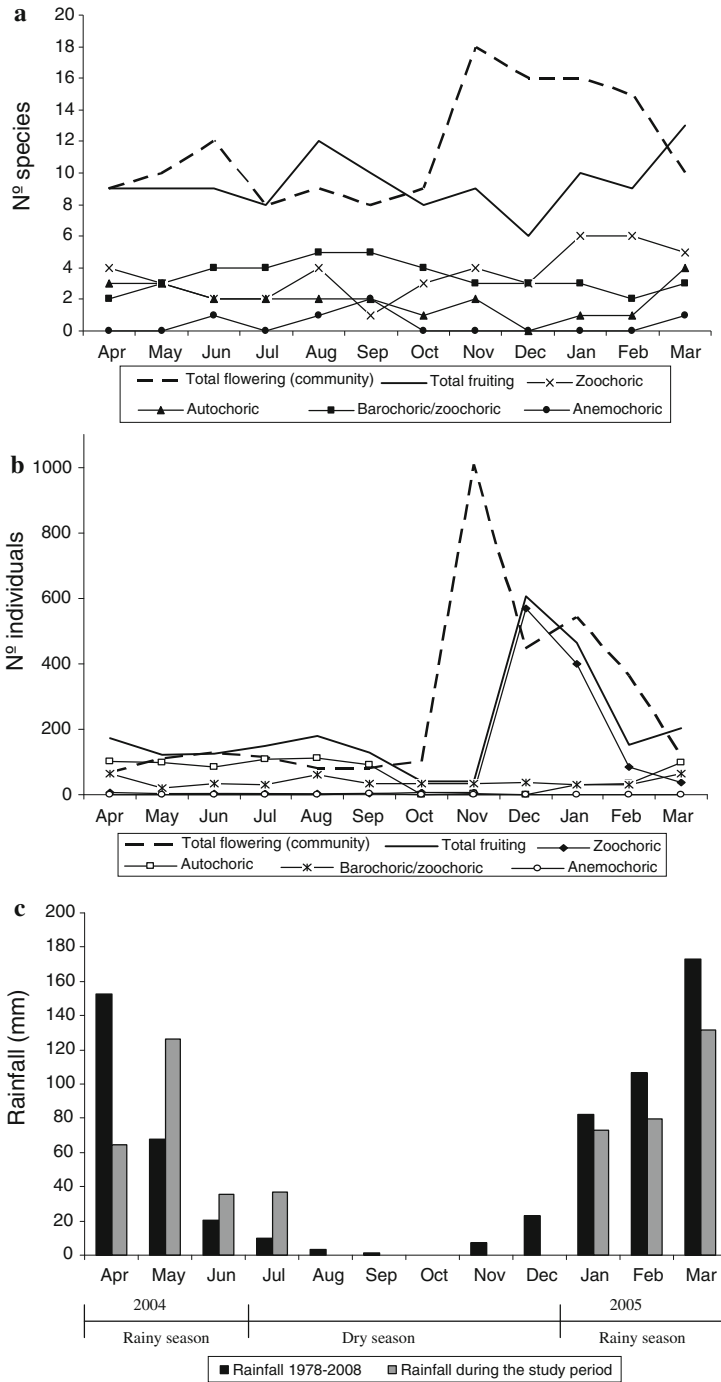
**Fig. 6** Number of species (**a**) and individuals (**b**) flowering and fruiting, with respective dispersal modes in the Carrasco vegetation of the Ibiapaba plateau, Crateús municipality, Ceará State, Brazil, during the period of April/2004–March/2005, and mean rainfall during 1978–2008 and during the study period (**c**)

delimitation of the Brazilian semiarid. The Caatinga dominium occur where the highest precipitation usually is less than 750 mm per year (Andrade-Lima 1981).

Despite this synchrony, we did not observe correlation between flowering and rainfall or the other variables tested here. Likewise, in some savannas of West Africa no climatic factors was found to be highly significant of flowering occurrence (cf. Seghieri et al. 2009). In the Carrasco rainfall is better distributed throughout the year, i.e., there is a shorter dry period. Although both the Carrasco and the Caatinga are under a regional semiarid climate, the Carrasco benefits from the topoclimate and soil moisture conditions thus making them functionally different. The soils in the Carrasco are deep and, as mentioned by Araújo et al. (2005), this may provide a lower water stress in this ecosystem due to a decrease in temperature and an increase in water availability in the soil. In fact, soil moisture also affects plant phenological behavior (Sing and Kushwaha 2005). In savannas of the West Africa, for example, the strategy of sprouting before the rainy season indicates that some water remains available to deep-rooting woody plants during the year (de Bie et al. 1998).

The occurrence of the flowering intensity peak (sensu Fournier 1974) in the community (26.8%) at the end of the dry season (November) is perhaps a response to the first rains since the existence of sporadic rains at the end of the dry season can reduce the water stress and, consequently, end the dormancy of flower buds (see Reich and Borchert 1982).

In the Caatinga, most species are generally deciduous in the dry season, beginning to flower during the rainy season and fruiting immediately after that, with a small number of species flowering in the dry season. There is, therefore, synchrony between the phenological events and the rainy season, as observed by Machado et al. (1997), Griz and Machado (2001) and Barbosa et al. (2003). Comparing the Carrasco with other seasonal tropical Brazilian formations, despite this ecosystem has deciduous vegetation and occur in the semiarid region, its phenological behavior is, in many aspects, similar to that of the semi-deciduous savanna (Cerrado) vegetation, typical of the Brazilian central plateau, and less similar to the deciduous savanna (Caatinga), which is the dominant surrounding vegetation. In most of the dry areas of the semiarid region, which is dominated by the Caatinga, the dry period varies from 8 to 9 months, with an annual average rainfall lower than 700 mm and an average annual temperature of up to 28°C (Sampaio 1995). On the other hand, in the core area of the Cerrado (in the Brazilian central plateau), soils are predominantly deep, the dry period varies from 4 to 5 months (similar to the Carrasco), and average annual temperatures are mild, between 20 and 25°C (Furley and Ratter 1988).

In the more humid Cerrado (outside the core area) as in the State of Pará, flowering and fruiting of the woody flora occur in the dry season, repeating the pattern found in studies conducted in the areas in the State of São Paulo (e.g., Mantovani and Martins 1988; Batalha et al. 1997; Batalha and Mantovani 2000; Silberbauer-Gottsberger 2001; Batalha and Martins 2004; Lenza and Klink 2006), where most species flowered and fruited during the dry season or in the transition period between the dry and the rainy season. Independent of the regional climatic conditions, the Cerrado is located in areas of deep soil and therefore benefits from soil moisture conditions.

The annual type of flowering and fruiting observed in this study confirm the pattern expected for semiarid regions, as recorded for the Caatinga (Machado et al. 1997). The fact that three species did not flower during the study period (*Copaifera martti*, *Maytenus* sp., and *Alibertia* sp.) can be attributed to two factors: they may be supra-annual species or the individuals of these species had not yet reached the reproductive phase and a greater observation period is necessary. In fact, Pedroni et al. (2002) studied the phenology of *C. martti* in a semi-deciduous forest in southeastern Brazil, and showed that fruiting occurred in supra-annual cycles, with years of intense production followed by years

without fruiting. Non-flowering species is a common phenomenon in phenological community studies (e.g., Griz 1996; Machado et al. 1997; Costa et al. 2004; Medeiros et al. 2007).

Continuous patterns of flowering and fruiting (sensu Newstrom et al. 1994) observed in some of the species studied (species flowering and fruiting throughout the year) were also observed for Caatinga (Machado et al. 1997) and Cerrado areas (Silberbauer-Gottsberger 2001; Batalha and Martins 2004). The occurrence of species with continuous phenological patterns in a community, such as *Bauhinia acuarana*, one of the most abundant species in the Carrasco, indicates an important resource for pollinators occurring in seasonal eco-systems as has been observed in the Caatinga (Machado et al. 1997).

The intra-specific flowering synchrony found in this study was also observed in the Caatinga (cf. Machado et al. 1997). In the Cerrado, Miranda (1995) also noted that leaf fall and flush, flowering and fruiting, occurred with high intra-specific synchrony.

The high percentage of species (33.3%) showing extended flowering (>5 months sensu Newstrom et al. 1994) differs from that observed for the Caatinga (see Machado et al. 1997), where few species have extended flowering. This fact confirms the expected pattern for the Carrasco, since this ecosystem is under a less arid climate.

The absence of a fruiting peak, when examining only the number of species, shows the occurrence of a non-seasonal pattern, different to that found for the Caatinga (Machado et al. 1997; Griz and Machado 2001), where most species bear fruit in the rainy season. Considering only the presence/absence of species fruiting in the Carrasco, this phenophase is evenly distributed throughout the year, similar to that found in less seasonal ecosystems, which offer less severe conditions for the development and ripening of fruit throughout the year, as highlighted by Talora and Morellato (2000). This strategy may be related to the maintenance of resources for seed dispersals since most species are zoochoric (cf. Snow 1965; Hilty 1980). In fact, animal-dispersed species, even in seasonal forests, tend to be less seasonal, with fleshy fruits produced throughout the year (Haugaasen and Peres 2005). Thus, physical factors may be important in determining the fruiting season, but the competition for dispersals may act as an additional selective pressure (Smythe 1970). The occurrence of a high percentage of zoochory in the Carrasco and the uniformity in the occurrence of fruiting species throughout the year, regardless of the distribution of rainfall, may be associated with soil water availability. In savannas of West Africa, sig-nificant relationships between fruiting and soil moisture may reflect a selection on fruiting periods that maximizes seed dispersion and germination (Seghieri et al. 2009).

## Types of fruits and dispersal modes

Berries and drupes, the most representative types of fruit among the Carrasco species, were also more frequent in the regional analysis for the Caatinga (cf. Tabarelli et al. 2003). However, Griz and Machado (2001) recorded that legume pods, followed by berries, were the most common among species in an area of Caatinga.

The high percentage of species (40.6%) showing medium-sized fruits, followed by very large ones (31.3%) in the Carrasco, was also registered for the Caatinga (Tabarelli et al. 2003; Vicente et al. 2003). The authors reported 46.7% of medium-sized fruit and 25.2% of very large ones for the Caatinga and 37.8% of medium-sized fruits and 25.4% of small fruits for the Atlantic forest. Tabarelli et al. (2003) mentioned that among species dispersed by vertebrates, the medium-sized and the very large fruits prevailed, a pattern also observed in this study.

The fact that most species (65.7%) in the Carrasco have fleshy fruits is different to that found for an area of Caatinga by Griz and Machado (2001), where 69% of species had dry fruits.

The percentage of zoochoric species (51.6%) observed in this study is even higher if the barochoric species that are secondarily zoochoric are added, totaling 67.7%, while the species dispersed abiotically (anemochoric and autochoric) account for 32.3%. In fact, the frequency of plants dispersed by animals is high in most tropical communities (Howe and Smallwood 1982). In tropical forests, at least 50% and generally 75% or more of the species of a given community produce fruits that are dispersed by birds or mammals (Fleming 1979; Gentry 1982; Howe and Smallwood 1982).

In areas of Caatinga, zoochory was observed in 36% of the species while the percentage of species dispersed abiotically (anemochoric, autochoric, and barochoric) corresponded to 64% (Griz and Machado 2001). Even adding to the zoochoric ones the percentage of barochoric species that may be secondarily zoochoric, the percentage rises to 48%, which is still below that found in the Carrasco (67.7%). This was expected due to the more arid climate of the Caatinga in comparison with the studied ecosystem. Machado et al. (1997) also found a predominance of species dispersed abiotically in another area of Caatinga.

In a deciduous forest in Venezuela, 42% of anemochory, 30% of zoochory, 19% of barochory, and 9% of autochory were observed by Wikander (1984). In tropical forests, the proportion of zoochoric species decreases as one moves from the humid areas toward the dry areas (Gentry 1982). These results were also observed in northeastern Brazil by Vicente et al. (2003) when examining changes in the mode of dispersal of woody species between dry and humid forests. In humid tropical forests, the proportion of anemochoric species are generally lower than 20% while zoochoric species respond to more than 80% (Fleming 1979; Gentry 1982; Morellato and Leitão-Filho 1996; Talora and Morellato 2000).

In the Cerrado, a high percentage of zoochory and a low percentage of autochory were documented (Gottsberger and Silberbauer-Gottsberger 1983; Batalha and Mantovani 2000; Batalha and Martins 2004), the latter being a dispersal strategy rarely observed in this ecosystem (see Vieira et al. 2002). Therefore, the higher percentage of zoochory in the Carrasco compared to the Caatinga reflects the lower aridity of the studied community. The results show that the studied community shows a percentage of zoochory similar to that found in the Cerrado and tropical rain forests.

In the Caatinga there is no record of zoochoric species fruiting throughout the year, which was observed in the Carrasco. In the Caatinga there is a predominance of zoochoric species fruiting during the rainy season and anemochoric species during the dry season (Machado et al. 1997; Griz and Machado 2001). This seems to be the most common pattern in seasonal ecosystems, and was also recorded in the Cerrado (Batalha and Martins 2004) and in seasonal tropical forests (Morellato et al. 1990; Morellato and Leitão-Filho 1996; Selwyn and Parthasarathy 2006, 2007). It is important to note that the frequency of zoochory is not always associated with precipitation, but also with areas that are dry or humid due to local topography (Bullock 1995). These areas, therefore, may bear higher or lower frequencies of zoochoric species. In tropical forests, for example, the proportion of zoochoric species decreases from humid areas toward dry areas (Gentry 1982).

Briefly, the Carrasco differs from the Caatinga in terms of functional traits due to the increased intensity and duration of phenological events, and also because it has a higher percentage of zoochoric species in comparison to the Caatinga. This highlights the importance of local environmental variables in triggering phenological events what makes the Carrasco to be more similar to ecosystems under less arid climates. Our results show

that the Carrasco, with its peculiar physiognomy and floristic composition, may also reveal differences regarding ecological processes when compared, in regional and global scales with other ecosystems under semiarid climates, and that local environmental factors, such as soil, relief, and edaphic water, seem to be the main reasons for these differences. This environmental heterogeneity may reflect not only in higher plant diversity but also in higher diversity of ecological processes in the Brazilian semiarid dominium.

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