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Pollination and breeding system of *Melochia tomentosa* L. (Malvaceae), a keystone floral resource in the Brazilian Caatinga

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Abstract

The main goals of the present paper were to investigate the floral biology and the breeding system of *Melochia tomentosa* in a semi-arid region in Brazil, comparing the role of *Apis mellifera* with other native pollinators, and to discuss the importance of this plant species as a floral resource for the local fauna in maintaining different guilds of specialized pollinators in the Caatinga. *M. tomentosa* is very common in Caatinga areas and blooms year-round with two flowering peaks, one in the wet and another in the dry period. The pink, bright-colored flowers are distylous and both morphs are homogamous. The trichomatic nectary is located on the inner surface of the connate sepals, and the nectar (ca. 7 μl) is accumulated in the space between the corolla and the calyx. Nectar sugar concentration reaches an average of 28%. The results of controlled pollination experiments show that *M. tomentosa* is self-incompatible. Pollen viability varies from 94% to 98%. In spite of being visited by several pollen vectors, flower attributes of *M. tomentosa* point to melittophily, and *A. mellifera* was the most frequent visitor and the principal pollinator. Although honeybees are exotic, severely competing with native pollinators, they are important together with other native bees, like *Centris* and *Xylocopa* species, for the fruit set of *M. tomentosa*. This species represents a keystone floral resource favoring the maintenance of many species of bees, butterflies and hummingbirds through the year in this deciduous tropical dry forest.

Keywords: Melittophily; Heterostyly; *Centris*; *Apis mellifera*; Dry-forest; Self-incompatibility

Introduction

Information concerning the floral biology of the genus *Melochia* (Malvaceae), which comprises 65 species (Willis, 1960) is very scarce. Knuth (1898–1905) referred to *M. parvifolia* as presenting heterostylous flowers, while Brizicky (1966) noted that the presence of nectaries and the intense coloring of the petals pointed towards entomophily in the genus, although no pollinators were reported. The only detailed study of the taxa was undertaken by Martin (1967) who studied the reproductive system of four *Melochia* species (including *Melochia tomentosa*) in Central America. According to this author, *M. tomentosa* is found almost exclusively in dry regions exposed to prolonged droughts, and it is capable of colonizing disturbed habitats such as roadsides and pasturelands.

M. tomentosa is a common species in the Caatinga (Giulietti et al., 2006; Machado, 1990), region characterized by a semi-arid climate with sparse rainfall that is

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irregularly distributed throughout the year. Its deciduous vegetation, a seasonally dry forest (Mooney et al., 1995; Pennington et al., 2000), has various physiognomies, including arboreal and shrubby formations with many xerophytic species, covering a semi-arid region of ca. 730,000 km^2 in north-east Brazil (Andrade-Lima, 1981; IBGE, 1985; Prado, 2003; Sampaio, 1995). *M. tomentosa* offers floral resources for various groups of animals, including many species of bees (Aguiar, 2003a, b; Aguiar et al., 2003; Machado, 1990), and its floral resources are especially important considering that it blooms year-round and occurs in an extremely dry, fragmented, and inhospitable environment.

This work presents information on floral biology and the reproductive system of *M. tomentosa* aiming to analyze its relationships with floral visitors and addresses the following questions: (1) Is *M. tomentosa* a typical distylous species with a heteromorphic self-incompatible breeding system? (2) Is *Apis mellifera*, compared with autochthonous floral visitors, an important pollinator? (3) How important is *M. tomentosa* as floral resource for the local fauna?

Material and methods

Field observation and experiments were carried out from January 1987 to March 1988, with additional studies in March and April of 2003 and 2004, totaling 160 h of observation on more than 100 individual focal plants of *M. tomentosa*. These focal plants were grouped in 10 patches distributed in a natural area of the Caatinga vegetation, a deciduous dry forest, in the municipality of Alagoinha (8°27′S × 36°46′W), in a semi-arid region of Pernambuco State, Northeastern Brazil. The local climate is "very hot, semi-arid" (Bs s'h'), according to the Köppen classification. Despite the long rainy season (5–6 months), the distribution of the rain within this time period is very irregular and the mean annual rainfall is very low (ca. 550 mm). Most rainfall occurs between March and May, and the mean annual temperature is around 21.6 °C (Griz and Machado, 2001). Local vegetation is hypoxerophytic, with a dense cover of shrubby species, in leaved state and flower especially during the rainy season (Griz and Machado, 2001, for details; Machado, 1990).

Monthly records were made about the reproductive phenology of the focal individuals. Data on floral morphology, flower color, and time of flower opening and anthesis duration were registered. Nectar sugar concentration was measured in the field (at approximately 10:00 h) in 20 bagged flowers of each morphotype from different individuals using a portable refractometer. Nectar volume was determined using graduated glass capillary tubes also in 20 flowers of each morphotype from different individuals. Pollen viability was examined in both long- and short-styled flowers using acetocarmine (Dafni et al., 2005; Radford et al., 1974). Hand self-pollinations in the two floral morphs, as well as hand cross-pollinations (intra- and inter-morph) were performed in 50–60 flowers from different individuals. For hand cross-pollinations, buds were enclosed in paper bags and emasculated just prior anthesis. A set of 100 flowers of each morph was used to estimate fruit set in natural conditions (control).

The behavior of floral visitors was analyzed by direct observations on focal flowers, and was complemented by photographs. Aspects related to the time, duration, and the frequencies of visitors were recorded, during a total of 120 h of field observations. Animal visitors were classified according to their visitation frequency as: (a) very frequent (VF), when present for more than 50% of the floral visits; (b) frequent (F), when present in $\geqslant 20\%$ and $< 50\%$ of the visits; and (c) rare (R), when observed in $< 20\%$ of the visits. Insects were captured, prepared for storage, and subsequently sent to specialists for identification. Voucher specimens are deposited in the Laboratório de Biologia Floral e Reprodutiva of the Universidade Federal de Pernambuco and at the Museu de História Natural, Universidade Estadual de Campinas (ZUEC, Unicamp). Hummingbirds were identified with the aid of a zoologist and by comparisons with literature (Grantsau, 1988; Sick, 1997). Plant voucher specimens were deposited in the Geraldo Mariz Herbarium of the Departmento de Botânica, Universidade Federal de Pernambuco (UFP no. 07022).

Results

Flowering phenology, floral biology and reproductive system

M. tomentosa is a perennial shrubby species, commonly occurring in clusters and individuals may reach up to 2.5 m tall. It flowers year-round, peaking twice a year from January to April and from June to August. The species is heterostylous–distylous (Fig. 1, Table 1), with an isopletic population structure and approximately equal proportions of long-styled (pin) and short-styled (thrum) flowers.

Flowers occur in axillary or terminal cymose inflorescences are zygomorphic and have a pink corolla. The petals are free but overlapping at the lower part giving the corolla a tubular shape and at the entrance their lobes are expanded and deflexed providing a landing platform (Fig. 2). The nectaries are trichomatic and are located on the inner surface of the connate sepals (Fig. 2C and D). Between the calyx and the basal tubular part of the corolla there are small spaces where nectar accumulates. The filaments are white,

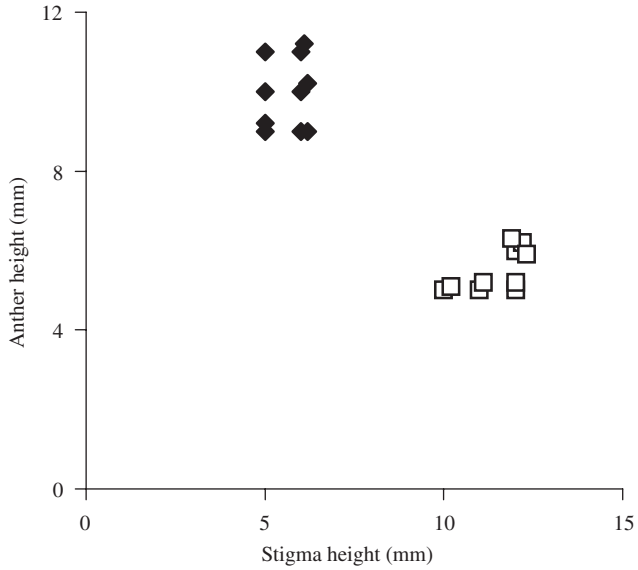

Fig. 1. Stigma and anther heights (mm) of short- (black squares) and long-styled (white squares) flowers of *Melochia tomentosa* in a deciduous tropical dry forest in northeastern Brazil.

Table 1. Mean values ± S.D. (mm) of floral traits of the short- and long-styled flowers of *Melochia tomentosa* in a deciduous tropical dry forest in northeastern Brazil

Floral morphs	Corolla length	Corolla width	Stigma height	Anther height
Short-styled	11.8 ± 1.1	12.4 ± 2.9	6.3 ± 0.6	11.1 ± 1.2
Long-styled	10.9 ± 0.7	13.0 ± 1.9	11.4 ± 0.9	6.2 ± 0.6

individually adnate to the median ventral part of each petal, being slightly curved especially in the long-styled flowers. The anthers maintain their ventral surfaces, where the dehiscent opening is located, facing the apex of the flower. They are yellow in color as is the case with the pollen as well. The style has five stigmatic branches whose thickened apices form papillate lobes (Fig. 2C and D). Filament and style dimensions of both long- and short-styled flowers are presented in Table 1.

Flower anthesis was initiated at 06:30–07:00 h, and anther dehiscence occurred shortly after bud opening. The flowers remained fresh and active during the morning, producing a light and pleasant odor. By approximately 14:00 h, the anthers had almost exhausted their pollen stocks. Pollen viability in both floral morphs varied between 94% and 98%. The flowers produced nectar throughout most part of the day, but the total volume was relatively small (ca. 7 μl/flower), being liberated very gradually and having an average solute concentration of 28% (25–30%). At approximately 16:00 h, most of the flowers were no longer producing nectar, the styles had withered, and the anthers were completely empty.

The results of the experiments of controlled pollinations with the two floral types are presented in Table 2. *M. tomentosa* demonstrates a classical pattern of heteromorphic self-incompatibility, with no fruit set from self- or intramorph cross-pollinations. Approximately, 100% of the manual intermorph pollinations set fruit. Under natural conditions fruit set was 82% and 78% in pin and thrum flowers, respectively.

Floral visitors

The flowers of *M. tomentosa* were visited by 10 species of bees, five butterfly species, and three species of hummingbirds (Table 3). Bees of the genera *Centris* and *Xylocopa* as well as *A. mellifera* (Fig. 2B) began their floral visits soon after floral opening, and continued in activity until the end of anthesis. Both floral morphs were visited indiscriminately by these bees, and their behavior was similar on the two morphs. Visits were short lasting, only about 5 s; the bees landed on the flower and introduced their heads into the corolla to take nectar. Contact with anthers and stigma took place at the ventral region of the animal's thorax or at the ventral region near the abdomen, depending on the size of the bee, as well as on the floral morph. *A. mellifera* was the most frequent visitor on *M. tomentosa* flowers (Table. 3), being recorded in 60% of the total of bee visits. Various individuals of this species foraged at the same time on different flowers of *M. tomentosa*, performing sequential visits on numerous flowers of the same floral group before leaving. *Coelioxoides punctipennis* was a legitimate visitor of *M. tomentosa* flowers, but made less than 20% of the visits. *Trigona spinipes* although frequent on flowers of *M. tomentosa* perforated the corolla base to take nectar (Table 3).

Among the butterflies, *Parides agavus* contacted anthers and the stigma since individuals hovered during nectar intake, whereas *Agraulis vanillae maculosa*, *Anartia jatrophae*, *Urbanus simplicius*, and *Phoebis sennae* landed on the flowers to probe for nectar, but without contacting anthers and the stigma.

Hummingbird species were recorded visiting the flowers of *M. tomentosa* frequently. During nectar intake, they contacted anthers and stigma with the bill. Visits to each flower lasted approximately 2 s, after which the hummingbirds moved on to other flowers of the same group before leaving. These birds visited up to 100 flowers in a sequence in the same floral cluster during each visiting bout, and an average of three bouts was recorded during each half hour of observation. On some occasions, the hummingbird species alternated their visitation to *M. tomentosa* visiting flowers of *Cnidoscolus urens* (Euphorbiaceae), *Nicotiana* sp. (Solanaceae), and *Ruellia asperula* (Acanthaceae).

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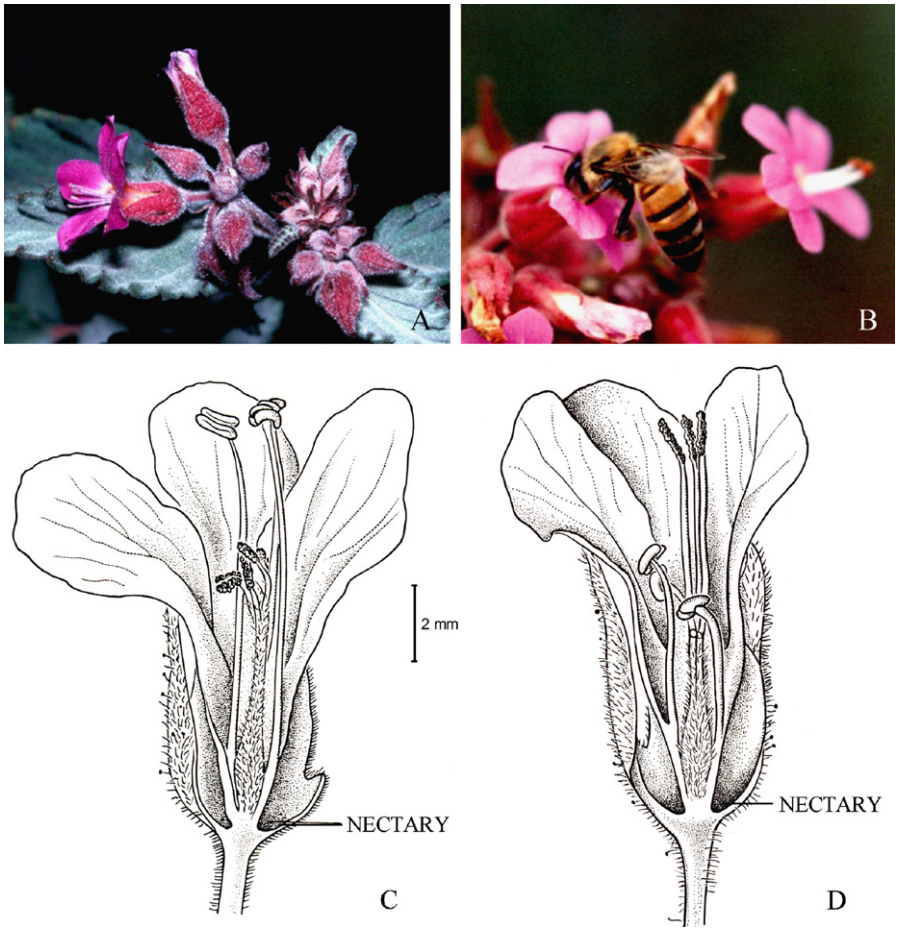

Fig. 2. Flower and pollinator of *Melochia tomentosa* in a deciduous tropical dry forest in northeastern Brazil. (A) Long-styled flower and inflorescence, (B) *Apis mellifera* visiting a short-styled flower. Note the stamens touching the ventral portion of the bee's thorax and abdomen, (C and D) longitudinal sections of the thrum (C) and pin (D) flowers.

Discussion

Flowering phenology, floral biology and reproductive system

The flowering pattern at the population level of *M. tomentosa* is defined as continuous by Newstrom et al. (1994). As such and offering two floral resources (nectar and pollen) at the population and community levels during both the rainy and the dry season, this species favors the maintenance of populations of bees, butterflies and hummingbirds year-round, but especially during the prolonged dry season.

The various attributes of *M. tomentosa* flowers indicate that the species is melittophilous (Faegri and Van der Pijl, 1979), including bold colors, pleasant odor, and the production of small quantities of nectar that is hidden in the basal part of the sepals – like many Malvaceae (S. Vogel, personal communication). Sugar concentration in the nectar of *M. tomentosa* was similar to records of other melittophilous species from several families (Baker, 1975). Although its floral attributes indicate melittophily and bees were the most important pollinators in terms of both the number of species and the frequency of visitation, this species is also pollinated by other groups of animals, such as butterflies and hummingbirds.

The floral dimorphism in *M. tomentosa* is well-documented in the scientific literature (Martin, 1967) and has been reported also in other genera of Malvaceae (Barrett and Richards, 1990; Ganders, 1979; Ornduff, 1974, 1992; Vuilleumier, 1967). The isopletic populational equilibrium detected in this species is common and expected in heterostylous species of this and other families (Barrett and Shore, 1985; Ornduff, 1971; Santos and Machado, 1998; Sobrevila et al., 1983) due to the diallelic heteromorphic system of incompatibility commonly associated with heterostyly (Barrett, 1992; Barrett and Richards, 1990; Barrett and Shore, 1985; Ganders, 1979; Gibbs, 1986; Vuilleumier, 1967).

M. tomentosa is self-incompatible and is fertilized only by intermorph cross-pollination. Such reproductive

Table 2. Fruit set of hand-pollinated flowers and flowers pollinated under natural conditions of short-styled (SS) and long-styled (LS) flowers of *Melochia tomentosa* in a deciduous tropical dry forest in northeastern Brazil

Treatments	Fruits/ flowers (n/n)	Success (%)
Cross-pollination		
SS × SS (≠individuals)	0/50	0
LS × LS (≠individuals)	1[a]/50	2[a]
SS × LS	50/50	100
LS × SS	58/60	96.6
Manual self-pollination		
LS	0/50	0
SS	0/60	0
Natural conditions (control)		
LS	82/100	82
SS	78/100	78

[a]Small and asymmetric fruit, with aborted seeds.

Table 3. Visitors of *Melochia tomentosa* flowers in a deciduous tropical dry forest in northeastern Brazil, with their respective frequency and importance as pollinators

Visitors	Frequency	Importance as pollinators
Insects		
Hymenoptera		
Apis mellifera	VF	1
Centris fuscata	F	2
Centris tarsata	F	2
Centris trigonoides	F	2
Centris xanthomelaena	F	2
Centris sp.	R	3
Coelioxoides punctipennis	R	3
Trigona spinipes	F	4
Xylocopa grisescens	F	2
Xylocopa sp.	F	2
Lepidoptera		
Agraulis vanillae maculosa	F	4
Anartia jatrophae	F	4
Parides agavus	R	3
Phoebis sennae	F	4
Urbanus simplicius	F	4
Birds/Trochilidae		
Amazilia versicolor	F	2
Chrysolampis mosquitus	F	2
Hylocharis sapphirina	F	2

1, High; 2, medium; 3, low; 4, nectar thieves (high, medium and low is the importance of those animals with a behavior appropriate to pollination and which visits were, respectively; VF, very frequent; F, frequent; or R, rare).

behavior was reported for this species in Porto Rico, although other species of the genus may be self-compatible, such as *M. pyramidata* (Martin, 1967). In the opinion of Vuilleumier (1967), heterostyly seems to have evolved in two directions: (1) towards dioecious and sub-dioecious forms, as in the genus *Cordia* (Boraginaceae), in which dioecia probably arose among distylous species (e.g. *C. inermis* and *C. colococca*) that were intermediate between the distylous and dioecious conditions (Opler et al., 1975); or (2) in the direction of a homostylous form and self-fertilization (see also Barrett, 1989). According to Martin (1967), self-incompatible distylous species of *Melochia* have given rise to self-compatible distylous species like *M. pyramidata*. Examples of reversing self-incompatibility, and/or monostylous populations, have been reported for species of Iridaceae (Goldblatt and Bernhardt, 1990) and Rubiaceae (Barrett, 1989; Consolaro et al., 2005).

The high reproductive success of *M. tomentosa* in natural conditions (78% of fruit set) even within a self-incompatible heteromorphic system, may be related to the fact that this species attracts a wide diversity of pollinators, including the social bee *A. mellifera*, which is well-known for its intensive foraging behavior (Paton, 1993).

Floral visitors: the role of *A. mellifera* and of autochthonous animals in the pollination of *M. tomentosa*

All of the bee visitors to *M. tomentosa*, in spite of flower size and morphology in relation to animal body size, acted as pollinators in the light of their behavior on the flowers and their visitation frequency, with the exception of *T. spinipes*, that is considered as a nectar-thief. Nectar or pollen robbing is a role frequently reported for *Trigona* bees (Renner, 1983; Roubik, 1989; Sazima and Sazima, 1989; Snow and Roubik, 1987).

An analysis of the behavior and the visitation frequency of *A. mellifera* indicate that it is the principal pollinator of *M. tomentosa*. The high constancy and the visitation behavior of *A. mellifera* together with other medium and large bees, like *Centris* and *Xylocopa* species, resulted in abundant fruit set of *M. tomentosa*. On the other hand, *M. tomentosa* is an important nectar source for many autochthonous bees. In a survey of the utilization of floral resources by bees, Aguiar (2003b) pointed out that *M. tomentosa* was one of the four angiosperm species of the Caatinga vegetation most frequently sought after by 24 bee species from a number of different tribes. *M. tomentosa* also represents an important floral resource especially for *Centris* species, as recorded by Aguiar (2003a) and Aguiar et al. (2003) in four Caatinga areas. Considering that Centridini are the main pollinators of plant species that offer floral oil

resources, the role of *M. tomentosa* in maintaining different guilds of specialized pollinators in the Caatinga takes on even more important. The importance of *M. tomentosa* for bee faunas was pointed out also by Carvalho and Marchini (1999), Aguiar et al. (2002), Machado and Lopes (2006) and Santos et al. (2006), for different sites of the Caatinga in NE Brazil.

Concerning the butterflies, only *P. agavus* was a pollinator, the other species being nectar thieves. As a general rule, butterflies are not considered good pollinators in tropical areas (Machado and Sazima, 1987). Although visiting a diverse array of flower species, hummingbirds were of medium importance in the pollination of *M. tomentosa* and their generalist behavior probably reflects the reduced diversity of true ornithophilous flowers in the study area (Machado, 1990; Machado and Lopes, 2003, 2004). Additionally, this behavior reinforces the observation that hummingbirds do not usually demonstrate high fidelity in their visits to any given plant species (Faegri and Van der Pijl, 1979; Grant, 1949), frequently visiting also many non-ornithophilous plant species (Araujo and Sazima, 2003).

In conclusion, *M. tomentosa* represents an important food source for the exotic *A. mellifera*, as well as for many native solitary short-tongued bees, other insects and hummingbirds, by flowering year-round, but it is especially important during the dry season which is marked by high scarcity of resources for the fauna in this deciduous tropical dry forest (Aguiar, 2003b; Machado et al., 1997; Quirino, 2006; Quirino and Machado, unpublished data). As such *M. tomentosa* may be characterized as a keystone floral resource (*sensu* Schaik et al., 1993; Terborgh, 1986) in the semi-arid Caatinga of north-east Brazil.

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References

Aguiar, C.M.L., 2003a. Flower visits of *Centris* bees (Hymenoptera: Apidae) in an area of Caatinga (Bahia, Brazil). Stud. Neotrop. Fauna Environ. 38, 41–45.

Aguiar, C.M.L., 2003b. Utilização de recursos florais por abelhas (Hymenoptera, Apoidea) em uma área de Caatinga (Itatim, Bahia, Brasil). Revta. Bras. Zool. 20, 457–467.

Aguiar, C.M.L., Monteiro, V.M., Santos, G.M.M., Resende, J.J., França, F., Melo, E., 2002. Plantas visitadas por *Apis mellifera* L. (Hymenoptera, Apidae) em uma área de Caatinga em Itatim, Bahia, Brasil. Sitientibus 2, 29–33.

Aguiar, C.M.L., Zanella, F.C.V., Martins, C.F., de Carvalho, C.A.L., 2003. Plantas visitadas por *Centris* spp. (Hymenoptera: Apidae) na Caatinga para obtenção de recursos florais. Neotrop. Entom. 32, 1–13.

Andrade-Lima, D., 1981. The caatingas dominium. Rev. Bras. Bot. 4, 142–153.

Araujo, A.C., Sazima, M., 2003. The assemblage of flowers visited by hummingbirds in the "capões" of Southern Pantanal, Mato Grosso do Sul, Brazil. Flora 198, 427–435.

Baker, H.G., 1975. Sugar concentrations in nectars from hummingbird flowers. Biotropica 7, 37–41.

Barrett, S.C.H., 1989. The evolutionary breakdown of heterostyly. In: Bock, J.H., Linhart, Y.B. (Eds.), The Evolutionary Ecology of Plants. Westview Press, Boulder, CO, pp. 151–169.

Barrett, S.C.H., 1992. Heterostylous genetic polymorphisms: model systems for evolutionary analysis. In: Barrett, S.C.H. (Ed.), Evolution and Function of Heterostyly. Springer, Berlin, pp. 1–29.

Barrett, S.C.H., Richards, J.H., 1990. Heterostyly in tropical plants. Mem. New York Bot. Gard. 55, 35–61.

Barrett, S.C.H., Shore, J.S., 1985. Dimorphic incompatibility in *Turnera hermannioides* Camb. (Turneraceae). Ann. Mo. Bot. Gard. 72, 259–263.

Brizicky, G.K., 1966. The genera of Sterculiaceae in the Southeastern United States. J. Arn. Arb. 47, 60–74.

Carvalho, C.A.L., Marchini, L.C., 1999. Plantas visitadas por *Apis mellifera* L. no vale do Rio Paraguaçu, Município de Castro Alves, Bahia. Rev. Bras. Bot. 22, 333–338.

Consolaro, H., Silva, E.B., Oliveira, P.E., 2005. Variação floral e biologia reprodutiva de *Manettia cordifolia* Mart. (Rubiaceae). Rev. Bras. Bot. 28, 85–94.

Dafni, A., Kevan, P.G., Husband, B.C., 2005. Practical Pollination Biology. Cambridge, Enviroquest.

Faegri, K., Van der Pijl, L., 1979. The Principles of Pollination Ecology. Pergamon Press, New York.

Ganders, F.R., 1979. The biology of heterostyly. New Zealand J. Bot. 17, 607–635.

Gibbs, P.E., 1986. Do homomorphic and heteromorphic self-incompatibility systems have the same sporophytic mechanism? Plant Syst. Evol. 154, 285–323.

Giulietti, A.M., Conceição, A., Queiroz, L.P., 2006. Nordeste semi-árido: caracterização geral e lista das fanerógamas. In: Giulietti, A.M., Conceição, A., Queiroz, L.P. (Eds.), Diversidade e caracterização das fanerógamas do semi-árido brasileiro. IMSEAR, MCT, APNE, Recife, pp. 15–364.

Goldblatt, P., Bernhardt, P., 1990. Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. Israel J. Bot. 39, 93–111.

Grant, V., 1949. Pollination systems as isolating mechanisms in Angiosperms. Evolution 3, 82–97.

Grantsau, R., 1988. Die Kolibris Brasiliens. Editora Expressão e Cultura, Rio de Janeiro.

Griz, L.M.S., Machado, I.C.S., 2001. Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in northeast Brazil. J. Trop. Ecol. 17, 303–321.

IBGE, 1985. Atlas Nacional do Brasil: Região Nordeste. IBGE, Rio de Janeiro.

Knuth, P., 1898–1905. Handbuch der Blütenbiologie, vols. I–III. Engelmann, Leipzig.

Machado, I.C., 1990. Biologia floral de espécies de Caatinga em Alagoinha – PE. Tese de Doutorado. Universidade Estadual de Campinas, SP.

Machado, I.C., Lopes, A.V., 2003. Recursos florais e sistemas de polinização e sexuais em caatinga. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (Eds.), Ecologia e Conservação da Caatinga. Editora Universitária UFPE, Recife, pp. 515–563.

Machado, I.C., Lopes, A.V., 2004. Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry Forest. Ann. Bot. 94, 365–376.

Machado, I.C., Lopes, A.V., 2006. Melitofilia em espécies de Caatinga em Pernambuco e estudos relacionados existentes no ecossistema. In: Santos, F.A.R. (Ed.), Apium Plantae. IMSEAR, MCT, APNE, Recife, pp. 33–60.

Machado, I.C.S., Sazima, M., 1987. Estudo comparativo da biologia floral em duas espécies invasoras: *Ipomoea hederifolia* e *I. quamoclit* (Convolvulaceae). Rev. Bras. Biol. 47, 425–436.

Machado, I.C., Barros, L.M., Sampaio, E.V.S., 1997. Phenology of Caatinga species at Serra Talhada, PE, Northeastern Brazil. Biotropica 29, 57–68.

Martin, F.W., 1967. Distyly, self-incompatibility, and evolution in *Melochia*. Evolution 21, 493–499.

Mooney, H.A., Bullock, S.H., Medina, E., 1995. Introduction. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, pp. 1–8.

Newstrom, L.E., Frankie, G.W., Baker, H.G., 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. Biotropica 26, 141–159.

Opler, P.A., Baker, H.G., Frankie, G.W., 1975. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). Biotropica 7, 234–247.

Ornduff, R., 1971. The reproductive system of *Jepsonia heterandra*. Evolution 25, 300–311.

Ornduff, R., 1974. Heterostyly in South African flowering plants: a conspectus. J.S. Afr. Bot. 40, 169–187.

Ornduff, R., 1992. Historical perspectives on heterostyly. In: Barrett, S.C.H. (Ed.), Evolution and Function of Heterostyly. Springer, Berlin, pp. 31–39.

Paton, D.C., 1993. Honeybees in the Australian environment. BioScience 43, 95–103.

Pennington, R.T., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and quaternary vegetation changes. J. Biog. 27, 261–273.

Prado, D.E., 2003. As caatingas da América do Sul. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (Eds.), Ecologia e Conservação da Caatinga. Editora Universitária UFPE, Recife, pp. 3–73.

Quirino, Z.G.M., 2006. Fenologia, síndromes de polinização e dispersão e recursos florais de uma comunidade de Caatinga no Cariri paraibano. Tese de Doutorado, Universidade Federal de Pernambuco, PE.

Radford, A.E., Dickinson, W.C., Massey, J.R., Bell, C.R., 1974. Vascular Plant Systematics. Harper & Row Publishers, New York.

Renner, S., 1983. The widespread occurrence of anther destruction by *Trigona* bees in Melastomataceae. Biotropica 15, 251–256.

Roubik, D.W., 1989. Ecology and Natural History of Tropical Bees. Cambridge University Press, New York.

Sampaio, E.V.S.B., 1995. Overview of the Brazilian Caatinga. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge, pp. 35–63.

Santos, F.A.R.S., Oliveira, J.M., Oliveira, P.P., Leite, K.R.B., Carneiro, C.E., 2006. Plantas do semi-árido importantes para as abelhas. In: Santos, F.A.R. (Ed.), Apium Plantae. IMSEAR, MCT, APNE, Recife, pp. 61–86.

Santos, M.J.L., Machado, I.C., 1998. Biologia floral e heterostilia em *Vismia guianensis* (Aubl.) Choisy (Clusiaceae). Acta Bot. Bras. 12, 451–464.

Sazima, I., Sazima, M., 1989. Mamangavas e Irapuás (Hymenoptera, Apoidea): visitas, interações e consequências para polinização do maracujá (Passifloraceae). Rev. Bras. Entom. 33, 109–118.

Sick, H., 1997. Ornitologia Brasileira. Nova Fronteira, Rio de Janeiro.

Snow, A.A., Roubik, D.W., 1987. Pollen deposition and removal by bees visiting two tree species in Panamá. Biotropica 19, 57–63.

Sobrevila, C., Ramirez, N., Enrech, N.X. de., 1983. Reproductive biology of *Palicourea fendleri* and *P. petiolaris* (Rubiaceae), heterostylous shrubs of a tropical cloud forest in Venezuela. Biotropica 15, 161–169.

Terborgh, J., 1986. Keystone plant resources in the Tropical Forest. In: Soulé, M.E. (Ed.), Conservation Biology. Sinauer, Massachusetts, pp. 330–344.

van Schaik, C.P., Terborgh, J.W., Wright, S.J., 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu. Rev. Ecol. Syst. 24, 353–377.

Vuilleumier, B.S., 1967. The origin and evolutionary development of heterostyly in the angiosperms. Evolution 21, 210–226.

Willis, C., 1960. A Dictionary of the Flowering Plants and Ferns, 6th ed. Cambridge University Press, Cambridge.

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