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Reproductive biology of woody species in Caatinga, a dry forest of northeastern Brazil☆

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A B S T R A C T

Studies concerning reproductive biology at the community level have not yet been reported for Caatinga. In this study, we analyzed the flowering phenology, floral longevity, and breeding system of 15 typical woody species in this ecosystem. Flowering occurred mostly during the dry season for ten species. Among dioecious plants, male individuals predominate for two out of three species analyzed. In *Maytenus rigida*, a gynodioecious species, female individuals predominate in the population; the number of flowers per inflorescence is the same between hermaphrodite (14.0 ± 4.4) and female (14.8 ± 4.6) individuals, but significant differences are found with respect to fruit set by hermaphrodite (1.9 ± 0.9) and pistillate flowers (4.0 ± 2.4). Self-compatibility occurs in 26.7% of the studied species, whereas 73.3% present obligatory xenogamy. Among self-incompatible species, two have a stylar site of rejection, while self-pollen tubes reach the ovules in five. Late-acting self-incompatibility in *Sideroxylon obtusifolium* constitutes the first record of this mechanism in Sapotaceae. The majority of the species studied have a lower fruit/flower than seed/ovule ratio. Reproduction of woody plants in this arid ecosystem depends upon biotic vectors that can promote cross-pollination and gene flow.

1. Introduction

Knowledge of plant reproductive biology is important for understanding the structure and diversity of communities as well as the ecological interdependence of plants and their pollination and dispersal agents (Bawa, 1974). Many studies concerning reproductive biology have been undertaken in tropical ecosystems, such as wet forests (e.g. Sobrevila and Arroyo, 1982; Bawa et al., 1985; Ramírez and Seres, 1994), semi-deciduous, deciduous and dry forests (Zapata and Arroyo, 1978; Bullock, 1985; Aronne and Wilcock, 1994), Chaco vegetation (Aizen and Feinsinger, 1994), Savanna (Oliveira and Gibbs, 2000) and island environments (McMullen, 1987; Bernardello et al., 2001). However, reproductive biology at the community level has yet to be adequately described in the Caatinga ecosystem in Brazil.

Although some studies have focused on phenology and pollination and dispersal syndromes in Caatinga (Machado et al., 1997; Griz and Machado, 2001; Machado and Lopes, 2004) case histories describing the pollination and reproductive strategies of individual species are more frequent (e.g. Lewis and Gibbs, 1999; Machado and Sazima, 2008). Recently, Machado et al. (2006) estimated the frequency of different sexual systems in Caatinga and also argued that data on breeding systems is still lacking for this ecosystem, particularly for most of the typical woody species.

The Caatinga ecosystem is considered to be one of the 37 Wilderness Areas of the World, and it plays an important role in the maintenance of regional macro-ecological process, as well as indirectly supporting regions with the greatest diversity and endemism in both Brazil and the world. Plant species of this ecosystem are constantly subjected to the influence of water stress, which can influence the flowering period (Pavón and Briones, 2001), floral traits (Carroll et al., 2001) and also sex ratio in dioecious species (Soldaat et al., 2000). Although the limitation of resources such as nutrient and water stress can affect the diversity of pollination and reproductive system (Aronne and Wilcock, 1994), increasing inbreeding depression (see Cheptou et al., 2000), no consideration has been made in this direction especially in the Caatinga.

In this study, we analyzed the flowering phenology, floral longevity and reproductive systems of some woody species of the Caatinga, aiming to test the following hypothesis: 1) in gynodioecious species the fruit set of hermaphrodite flowers is in average fewer than in pistillate ones; 2) the frequency of self-compatible

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species in Caatinga is higher than the obligatory xenogamous; 3) in self-compatible species the frequency of fruits produced by cross-pollination is higher than the frequency of fruits produced by self-pollination, and 4) in late-acting self-incompatible species pollen tubes from cross-pollination reach the ovules more often than tubes from manual self-pollination. We also answered what are the types of self-incompatibility mechanisms observed among the examined species.

2. Materials and methods

2.1. Study area and species

Fieldwork was carried out at the Dona Soledade farm (7°20′30.7″S, 36°18′5.8″W), a private area of 690 ha in municipalities of Cabaceiras and Boa Vista, Paraíba State, Brazil. The study site is situated in a region known as "cariris velhos", one of the driest areas in arid northeastern Brazil. The rainy period occurs from February to June, and the average annual rainfall in the region of Cabaceiras and Boa Vista is around 330 mm yr^{-1}. Precipitation rates as low as 252 mm yr^{-1} have been reported (Governo da Paraíba, 2005). Mean annual temperature can be as high as 32 °C (Governo da Paraíba, 2005) (Appendix electronic version only). The study site is covered predominantly by open shrub-arboreal vegetation, with tree species characteristic of the Caatinga vegetation, such as *Aspidosperma pyrifolium* (Apocynaceae), *Bauhinia cheilantha* and *Caesalpinia pyramidalis* (Leguminosae), *Commiphora leptophloeos* (Burseraceae), *Pilosocereus* spp. (Cactaceae), *Schinopsis brasiliensis* and *Spondias tuberosa* (Anacardiaceae). Most of these species were included in the present study.

We analyzed 15 typical woody species of Caatinga, nine of which appears as very frequent in floristic and phytosociological surveys of this ecosystem (see Rodal et al., 2008 and references there in). Six studied species are endemic, and three are widely valued as fruit trees (for species see Table 1; Machado and Lopes, 2004). Nine are hermaphroditic, three are dioecious, one is andromonoecious, one is gynodioecious, and one is monoecious (Table 1). Voucher collections are deposited in the UFP Herbarium at the Federal University of Pernambuco, Brazil.

2.2. Flowering phenology, floral longevity and breeding systems

Monthly observations of the flowering period of each species were made between April 2003 and December 2005, in 10–15 individuals per species. We examined floral longevity and mechanisms to avoid self-pollination in about 10–20 flowers from 10 inflorescences and five individuals of each species (see Table 1). To analyze the floral longevity, pre-anthesis buds were tagged and examined in the next day for determination of the beginning of flower lifespan. These flowers were monitored daily until senescence or corolla fall. In this period we also checked if the reproductive structures show any temporal (dicogamy) or spatial (hercogamy) mechanism.

To determine the proportions of individuals with pistillate or staminate flowers in the dioecious species and of individuals with pistillate and hermaphrodite flowers in the gynodioecious species, we made surveys of plant sexuality during random walks throughout the study area. We also counted the numbers of pistillate and staminate flowers (in dioecious) and hermaphrodite and pistillate flowers (in gynodioecious) per inflorescence. We used

Table 1
Number of studied individuals, floral longevity, sexual system, pollination tests, Index of Self-Incompatibility (ISI), breeding system and incompatibility in 15 woody species in Caatinga, Boa Vista, Paraíba, Brazil. H: hermaphrodite, M: monoecious, D: dioecious, GD: gynodioecious, AM: andromonoecious, SC: self-compatible, SI: self-incompatible, LSI: late-acting self-incompatible, G: gametophytic. Agamospermy was zero for *Parkinsonia aculeata*.

Family/Species	Individuals studied	Longevity (flowers)	Sexual system	Self-pollination Fl/Fr	Manual self-pollination Fl/Fr(%)	Cross-pollination Fl/Fr(%)	Natural pollination Fl/Fr(%)	ISI[a]	Breeding system/ incompatibility
Anacardiaceae									
Myracrodruon urundeuva	5	1 day (10)	D	–	–	–	1335[d]/433 (32)	–	–
Schinopsis brasiliensis	5	2–3 days (10)	D	–	–	–	80/62 (78)	–	–
Spondias tuberosa[b,c]	12	2–3 days (15)	AM	100/0	55/0	55/12 (22)	176[e]/2 (1)	0	SI/G
Burseraceae									
Commiphora leptophloeos[b]	9	2–3 days (10)	D	–	–	–	130/37 (28)	–	–
Celastraceae									
Maytenus rigida[b]	5	2 days (15)	GD	50/0	50/0	50/0	122[e]/1 (0,8)	–	–
Cochlospermaceae									
Cochlospermum insigne	7	2 days (12)	H	70/0	30/9 (30)	30/13 (43)	125/30 (24)	0,60	SC
Euphorbiaceae									
Croton sonderianus	10	2 days (10)	M	–	20/8 (40)	30/13 (43)	63/17 (27)	0,93	SC
Leguminosae									
Bauhinia cheilantha	16	1 night (15)	H	65/0	34/0	42/20 (47)	93/23 (25)	0	SI/LSI
Caesalpinia pyramidalis[b]	17	3 days (15)	H	60/0	30/0	33/7 (21)	130/17 (13)	0	SI/LSI
Erythrina velutina	5	2 days (10)	H	75/0	30/3 (10)	–	90/4 (4)	–	SC?
Parkinsonia aculeata	10	3 days (15)	H	30/7 (23)	31/24 (77)	10/6 (60)	116/37 (32)	1,28	SC
Senna martiana[b]	15	1 day (20)	H	100/0	37/0	34/2 (6)	100/44 (44)	0	SI/LSI
Senna spectabilis	6	1 day (10)	H	100/0	30/0	30/3 (10)	102/3 (3)	0	SI/LSI
Rhamnaceae									
Ziziphus joazeiro[b,c]	10	12 h (20)	H	90/0	50/2 (4)	50/11 (22)	190/3 (1,5)	0,18	SI/G
Sapotaceae									
Sideroxylon obtusifolium[c]	5	3 days (10)	H	100/0	31/0	31/7 (23)	100/0	0	SI/LSI

– Information lacking;? Uncertain.
[a] According to Bullock (1985).
[b] Endemics.
[c] Fruitful.
[d] Flowers in 10 inflorescences.
[e] Hermaphrodite flowers.