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Dynamics of Brazilian Caatinga – A Review Concerning the Plants, Environment and People

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ABSTRACT

The Caatinga is a xerophyte, deciduous plant formation that occupies more than 50% of the northeastern region of Brazil (approximately 800.000 km^2). This formation presents a high biological and cultural diversity, including several endemic species of plants and animals, as well as many ethnic groups such as indigenous and rural communities. Distinct scenario types found within the Caatinga domain can be interpreted as a result of the interaction of many factors, such as the soil and the climate, which greatly influence the vegetation type, as well as the historical processes of occupation by man, and the socio-cultural features of local populations. The interaction of all these factors induces dynamic processes in Caatinga that influence local diversity, affecting the structure and dynamics of plant populations and communities, as well as social processes. The objective of this study is to present an overview of the diversity of plants (Angiosperms) and of ecological processes in Caatinga, discussing the manners in which people use this diversity. We also suggest some studies that may contribute to the conservation and management of Caatinga resources, considering the structure and the functioning of this ecosystem.

Keywords: dry forest, dynamics, ecology, ethnobotany, semi-arid vegetation, xerophytes

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INTRODUCTION

The Caatinga is a tropical semi-arid vegetation type that is exclusive to Brazil, and represents the fourth largest plant formation of the country (Sampaio 1995; MMA 2002; Castelletti *et al*. 2004) that occupies 734.478 Km^2 of the northeastern region (**Fig. 1**). Some evidences strengthen the existence of floristic links between the Caatinga and other seasonal dry forests in South America, due to, among other factors, the disjunctive distribution of important and characteristic species (Prado and Gibbs 1993).

The climate type is semi-arid (Köppen's BSh), mainly characterized by an extremely high energy entrance and elevated temperatures, evaporation and evapotranspiration rates. Annual precipitation varies from 250 to 1.200 mm, but a mean for the entire biome is less then 620 mm, generally distributed irregularly in time and space; dry season comprises from five to nine months (Ab'Saber 1974; Reis 1976; Sampaio 1995, 1996). The Caatinga occupies predominantly areas of crystalline basement, although sometimes it occurs in areas of sedimentary basins. Plain areas predominate in Caatinga, which contrast with the steep residual slopes reaching 1000 m tall (Andrade 1977; Souza *et al*. 1996).

Caatinga is a xerophilous vegetation that include many deciduous and thorny species, as well as succulents ones. According to Veloso *et al*. (1991) system, it is classified as a steppic savanna. However, depending on its geographical position and climatic features, it may also be classified as a dry tropical forest (Tosi and Vélez-Rodríguez 1983). Beyond the Caatinga, NE Brazil also include small patches of Semidecidual or Ombrophilous Montane Forests (*brejos de altitude*), and also of Cerrado vegetation (tropical savanna; Sampaio 1996; Ferraz *et al*. 2004), which are conditioned by topography and soils; these vegetation types will not be discussed here.

The Caatinga is represented by different physiognomic types, locally denominated as shrubby, woody, shrubby/

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Invited Review

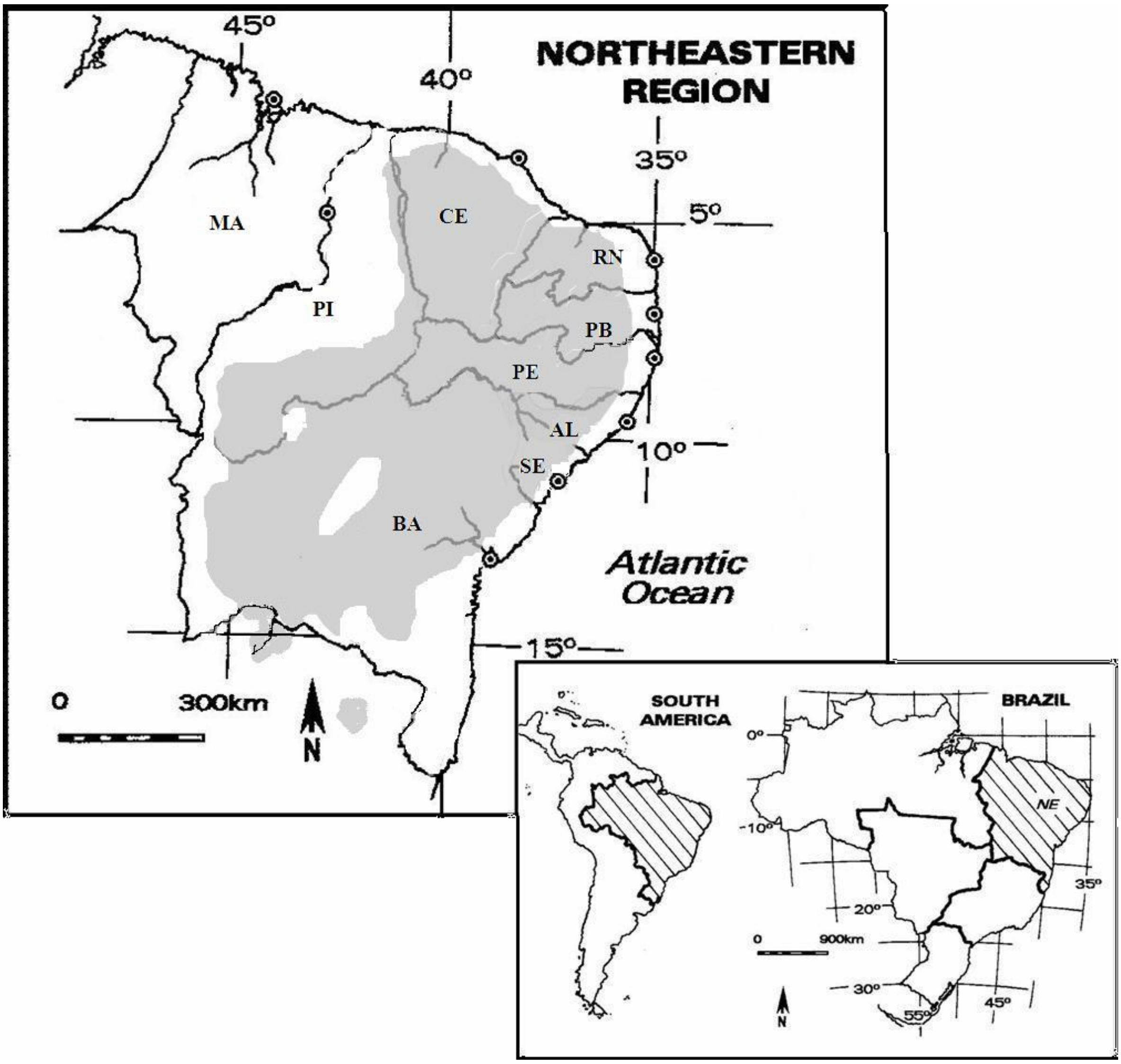

Fig. 1 Map showing the location of the Caatinga domain (gray). AL: Alagoas, BA: Bahia, CE: Ceará, MA: Maranhão, PB: Paraíba, PE: Pernambuco, PI: Piauí, RN: Rio Grande do Norte, SE: Sergipe.

woody and park (**Fig. 2A-F**). The park type is characterized by large quantities of Poaceae and Cyperaceae, and trees being distributed in disjoint patches. In all physiognomic types of Caatinga, the richness of herbaceous stratum is high, however this is the less studied component: there are only a few studies concerning floristic, structure and population dynamics of herbs (Rodal *et al.* 1999; Araújo and Ferraz 2003; Reis *et al.* 2006; Costa *et al.* 2007), similarly to what occur in other tropical formations (Royo and Carson 2005). Studies including only three NE states showed the presence of 624 herb species (Araújo *et al.* 2002a; Silva 2005; Costa *et al.* 2007), mainly distributed in the families Poaceae, Convolvulaceae, Asteraceae, Fabaceae, Euphorbiaceae, Convolvulaceae, Cyperaceae, Malvaceae, Scrophulariaceae and Rubiaceae (Feitosa 2004; Pessoa *et al.* 2004; Silva 2005; Araújo *et al.* 2005a; Reis *et al.* 2006), indicating that the richness of herbaceous flora is approx. three times that of woody stratum (Araújo 2003).

There are an elevated number of floristic and phytosociological studies on the woody component of Caatinga, which employed different sample methods and showed high floristic and structural heterogeneity (**Table 1**). There are approx. 1.102 species of trees and shrubs (Gamarra-Rojas and Sampaio 2002), 318 of them are endemic (Giulietti e*t al.* 2002). The most common families are Euphorbiaceae, Leguminosae, Cactaceae and Anacardiaceae (Araújo *et al.* 1995), and the species C*aesalpinia pyramidalis* Tul. (Caesalpiniaceae), *Anadenanthera colubrina* (Vell.) Brenan (Mimosaceae), *Schinopsis brasiliensis* Engl. and *Myracrodruon urudeuva* Allemão present wide distribution (Prado and Gibbs 1993; Sampaio 1995).

Generally-speaking, the Caatinga suffers strong anthropogenic pressures, as a consequence of space occupation by man and exploration of natural resources (Sampaio 2002; Albuquerque and Andrade 2002a, 2002b; Agra *et al.* 2005; Albuquerque *et al.* 2005a, 2005b). Recognized as one of the "Earth's last wild places' and classified as one of the 37 'Wilderness Areas of the World' (Gil 2002), the Caatinga is now fragmented in areas of several degrees of disturbance (MMA 2002). Until now, only 16% of Caatinga areas are protected as conservation unities of total protection (Tabarelli and Vicente 2004). In intensively degraded areas, desertification may occur, in which plant cover is almost totally removed, the soils are degraded, farming productive capacity is low and social conditions of local populations are deteriorated (Sampaio and Araújo 2005).

The most recent review related to Caatinga ecosystem is found in Leal *et al.* (2003), that focused on plant and animal diversity, ecology and conservation. In this review, we aim to present an overview related to the state-of-art of the ecological processes and dynamics of Caatinga ecosystem. We divided the text in three parts: in the first, we focused plant responses to climatic seasonality; in the second, we discuss the main ecological processes that originate and maintain biological and cultural diversity; finally, we discuss how this diversity is used by people that live within Caatinga limits.

Fig. 2 Some physiognomic types and microhabitats of Caatinga vegetation in the rainy season. (**A**) park; (**B**) shrubby; (**C**) shrubby/woody; (**D**) woody; (**E**) stone microhabitat; (**F**) riparian microhabitat.

PLANT ECOPHYSIOLOGICAL RESPONSES TO RAINFALL SEAZONALITY

Hierarchically, the most important abiotic factor influencing plant life in Caatinga is water availability (Sampaio 1995; Araújo 2005), although light and nutrients represent very important factors that affect productivity of the herbaceous component, as well as biomass of the woody one (Sampaio 2003). About 85-90% of the total rainfall occurs during the rainy season, but precipitation values may vary between years, affecting germination, recruitment, growth and production of flowers and fruits (Araújo 2005; Lima 2007). Similarly, the total rainfall in other arid and semiarid forests of the world present a high variation coefficient between years, and water is also an important factor influencing plant performance and ecosystem functionality (Knaap and Smith 2001; Knapp *et al*. 2002; Weltzin *et al*. 2003; Nippert *et al*. 2006; Wiegand *et al*. 2006).

Climatic seasonality induces a stress state in Caatinga plants, which show ecophysiological responses that favor their capacity of survivor. The occurrence of a year without drought is extremely rare, but, when it happens, plants maintain their leaves; this data shows the extension to which water affects their productivity and development (Araújo 2005). After five to nine months of dry season (**Fig. 3A-B**), the vegetation rapidly responds to the rain, and produce leaves (Araújo and Ferraz 2003), which may minimize light incidence upon the soil, the temperature and the evapotranspiration, favoring general conditions for plant development.

The reduction on rainfall rates between consecutive years may induce great variations in leaf size and duration of some Caatinga species, suggesting the existence of more favorable years for light absorption and to carbon sequestration (Araújo *et al*. 2002b). An increased leaf area affects shading and soil temperatures, and may influence water infiltration and draining, as well as litter production.

Other leaf morphological features such as the presence and distribution of trichomes, epicuticular waxes and stomata may also influence plant performance, directly or indirectly affecting their water potential (Lambers *et al*. 1998). Trichomes and stomata, for example, may be concentrated near the base, apex, middle or abaxial surface of the leaf blade of some species, such as *Croton rhamnifolius* Müll. Arg. and *C. sonderianus* Müll. Arg. (Euphorbiaceae), *Myracrodruon unrundeuva* Fr. Allemão (Anacardiaceae) and *Commiphora leptophloeos* (Mart.) Gillet (Burseraceae) (Araújo *et al*. 2002b; **Fig. 4**). The biological implications of these variations are not well understood, but it is suggested that they may favor CO_2 uptake and diminish water loss, resulting in variations in leaf water potential between species (Campos 1991; Nogueira and Barbosa 1998; Mansur and Barbosa 2000; Araújo *et al*. 2002b).

One of plants' physiological strategies related to temporal adjustment to the dry season is the mechanism of CAM photosynthesis (Crassulaceae acid metabolism), which favors carbon capture along the year (Lambers *et al*. 1998; Larcher 2000). However, many deciduous species of Caatinga that do not have CAM mechanism have large quantities of lenticels in the stem, and also a chlorophyll tissue

Table 1 Variations in sample criteria, species richness and vegetation structure of Caatinga woody vegetation in NE Brazil.

Locality	ST	P	A (ha)	C	S	TD	BA	Reference
Xique-Xique	BA	617	0.75	H≥1 m	14	960	-	Silva 1991
Quixadá	CE	-	5.00	H≥50 cm/D≥3 cm	10	610	-	Tavares *et al.* 1969a
Barbalha	CE	730	5.00	H≥50 cm/D≥3 cm	28	730	-	Tavares *et al.* 1974a
Tauá	CE	620	5.00	H≥50 cm/D≥3 cm	11	300	-	Tavares *et al.* 1974b
CBHistrano	CE	848	0.50	DSL≥3 cm	48	4250	34.70	Medeiros 1995
Aiuaba	CE	637	0.40	DSL≥3 cm	29	3780	-	Oliveira *et al.* 1988
Piranhas-Açu	PB	-	5.00	H≥50 cm/D≥3 cm	24	537	12.50	Tavares *et al.* 1975
Barra de São Miguel	PB	363	0.10	DSL≥5 cm	7	870	-	Lira 1979
Cabaceiras	PB	246	0.10	DSL≥5 cm	9	3190	-	Lira 1979
São João do Cariri	PB	386	0.20	DSL≥5 cm	10	1870	-	Lira 1979
Serra Branca	PB	386	0.20	DSL≥5 cm	9	1930	-	Lira 1979
São José do Belmonte	PE	-	5.00	H≥50 cm/D≥3 cm	61	897	14,80	Tavares *et al.* 1969b
Ourucuri	PE	-	5.00	H≥50 cm/D≥3 cm	16	689	10.19	Tavares *et al.* 1970
Petrolina	PE	570	5.00	H≥50 cm/D≥3 cm	45	534	7.30	Tavares *et al.* 1970
Santa Maria da Boa Vista	PE	454	0.42	DSL≥5 cm	26	459	5.50	Drumond *et al.* 1982
Fazenda Nova	PE	557	0.30	H≥20 cm	37	1390	-	Lyra 1982
Parnamirim	PE	585	0.35	All species	31	1240	-	Santos *et al.* 1992
Boa Vista I	PE	651	0.25	DSL≥3 cm	28	1872	20.80	Rodal 1992
Boa Vista II	PE	651	0.25	DSL≥3 cm	22	1076	34.29	Rodal 1992
Fasa	PE	632	0.25	DSL≥3 cm	23	1876	16.51	Rodal 1992
Poço do Ferro II	PE	632	0.25	DSL≥3 cm	24	2172	15.62	Rodal 1992
Baixa do Faveleiro	PE	585	1.40	CNS≥5 cm	35	3973	19.84	Araújo *et al.* 1995
Poço do Ferro I	PE	585	1.60	CNS≥5 cm	28	3098	31.80	Araújo *et al.* 1995
Custódia	PE	574	1.50	CNS≥5 cm	30	5385	32.24	Araújo *et al.* 1995
Petrolina	PE	570	1.40	DSL≥3 cm	48	3100	33.40	Nascimento *et al.* 2003
Serra Talhada	PE	679	0.30	DSL≥3 cm	35	3555	30.60	Ferraz *et al.* 1998
Brejo da Madre de Deus	PE	553	1.00	DSL≥3 cm	32	2828	19.45	Andrade 2000
Buíque	PE	600	1.00	DSL≥3 cm	33	1824	8.20	Figueredo and Rodal 2000
Caruaru	PE	612	1.00	DSL≥3 cm	39	3810	24.90	Alcoforado-Filho *et al.* 2003
São Raimundo Nonato	PI	689	1.00	DSL≥3 cm	40	5827	31.90	Lemos and Rodal 2002
Vale Açu	RN	-	4.00	H≥50 cm/D≥3 cm	19	1170	-	Tavares *et al.* 1975
Açu	RN	704	-	DBH≥5 cm	19	970	10.80	Ferreira 1988
Salineira	RN	707	0.40	DSL≥5 cm	17	1380	-	Figueredo 1987
Serra Negra	RN	600	1.00	CBH≥3 cm	15	3247	6.10	Amorim *et al.* 2005
Nossa Senhora da Glória	SE	650	0.40	DSL≥5 cm	60	1515	-	Souza 1983
Frei Paulo	SE	650	0.20	DSL≥5 cm	36	1222	-	Souza 1983
Barra da Onça I	SE	500	0.15	DSL≥3 cm	35	2913	37.60	Fonseca 1991
Barra da Onça II	SE	500	0.15	DSL≥3 cm	26	3947	36.40	Fonseca 1991
Fazenda Califórnia	SE	500	0.15	DSL≥3 cm	32	3340	48.20	Fonseca 1991
Curitiba I	SE	500	0.15	DSL≥3 cm	23	3360	44.40	Fonseca 1991
Curitiba II	SE	500	0.15	DSL≥3 cm	28	4427	39.50	Fonseca 1991

ST: Brazilian state, See Fig. 1; P = annual precipitation (mm); A = sampled area; C = criteria, S = number of species; TD = total density (ind.ha^{-1}); BA = Basal area (m^2.ha^{-1}); H = height; D = diameter; DSL = diameter at the soil level; DBH: diameter at breast height; CSL = circumference at the soil level; CBH = circumference at breast height.

under the ritidome (a part of the epidermis that is naturally discarded, and constituted by a thin layer in many species, **Fig. 3C-D**); this structure suggests the possibility of stem photosynthesis in these plants (Araújo 2005). This ritidome may function as a covering that attenuates transpiration rates and allows photosynthesis to occur in the dry season, when leaves are absent. Thus, carbon sequestration by deciduous species plants in Caatinga would occur constantly throughout the year. However, this hypothesis was not yet tested, but once corroborated, future studies could answer questions such as: (1) Do all woody deciduous species of Caatinga present this kind of photosynthetic process? (2) Are the biochemical pathways in stem photosynthesis similar to those of leaves?

In field conditions, plants may enlarge, reduce or maintain their stem size (height and diameter), both in the wet and in the rainy seasons; positive growth rates are higher in the rainy season, but may also be recorded in the drought (Araújo and Tabarelli 2002), what may be interpreted as an evidence of stem photosynthesis hypothesis discussed above (Araújo 2005). The negative growth in height has been interpreted as a result of the loss of some parts of the aerial system, which would represent a late expression of the stress occurred during the dry season (Araújo and Tabarelli 2002). Other plants loose their aerial parts due to the fall of other plants, both in the dry or in the wet season (Araújo 2005).

It is important to note that many herbaceous climbers (such as *Apodanthera glaziovii* Cogn. – Cucurbitaceae and *Cissus* cf. *simsiana* Schult. & Schultz.F. – Vitaceae) present lateral ramifications when they reach the canopy (5-12 m), resulting in an expansion of the individual. Then, the stems grow down, fix their roots in the soil and sometimes disconnect themselves from the original plant, generating a clone population, that compete with other woody plants for resources. Both connected and unconnected stems may create new stems that grow upon other plants, reaching again the canopy, a strategy that induces the breaking of aerial parts of several woody plant species, which stay longer in the juvenile stage (Araújo and Tabarelli 2002).

PHENOLOGY, REPRODUCTIVE BIOLOGY AND ECOSYSTEM DYNAMICS

Plant biological responses to climatic seasonality influence, direct and indirectly, important ecological processes that maintain plant diversity in different Caatinga habitats, such as pollination, dispersal, germination, recruitment, and consequently the population, community and ecosystem dynamics. These processes wil be discussed below.

Phenology

Generally, studies concerning phenology strategies in the Caatinga focused on isolated species, or some species from a family, mainly woody or succulents. The patterns most

Fig. 3 Caatinga vegetation physiognomy in the dry season and some functional aspects of the ecosystem. (**A, B**) Shrubby and shrubby-woody Caatinga, respectively; (**C, D, E**) Tissue with chlorophyll under the ritidome in *Amburana cearensis* (Fabaceae), *Commiphora leptoploeos* (Burseraceae) and *Cnidoscolus bahianus* (Euphorbiaceae), respectively. In **C** and **E** a thin layer was removed for better observation of the chlorophyll tissue. (**F**) a ramet of *Croton sonderianus* (Euphorbiaceae), resulted from vegetative propagation.

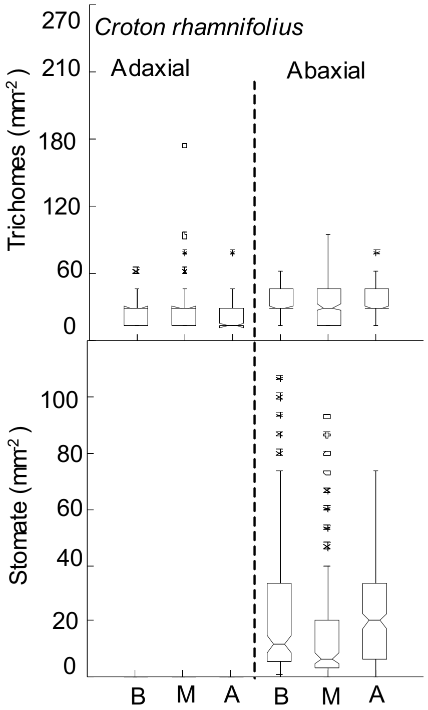

Fig. 4 Density and distribution of stomates and trichomes in the base (B), medium (M) and apex (A) of leave surface of the Caatinga shrub *Croton rhamnifolius* (Euphorbiaceae) in NE Brazil. * = extreme points; box = 50% of the size variation; line inside the box = median; narrow region around the median = confidence interval; superior and inferior bars = 25% of the size variation. (From Araújo *et al.* 2002b).

commonly recorded are (1) flushing and flowering as a consequence of precipitation; (2) variation in the fruiting period, depending on the dispersion syndrome: zoochorous species generally produce fruits between the dry and rainy seasons, autochorous in the rainy season and anemochorous in the dry one (Barbosa *et al*. 2003), when wind circulation is maximized because of leaves senescence (Griz *et al.* 2002); (3) leaf senescence in the dry season (Barbosa *et al.* 1989; Machado *et al*. 1997; Piedade-Kill and Ranga 2000; Lorenzon *et al*. 2003). However, generally-speaking, all phenophases occur along the year (Machado 1996; Machado *et al*. 1997; Machado and Lopes 2002; Araújo 2005). Several particular phenological strategies were already recorded in Caatinga, such as (1) flowering and fruiting in the wet season; (2) flowering in the wet season and fruiting in the dry one; (3) flowering and fruiting in the dry season; (4) flowering and fruiting twice a year (Machado 1996). As a consequence of these diverse strategies, there is a continuous resource availability for pollinators, dispersers and herbivorous along the year, in the different vegetation strata, although the amounts of these resources vary along the year. Seasonal rainfall was also considered the main factor influencing flowering and fruiting phenologies in other dry forests of the world (e.g., McLaren and McDonald 2005, but see Sloan et al. 2007).

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Sexual and breeding systems and asexual reproduction

A general review about the sexual and breeding systems of Caatinga species was published by Machado *et al.* (2006), and will be discussed here. In relation to sexual systems, 147 species of several life forms were evaluated, belonging to 91 genera and 34 families, what represent approx. 16% of Caatinga flora (MMA 2002). Similarly to what was showed by studies concerning sexual systems of plant communities, the hermaphroditism was the most frequent sexual system (83%); monoecy was recorded in 9.5% of species (associated to the high frequency of Euphorbiaceae species), followed by andromonoecy (4.8%, mainly represented by Solanaceae species), and dioecy (2.7%).

The proportion of dioecious species was lower than that estimated for Angiosperms (6%, Renner and Ricklefs 1995), and also to that which was recorded in studies developed in the majority of dry and wet forest formations, even if one takes into account the different life forms. This low proportion may be explained by the fact that this sexual system is generally associated with small, generalist flowers (i.e., pollinated by a large spectrum of animals, generally insects), which are not so frequent in Caatinga species (Machado and Lopes 2004), to zoochorous fruits (Bawa 1980; Bawa *et al.* 1985), which are not the most common in plants of this ecosystem (Griz and Machado 2001, see discussion in Pollination and dispersion section below), and to tree species (Bawa *et al.* 1985; Bullock 1985; Kress and Beach 1994; Renner and Ricklefs 1995) that present lower heights in this plant formation (Sampaio 1996).

In relation to breeding systems, the tendencies also corroborated the majority of studies related to reproductive biology in plant communities in Brazil (Oliveira and Gibbs 2000) and in the world (Bullock 1985; Ramírez and Seres 1994; Jaimes and Ramírez 1998). Self-incompatibility was predominant (61.5%), followed by self-compatibility (38.5%) for all life forms (except for herbs, which are in a general matter associated with self-compatibility, Jaimes and Ramirez 1999), and no agamospermic species was recorded. Taking into account the self-incompatible and the dioecious species, the total number of species that present obligate alogamy is almost 65%, a value higher than that observed for some humid ecosystems (Ramirez and Brito 1990), indicating the necessity of pollinators for satisfactory reproduction. Machado *et al.* (2006) pointed out the relatively low number of studied species, and the necessity of new studies concerning the breeding systems of Caatinga species.

Some Caatinga species, for example, although being self-compatible, set fruits mainly through cross pollination (Piedade-Kill and Ranga 2000; Quirino and Machado 2001). Moreover, although Machado *et al.* (2006) did not record agamospermic species, this reproductive mechanism was already observed for *Croton sonderianus* Müll. Arg. (Euphorbiaceae, Araújo 1998). The low frequency of agamospermy in Caatinga may indicate that pollination services seem to be satisfactory, since the high incidence of agamospermic species is generally related to low availability of adequate pollinators (Ramírez and Brito 1990)

Some Caatinga species are capable of other asexual reproduction strategies, such as through root shooting (**Fig. 3F**, Araújo and Ferraz 2003). Vegetative propagation allows: (1) a rapid colonization during the rainy season; (2) the maintenance of some allele frequencies; (3) the maintenance of population sizes in years with *veranicos* (see Population and communities dynamics). Because of the disconnection that may occur between ramets after vegetative propagation, population quantitative surveys may overestimate seed production rates. For this reason, the investigation of species presenting mixed reproduction systems (Araújo 1998) would be of great interest, and could also be useful in future restoration projects.

Pollination and seed dispersal

There are relatively few studies related to pollination biology in Caatinga (Machado *et al.* 2006). Similarly to what occurs for phenological and breeding system studies, those related to pollination processes investigate only a single species, or some species of the same genus. We will discuss here the most recent review of pollination patterns in Caatinga (Machado *et al.* 2006). This study showed the existence of a great diversity of colors, shapes, sizes and pollination systems, and the following tendencies: (1) large flowers (65.2%) more common than medium and small ones; (2) actinomorphy (61.7%) more common than zigomorphy; (3) predominance of disk and tubular floral shapes (48.6%), and a considerable proportion of flag flowers (15.3%, due to the presence of Fabaceae species); (4) bright colors (62.8%) more frequent than pale ones.

The higher frequency of showy flowers differed to what was observed in other vegetation community types, such as the Cerrado (Oliveira and Gibbs 2000), a Venezuelan shrubland (Ramírez *et al.* 1990) and some humid areas (Silva e*t al.* 1997). On the other hand, some community features were also observed in other studies, such as (1) the predominance of radial, isolated flowers and (2) the tendency of small size and collective unities among the pale colored ones (Ramírez *et al.* 1990).

The nectar was the most common floral resource (71.50%), followed by pollen (15.3%) and oil (9.0%), nectar + pollen (2.8%) and resin (1.4%). Machado and Lopes (2004) pointed out that, although climatic restrictions, pollination systems in Caatinga are diversified, similarly to what was recorded in other tropical communities. Entomophily was the syndrome most commonly observed, followed by ornitophyly and chiropterophily; among insects, the bees represented the main group of pollinators.

Honey bees visited species of the Mimosaceae, Fabaceae, Euphorbiaceae, Malvaceae and Convolvulaceae, a group of plants with economic potential (honey) in Caatinga (Carvalho and Marchini 1999). The higher availability of floral resources in the rainy season, as a consequence of phenological patterns discussed above, result in a greater diversity and abundance of pollinators in this period of the year (Zanella *et al.* 2003).

Although being of great importance for the structure and dynamics of populations, communities and ecosystems, seed dispersal studies in Caatinga are too scarce yet (Griz *et al.* 2002). Among woody plants, there is a predominance of medium-sized (46.7%) and large fruits (25.2%), as well as fleshly ones, followed by drupe, capsule, legume and others. Depending on the locality, similar proportions of dispersion syndromes may occur, such as zoochory, anemochorous and balistic + barochory (Griz and Machado 2001), or the predominance of any one of them, such as autochory being more common than zoochory and anemochory (Barbosa *et al.* 2002). On the other hand, dispersion patterns in Caatinga also reflect rainfall seazonality and may vary in relation to the distance from the ocean: precipitation is inversely proportional to the distance from the ocean, resulting in a humidity gradient and, consequently, a gradient of dispersion syndromes. Anemochory is more common in dry areas, and zoochory in humid ones (Vicente *et al.* 2003). Moreover, in Caatinga, similar to other dry forests (Gentry 1983), anemochorous species tend to present a broader distribution than zoochorous ones, which are more susceptible to endemisms (Vicente *et al.* 2003). A recent study showed that dispersion by monkeys may influence positively the regeneration of Caatinga (Moura and McConkey 2007).

Beyond primary dispersion, Caatinga seeds may be secondarily dispersed by ants, which allow a redistribution of seeds in the soil (affecting spatial distribution patterns) and influence germination rates (Oliveira *et al.* 1995; Araújo and Ferraz 2003; Leal 2003). Until now, 18 ant species were recorded (mainly the genera *Pheidole* and *Dorymyrmex*) acting as secondary dispersers of 27 woody caatinga species, mainly those of Euphorbiaceae (40.7%), but also non-mirmechocorous species of Anacardiaceae and Cactaceae (Leal 2003).

Seed bank dynamics in the soil

The Caatinga seeds present variable sizes, being smaller in herbaceous taxa (Araújo *et al.* 2006), whose species diversity in the seed bank is greater than that of woody ones (Costa and Araújo 2003; Pessoa 2007).

In the pre-dispersion phase, many species suffer high predation levels and pathogen attack (Ferraz EMN *et al.*, pers. comm.), reducing the chances of recruitment and consequently plant reproductive success (Leal 2003). Although there are very few studies related to seed predation in Caatinga (Silveira *et al.* 2005), it seems that, after dispersion, seed predation rates may be high, and differ between species, possibly because of (1) differences in chemical composition of their metabolites and hard tegument (Silveira *et al.* 2005); (2) temporal heterogeneity of rains, causing differences in predation rates between dry and wet seasons (Araújo EL, pers. comm.). Differences in predation rates between seasons may indicate that the bimodal fruiting presented by some species represent a strategy that compensate the unpredictability of seed survivor after dispersion (Araújo and Ferraz 2003).

Seed bank turn-over in the soil may be more than once a year for species whose flowering is bimodal or continuous (Araújo and Ferraz 2003). The destiny of healthy seeds when they arrive in the seed bank of Caatinga is variable. Part of them may (1) be removed by secondary dipersal (Leal 2003); (2) be attacked by pathogens or predators and die (Silveira *et al.* 2005); (3) be recruited to the seedling stage (Araújo *et al.* 2005b; Lima 2007) or (4) remain in the seed bank for a variable period (Araújo and Ferraz 2003). The scientific knowledge of these possibilities, as well as of seed production remains unclear for most Caatinga species.

Seed germination occurs mainly in the rainy season for herbaceous and woody taxa, allowing regeneration (Silva and Barbosa 2000; Costa and Araújo 2003; Araújo *et al.* 2005b, 2006). However, sporadic rains may eventually occur during the dry season and result in germination of herbaceous seeds. However, this is not an advantage, since these seedlings will die before the arrival of the rainy season, and represent a loss in the seed bank (Lima 2007).

Many Caatinga species exhibit tegument dormancy as an ecophysiological strategy of protection against predators, and also drought escape, allowing germination in the rainy season (Barbosa *et al.* 2002; Araújo and Ferraz 2003; Barbosa 2003). In laboratory conditions, scarification (mechanical and chemical) induced higher levels of germination in 60% of the total of 70 studied species; these results indicate that Caatinga seeds present a high frequency of exogenous dormancy (Araújo *et al.* 2006).

The depth to which seeds are deposited in the Caatinga soil affects the probability and velocity of germination (Costa and Araújo 2003). Thus, in areas subjected to degradation processes, the superficial revolving of the soil would be a strategy that could facilitate local regeneration; in field conditions, this action is performed by native fauna, which facilitate Caatinga diversity processes.

Until now, the period in which the viable seeds stay in Caatinga soil banks is unknown. The few studies related to seed longevity were developed in the laboratory and indicated that the conservation *ex situ* of some species' germplasm is possible using cold chambers. Actually, the number of Caatinga seeds that are conserved in cold chambers is very low, and include mainly woody species of economical importance (Araújo *et al.* 2006).

Population and community dynamics

Until now, in field conditions, there are a few studies related to population dynamics in Caatinga (Barbosa and Barbosa 1996; Araújo *et al.* 2005b; Reis *et al.* 2006). A study that investigated seedling establishment of five woody species with adult individuals showed that the recruitment was more intense during the rainy season; recruitment in the dry season varies between species (Barbosa and Barbosa 1996).

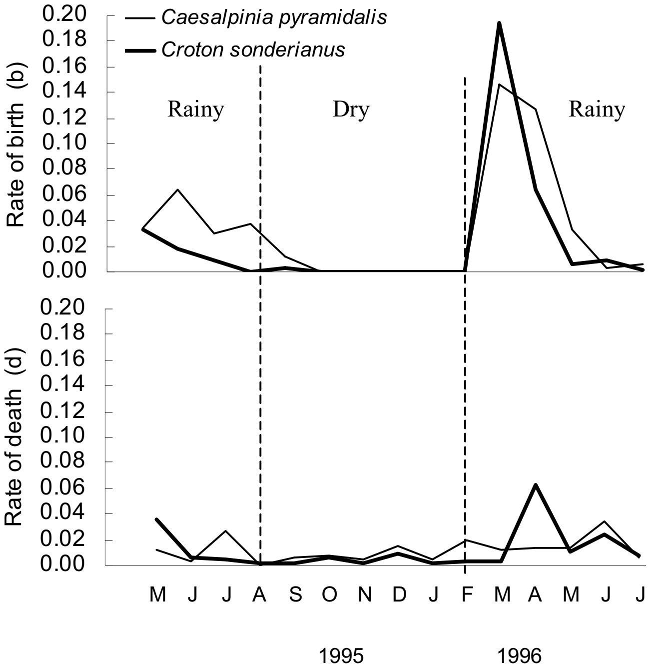

Fig. 5 Monthly rates of birth and death in populations of Caatinga woody species of NE Brazil. (From Araújo *et al.* 2005b).

Two dynamic models were described for woody species of Caatinga, based on a monthly census of births and deaths for all ontogenetic stages of *Croton sonderianus* and *Caesalpinia pyramidalis* (Caesalpinaceae). For the first species, germination occurs in the beginning of the wet season and, for the second, it occurs throughout this season (Araújo and Tabareli 2002; Araújo *et al.* 2005b). The two models include advantages and disadvantages for the plants (**Fig. 5**). The advantage of the first is that the seedling has water availability for a long time, a condition that allow its development and survivorship during the subsequent dry season; the disadvantage is represented by the risk of elevated mortality in years with the occurrence of periods of drought during the wet season (locally called *veranicos*). The advantage of the second model is the reduction of mortality risk during the *veranicos*, and the disadvantage is the high probability of mortality for seedlings recruited at the end of the wet season, because of the subsequent dry season. Both models show the inexistence of a seedling bank; this development stage is ephemeral and only occurs in the wet season, when birth rates are high; seedling mortality in wood plant species is higher in the wet season than in the dry one (Araújo *et al.* 2005b; Araújo 2005).

In Caatinga it may occur delays or anticipations of the wet and dry seasons; this unpredictability acts as an additional stressing factor that modifies demographic features of plant populations (Araújo 2005). Such unpredictable variations were also recorded in other arid and semi-arid environments around the world (Weltzin *et al.* 2003; Nippert *et al.* 2006; Wiegand *et al.* 2006).

Herb dynamics also depends on the seasonality of rains in the Caatinga, and the demographic models for this stratum may be consistent or not between years (Lima 2007). Therophyte herbs, such as *Gomphrena vaga* Mart. (Amaranthaceae), germinate in the beginning of the rainy season and present high mortality during drought. In perennial herbs such as *Dorstenia asaroides* Hook. (Moraceae), the births are distributed along the rainy months (**Fig. 6**; Lima 2004). Both annual and perennial herbs may present great differences in births between rainy seasons of subsequent

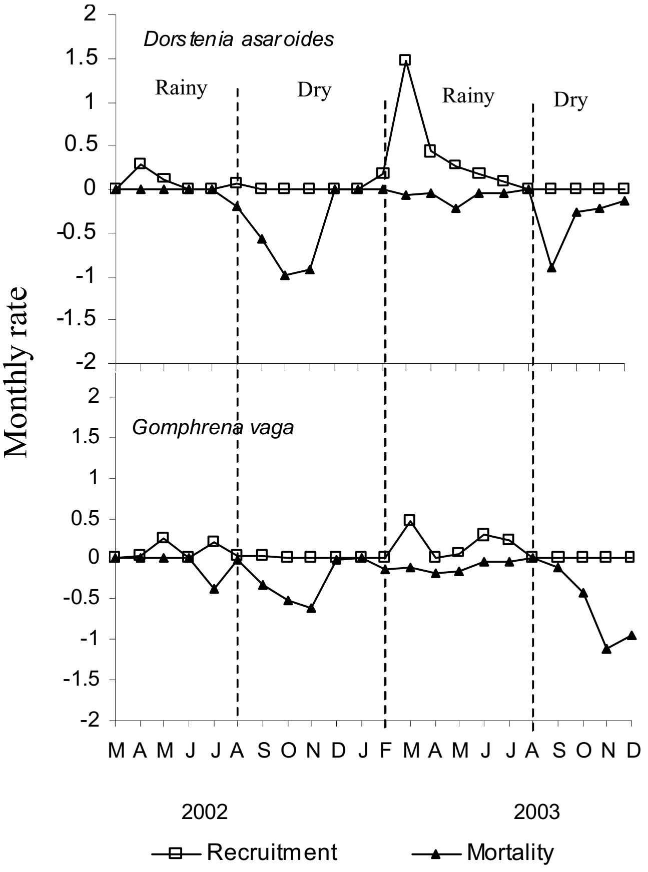

Fig. 6 Birth (birth.individual.month^{-1}) and death (death.individual. month^{-1}) monthly rates in populations of herb Caatinga species in NE Brazil. (From Araújo 2005).

years (Araújo 2005; Lima 2007). Spatial variations may also occur in the microhabitat conditions, represented by the presence of rocks and water courses (temporary or perennials), soil erosion ridges, shading differences and so on. Such variations, together with the rain seasonality, may modify birth, mortality and survivorship rates of Caatinga herb species (Lima 2007; Pessoa 2007).

Variations between years in total rainfall also modify the structure of the herb community, resulting in drastic reductions in population sizes, or even in local disappearance of some species in some years (Reis *et al.* 2006). The frequency and the occurrence of herbs seem to be variable in time and space: in a 5-year study, Araújo and Sampaio (pers. comm.), recorded 96 species in an area of 0.5 ha (distributed in 105 plots). Some of them (e.g., *Callisia repens* L., Commelinaceae, **Fig. 7**), were always present in the study area (frequent in time) but did not occur in the same plots between years (variable occurrence in space). Others (e.g., *Euphorbia insulana* Vell., Euphorbiaceae, **Fig. 8**) were frequent in time and space, and others (e.g. *Entodontopsis leucostega* (Brid.) Buck and Irel, Stereophyllaceae, *Desmodium glabrum* (Miller) DC., Fabaceae and *Cleome diffusa* Banks ex DC., Capparaceae, **Fig. 9**) were frequent and with variable occurrence in time and space (i.e., did not occur in the same plots between years or were absent in some years). These results indicate that the herbaceous component may present faster responses to inter-annual variations in rainfall than the woody one; this probably occurs because of the differences in the life cycles span of these strata.

In arid savannas, the dynamic of woody species is related to that of herbs. The interaction between their dynamic models is conducted by the high variability of precipitation, fire and competition, and allows their co-existence (Weiegand *et al.* 2006). Fire is not a natural factor in the Caatinga, but the interactivity between the dynamic models of these two components may also occur, since the births of these species coincide with the rainy season. Herbs, for example, may co-exist with tree seedlings, and sometimes may even "suffocate" them, causing their death (Lima 2007). The intensity of this interactivity between the dynamic models in Caatinga community was not measured yet.

Studies concerning plant cover regeneration in areas of Caatinga that suffered anthropogenic actions (such as burning and cutting) indicated a high capacity of sprouting and, consequently, regeneration through vegetative propagation (Sampaio *et al.* 1998; Carvalho *et al.* 2001; Pereira *et al.* 2001; Figuerôa *et al.* 2006). However, population structures

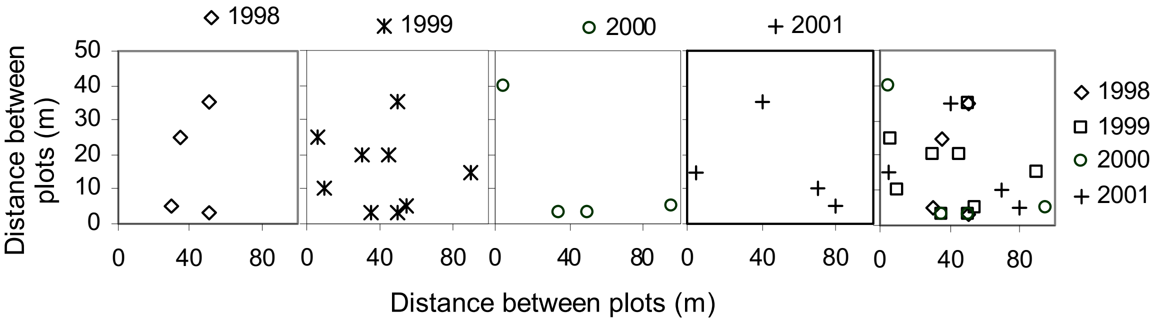

Fig. 7 Occurrence of the Caatinga herb *Callisia repens* (Commelinaceae) in an area of 0.5 ha between 1998 and 2002 in NE Brazil. (From Araújo 2005).

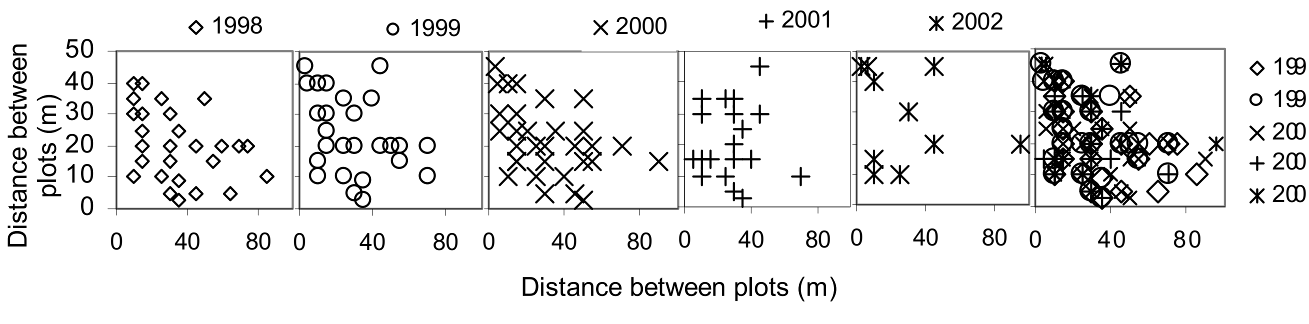

Fig. 8 Occurrence of the Caatinga herb *Euphorbia insulana* (Euphorbiaceae) in an area of 0.5 ha between 1998 and 2002 in NE Brazil. (From Araújo 2005).

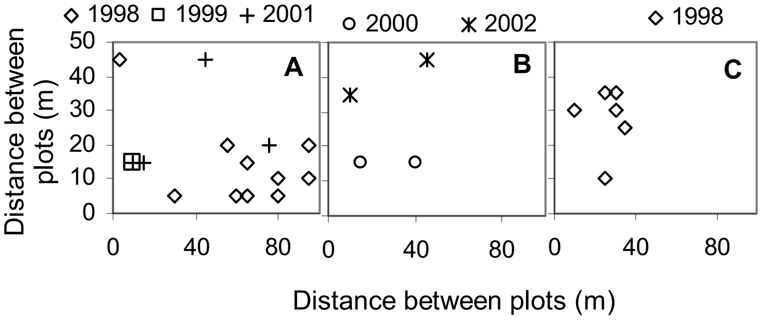

Fig. 9 Occurrence of the Caatinga herbs *Entodontopsis leucostega* (Stereophyllaceae, A), *Desmodium glabrum* (Fabaceae, B) and *Cleome diffusa* (Capparaceae, C) in an area of 0.5 ha between 1998 and 2002 in NE Brazil. (From Araújo 2005).

may hardly be altered: populations with greater capacity of regeneration after stress may exhibit disequilibrium features and dominate the space that were previously occupied by many species; this evidence shows that ecological processes were not totally restored, or, at least, were restored at different rates (Araújo and Ferraz 2003).

HOW DO PEOPLE INTERACT WITH CAATINGA RESOURCES?

Beyond the biological diversity and ecological processes discussed above, the Caatinga presents a great cultural richness due to its occupation by diverse ethnic groups, that are distributed in almost all region, and that may be divided generally speaking in indigenous groups, *quilombolas* (i.e., black descendents brought to Brazil as slaves, and that now are relatively isolated in some regions) and rural communities (Diegues and Arruda 2001).

Caatinga vegetation, although being very disturbed by historical occupation processes and irrational uses, constitutes an important source of subsistence for those communities, which also collect products that are necessary to maintain and reproduce their practices. The distinct ethnic groups explore differently the biological resources of Caatinga, as a function of social, cultural, economic and/or ecological aspects (Silva and Andrade 1998; Sampaio 2002; Silva 2003; Albuquerque *et al.* 2005a; Mota and Albuquerque 2006; Silva *et al.* 2006; Albuquerque *et al.* 2007)

From the local communities' point of view, plants may play several roles (Sampaio 2002), but the use of wood is the most commonly recorded. There are several studies concerning the uses of native Caatinga species, but relatively few systematic investigations of ethnobotany were made. Initially, the main objective of ethnobotanical projects was to describe useful plants; from 2000 until now, there is a tendency of comprehend the processes and patterns of use of those resources through the formulation of questions and specific hypothesis. In general, studies focused on the role of plant species in medicine (Silva and Albuquerque 2005), fodder (Ferraz *et al.* 2005, 2006), rural constructions (Lucena *et al.* 2007), as fuel (Ramos 2007), food and medicine for people (Albuquerque and Andrade 2002a, 2002b). Curiously, few native species are cited as food for people in the interviews made with local populations, probably due to the absence of specific studies, their little importance, or even to local people interpretation that eating these plants is a signal of poorness (Albuquerque 2006).

The role of seasonality in the use of plant resources

Peoples' choices concerning the use of plants in Caatinga seem to be greatly conditioned to plant responses to the climatic seasonality; other variables, such as social structure and economy, are also important (Albuquerque 2006), but will not be discussed here. Data show that preferred plants, or the most used ones, are those whose availability is not affected by the local seasonal pattern (Albuquerque and Andrade 2002a; Albuquerque and Lucena 2005; Albuquerque *et al.* 2005b; Albuquerque 2006). The spontaneous herbaceous layer, as was discussed above, is the most affected by severe drought conditions, when its populations drastically diminish in number. Therefore, there is a preference for the shrub and arboreal plants, from which man's populations mainly obtain wood (for several uses) and/or stem bark for uses in local medicine (Albuquerque *et al.* 2005b; Albuquerque 2006; Monteiro *et al.* 2006a; Silva *et al.* 2006). Generally, herb species have major importance only because of the necessity of feeding domestic animals during the rainy season, even these plants are potential items for man food and medicine (Albuquerque and Andrade 2002a, 2002b).

An example of preference by available items along the year is the use of stem barks from *Myracrodruon urundeuva* (*aroeira*, Anacardiaceae) and *Anadenanthera colubrina* (*angico*, Mimosaceae) as anti-inflammatory. In fact, the bark has a high concentration of phenolic compounds, justifying the local indications (Monteiro *et al.* 2006a, 2006b). However, high concentrations of these substances were also found in leaves during some periods of the year, sometimes even with higher values than those recorded for stems (**Fig. 10**, Monteiro *et al.* 2006a). These data show that the continuous availability of bark may induce their choice by people, independently if the phenolic concentrations of leaves are similar or even better than that of bark.

In the set of plants used for medicinal purposes in the world, there is predominance of exotic herbs and/or from managed habitats, a fact that led Voeks (2004) to suggest that traditional medicines are based in a disturbance regime. However, conversely to what was proposed by some authors (Stepp and Moerman 2001; Voeks 2004), this high richness does not necessary imply peoples' preference for those plants. In Caatinga, for example, people often prefer to use native tree species rather than spontaneous or cultivated herbs (Albuquerque and Andrade 2002a, 2002b; Albuquerque *et al.* 2005b). Similar results were also recorded in other arid and semi-arid areas of the world (Estomba *et al.* 2006).

The apparent low importance of herbs for local communities of Caatinga may be also explained by the quantity of available information concerning these plants or by the seasonal pattern discussed above. From a total of 624 herb Caatinga species (Araújo *et al.* 2002a; Silva 2005; Costa *et al.* 2007), at least 16% are cited by people as being useful in local medicine (Sales and Lima 1985; Agra 1996; Rocha and Agra 1996; Cabral and Agra 1998; Silva and Andrade 1998; Costa-Neto and Oliveira 2000; Albuquerque and Andrade 2002a, 2002b; Almeida and Albuquerque 2002; Silva 2003; Marinho 2004; Trovão *et al.* 2004; Lucena 2005; Almeida *et al.* 2006). Moreover, at least 15% of these herbs are known as medicinal plants for other human communities in Brazil and in the world. Although these proportions seem to be expressive, it is necessary to consider if these species are, in fact, used by people, since the knowledge about plant properties does not prove its use, as was noted by Albuquerque *et al.* (2005b) for a local community in Caatinga. In this study, people knew many medicinal herb species of broad use, but preferred to use native tree species, even if they had to cover large distances to find them.

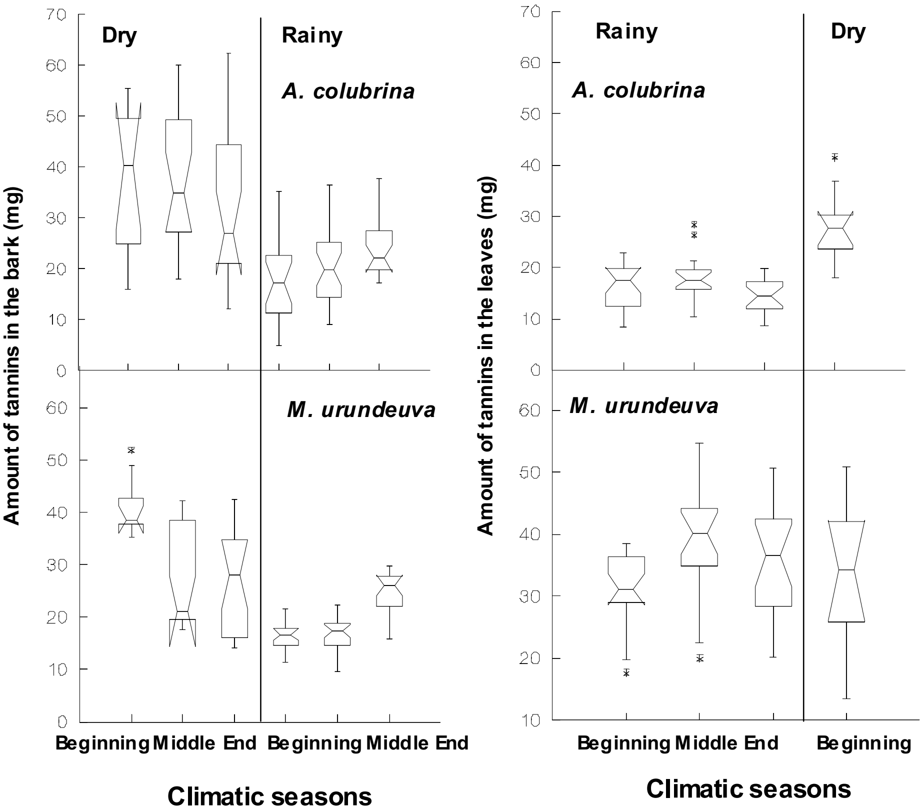

Fig. 10 Relationship between the amounts of tannins in barks and leaves, for a 500 mg sample of *Anadenanthera colubrina* (Vell.) Brenan (Mimosaceae) and *Myracrodruon urundeuva* (Engl.) Fr. All. (Anacardiaceae) and the climatic seasons in two rural communities of Caatinga, NE Brazil. * = extreme points; box = 50% of the size variation; line inside the box = median; narrow region around the median = confidence interval; superior and inferior bars = 25% of the size variation. From Monteiro *et al.* (2006a).

If the climatic seasonality and ecogeographic conditions of a region regulate the relations between people and plants, it is expected that their influence is expressed in several ways. Gottlieb *et al.* (1996) suggest that, even if one considers local ecological processes, some sets of secondary metabolites are shared by ecogeographically-related plants. Thus, a high production of plant phenolic compounds (polyphenols), for example, is expected to be produced in areas of high incidence of sun energy. In fact, a study in Caatinga corroborated this hypothesis. Almeida *et al.* (2005) studied a diversified sample of medicinal plants (including herbs, shrubs and trees) in Caatinga and recorded that all of them presented phenolic compounds. Trying to comprehend the choice criteria for the selection of plants by people, the authors investigated local preferences and also the chemical composition of plants. It was found that herbs (and other plants presenting short life cycles) are not more important for local medicine, and do not present higher incidences of bioactive compounds of low molecular weight (alkaloids, for example). These results indicate that cultural and ecological factors influence local strategies of plant selection and use by local people. The comprehension of these processes may contribute to the more rapid advance of studies related to conservation and bioprospection of biodiversity (Albuquerque and Lucena 2005).

Dynamics of use of woody plants

Woody species present a multiplicity of uses by local communities, and this feature seems to be common for Caatinga plants (Albuquerque *et al.* 2005a, 2005b; Albuquerque 2006). Some examples are *Myracrodruon urundeuva*, *Schinopsis brasiliensis*, and *Anadenanthera colubrina* (Lucena *et al.* 2007), which deserve special attention for conservation (Leite 2002; Lucena *et al.* 2007).

The availability (number individuals) seems not to present a significant relation with its potential use, or even may have a negative correlation (Ferraz *et al.* 2005, 2006). The last tendency seems also to be reflected at a regional scale for plants popularly recorded as medicinal (Silva and Albuquerque 2005). In the case of plants used as firewood in Caatinga, there are differences in the set of species that people cited during the interviews, that they truly use and that they prefer to use (Ramos 2007). The choice of these plants, however, is also influenced by intrinsic qualities (see Shackleton 1993; Abbot and Lowore 1999) that are locally perceived, such as the fuel properties of plants that are used for firewood, for example (Ramos 2007).

It is necessary to develop more studies with ethnobotanical approach, as well as to distinguish between potential use and real use, associated with pressures for use (Albuquerque *et al.* 2006). There is evidence that the frequency in which a plant species occurs in a Caatinga fragment may constitute an important aspect for its potential use as a medicinal (Lucena 2005). The spatial distribution pattern of a species, however, seems not to affect its extractive activities; total abundance seems to be a more important fact (Oliveira *et al.* 2007).

How do people affect ecological processes in Caatinga?

The land use history and the manner in which people relate themselves with plant resources influence ecological processes in Caatinga. The establishment of pastures and the expansion of agriculture have been recognized by ecologists and biologists as disturbances that modify structure and diversity in the ecosystem (Leal *et al.* 2005). Similarly, the proximity to cities and the construction of roads, for example, may predict the fragmentation and loss of habitats (Santos and Tabarelli 2002). Although Caatinga areas are subject to all these anthropogenic pressures, until now there is very few information to be used as a base of generalizations of human impact in this important ecosystem. Broad-scale events overlap little local events, which are a result of man's action upon specific resources, and are not recorded neither quantified. In Amazonia, for example, some areas of "primary" vegetation seem to be a result of manipulation by indigenous groups (Albuquerque 1999; Chazdon 2003). This data led us to believe that human impact upon tropical forests may be less apparent than is believed, and with effects even less perceptible. Thus, it is necessary to abolish the idea of virgin forests, and change the notions of climax and stability by a model of flux and dynamism (Chazdon 2003).

In our point of view, to adopt this model, and to include man's role in the ecosystem (not only as a destroyer) is a strong, very important and necessary paradigm change. The fact that people interact with different natural resources, present preferences by determined species, make selective cut and collection, may generate even more unexpected effects upon dynamic and ecological processes in plant communities, not necessarily negatives. Plant selective cuts, for example, may modify survival and mortality rates of plant populations, pollinator sharing, or even affect neighboring populations with which they are ecologically related. However, there are no studies that evaluate these aspects, and that join the approaches of plant ecological investigations (e.g., population structure and dynamics) with resource uses and management by people (e.g., ethnobotany). Although human actions upon forests is always seen as destructive, local practices of plant uses may constitute good models (see Florentino *et al.* 2007) to evaluate this complex resource interaction dynamics. Nascimento (2007), for example, observed that the use of wood from native species for the construction of fences (for delimitation of rural properties), can lead to a pressure upon a particular species group. On the other hand, the habit of using native plants in live fences may function as a source of germplasm and diaspores of these species, and also connect landscape elements. The impacts of these actions in the communities' dynamics are practically unknown.

The role of ethnobotanical studies in the comprehension of Caatinga dynamics

Ethnobotanical studies are not always considered in projects of other knowledge areas, such as ecology, however they could contribute as a key-element in the comprehension of variables that affect both communities and resource use dynamics. This is especially true for dry forests (Sánchez-Azofeifa *et al.* 2005). It is important to note the necessity of rigor in ethnobotanical studies (Albuquerque and Hanazaki 2006), since many misinterpretations may be made because of (1) the simplistic manner in which these studies are view or interpreted, (2) the wrong use of data collection tools (Albuquerque and Hanazaki 2006) or (3) the weak techniques of data analysis, which do not allow a consistent interpretation of what is important to say (Albuquerque *et al.* 2006). Future research programs related to Caatinga dynamics must change the discussions scenario, and include questions such as: (1) Is it possible to predict the manner in which people interact with Caatinga natural resources? (2) Can ecological models be used to explain these relations? (3) How can the use and management of natural resources affect ecological processes at population, community and ecosystem levels? (4) Which tools and/or theoretical focus must be related in these studies?

FINAL CONSIDERATIONS

Despite the considerable volume of data describing Caatinga structure and processes, it is necessary to consider the actual limitations of these studies in contributing to Caatinga conservation. Since plant responses change drastically as a function of spatial-temporal variations in rainfall, consistent generalizations about this ecosystem must be based on long-term studies. On the other hand, there is a necessity of rapid answers to problems related to management and conservation of natural resources. Our review also indicates the necessity of studies that consider the ecological processes and the use of natural resources by people together. This is an important action because it may allow a broad comprehension of the environment and the complex relations net that are developed.

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