

Plant species and habitat structure in a sand dune field in the Brazilian Caatinga: a homogeneous habitat harbouring an endemic biota

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ABSTRACT– (Plant species and habitat structure in a sand dune field in the Brazilian Caatinga: a homogeneous habitat harbouring an endemic biota). One dune habitat in the semi-arid Caatinga Biome, rich in endemisms, is described based on plant species composition, woody plant density, mean height and phenology and a multivariate analysis of the micro-habitats generated by variables associated to plants and topography. The local flora is composed mainly by typically sand-dweller species of Caatinga, suggesting the existence of a phytogeographic unity related to the sandy areas in the Caatinga biome, which seems to be corroborated by faunal distribution. Moreover, some species are probably endemic from the dunes, a pattern also found in vertebrates. The plant distribution is patchy, there is no conspicuous herbaceous layer and almost 50% of the ground represents exposed sand. Phenology is not synchronized among species, occurring leaves budding and shedding, flowers development and anthesis, fruits production and dispersion both in rainy and dry seasons. Leaf shedding is low compared to the level usually observed in Caatinga areas and about 50% of the woody individuals were producing leaves in both seasons. Spectrum of dispersal syndromes shows an unexpected higher proportion of zoochorous species among the phanerophytes, accounting for 31.3% of the species, 78.7% of the total frequency and 78.6% of the total density. The habitat of the dunes is very simple and homogeneous in structure and most of environmental variance in the area is explained by one gradient of woody plants density and another of increase of *Bromelia antiacantha* Bertol. (Bromeliaceae) and *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy (Cactaceae) toward valleys, which seem to determine two kinds of protected micro-habitats for the small cursorial fauna.

Key words - density, endemic species, phenology, phytogeography, semiarid

RESUMO – (Espécies vegetais e estrutura do hábitat em um campo de dunas arenosas na Caatinga brasileira: um hábitat homogêneo portando uma biota endêmica). Um ambiente de dunas no bioma Caatinga, rico em endemismos, é descrito a partir da composição florística, da densidade, altura média e fenologia das espécies lenhosas e de uma análise multivariada dos micro-habitats criados por variáveis associadas às plantas e à topografia. A flora local é composta principalmente por espécies típicas de áreas arenosas da caatinga, sugerindo a existência de uma unidade fitogeográfica na caatinga relacionada a áreas arenosas, o que parece ser corroborado por dados faunísticos. Além disso, algumas espécies são provavelmente endêmicas das dunas, padrão também observado nos vertebrados. A vegetação possui distribuição agregada, não há estrato herbáceo conspícuo e quase 50% do solo representa areia nua. A fenologia das espécies não é sincronizada, ocorrendo brotamento e queda de folhas, desenvolvimento e antese de flores e produção e dispersão de frutos nas estações seca e chuvosa. A caducifolia é particularmente baixa em comparação com outras áreas de caatinga e cerca de 50% dos indivíduos lenhosos produz folhas nas duas estações. O espectro de síndromes de dispersão mostra uma proporção de espécies zoocóricas inesperadamente alta entre as fanerófitas, representando 31,3% das espécies, 78,7% da frequência total e 78,6% da densidade total. O hábitat possui estrutura bastante simples e homogênea: a maioria da variância na área é explicada por um gradiente de densidade de lenhosas e outro de aumento de *Bromelia antiacantha* Bertol. (Bromeliaceae) e *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy (Cactaceae) em direção aos vales, determinando dois tipos de micro-habitats protegidos para a fauna cursora de pequeno porte.

Palavras-chave - densidade, espécies endêmicas, fenologia, fitogeografia, semi-árido

Introduction

The Caatinga Morphoclimatic Dominion extends over an area of about 700,000 km² of Northeast Brazil

(Ab'Saber 1974) and represents one of the most inhospitable Brazilian landscapes due to a peculiar conjunction of physical factors. The mean annual temperature of about 28° C makes it one of the hottest semiarid areas of the world. Its rains are scanty and unevenly distributed in time and space, its water courses are seasonally intermittent and its soils have scarce or even null water stocks (Ab'Saber 1974, Andrade-Lima 1981, Sampaio 1995).

The number of endemic plant species in the biome Caatinga is high (Rizzini 1979, Prado 2000) reaching almost 30% of the total flora (Giulietti *et al.* 2002).

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However, the vegetation of this biome is highly variable in structure and floristic composition in a local scale and different vegetations types had been proposed to highlight this heterogeneity (see summaries in Andrade-Lima 1981 and Rodal & Sampaio 2002). These include different caatinga vegetations based on tree profile, probably related to different soil and water conditions (Andrade-Lima 1981), and a vegetation with a particular floristic composition occurring on sandy soils and higher altitudes called carrasco (Araújo *et al.* 1998). More recently, Pennington *et al.* (2000) and Prado (2000) proposed the Neotropical seasonally dry forests as a new phytogeographical province and considered the Caatinga as one of its nucleus based on distribution patterns of genera present in different dry areas of the Neotropics. Moreover, the flora of the Caatinga shows several adaptations to deal with water scarcity. It is characterized by the presence of succulent plants (mainly Cactaceae and Euphorbiaceae), thorny bushes and terrestrial bromeliads. Additionally, most plants, especially trees and shrubs, have small, thin leaves and their abscission during droughts is the most significant response to the water stress (Holbrook *et al.* 1995). The activity of their stomata is fast, the stomata are kept closed most of time, and transpiration is restricted even during the wet season (Ferri 1955).

The terrestrial vertebrate fauna of the biome Caatinga, on the other hand, has been supposed to show very little adaptations to this stressful habitat: some works have proposed that small mammal populations aggregate on the rock outcroppings where microhabitat conditions are more mesic (Streilein 1982c) as there are no physiological adaptations in these animals to restrict water lose and to deal with long periods of droughts (Mares *et al.* 1985, Streilein 1982a, b). The number of endemic species of reptiles, birds and mammals has also been considered very low (Sick 1965 *apud* Mares *et al.* 1985, Vanzolini *et al.* 1980, Willig & Mares 1989). The mastofauna of Caatinga, for example, is supposed to represent an impoverished subset of those from Atlantic forest and Cerrados (Mares *et al.* 1985), including only 80 species (Willig & Mares 1989). More recent studies, however, have detected at least 143 species in the biome (Oliveira *et al.* 2003). Some authors suggested that some species may have physiological adaptations to the semi-arid conditions (Barros *et al.* 1998, Ribeiro *et al.* 2004) and that the causal factors underlying the pattern of small mammal abundances in the Caatinga probably includes variables other than structural complexity of the substratum and humidity and shelter availability, as amount of herbs and litter, plant species richness, and

amount of loose gravel (Rocha, unpublished data).

Moreover, recent zoological studies in the State of Bahia (Brazil) have lead to the discovering of a region that, in spite of its small extent relative to the Caatinga biome (c. 7.000 km², Oliveira *et al.* 1999), holds several endemic genera and species (Sauria, Serpentes, Amphisbaenia, Aves, Rodentia), many of which show morphological and behavioral adaptations to psammophily (Lencioni-Neto 1994, Rocha 1995, Rodrigues 1996). The area, referred to as “The Little Sahara along the São Francisco River” (Williams 1925 *apud* Oliveira *et al.* 1999) is a palaeodesert consisting of an extensive and inactive dune field that lies on the banks of the middle São Francisco River, between Barra and Pilão Arcado (Rodrigues 1996).

During the executions of two research projects focusing the ecology of squamates and rodents from the dunes (Rocha 1991, 1998), data were collected on the local flora in order to appreciate the resources available to the fauna. Due to the intrinsic biological importance of the dunes and to the general lack of quantitative information on the Caatinga vegetation, floristic and phytosociological data were collected in order to describe qualitatively and quantitatively the local plant community. The first objective of the present article is to present one description of this important ecosystem based on: (1) the plant species composition, (2) the density estimates and height distributions of the woody species, (3) data of the phenology and dispersion syndromes of the species and (4) a multivariate description of the microhabitat in the dunes based on the variables used in (2) and on topography, on the proportion of plants of different habits, on the level of shade, and on the amount of litter. The second objective is to discuss evidences suggesting that plant species in the dunes represent one phytogeographic unity related to other sandy areas and different from the Neotropical seasonally dry forests. The third objective is to discuss the ways the habitat structure in the dunes may influence the local fauna.

Methods

The study site – The dunes are located in one strip of arid and semiarid climates extending southwest from Raso da Catarina, along the valley of middle São Francisco River, where mean annual temperatures are the highest in the state of Bahia, exceeding 26.2 °C (Bahia-Septentec 1978). Records from meteorological station closest to Ibiraba, in Barra (ca. 50 km SW of Ibiraba), indicate annual mean rainfall of 692 mm (ranging from 400 to 800 mm), dry season of 7 to 8

months and rain season from October to March (Nimer 1979). The fieldwork was performed in sand dunes of Ibiraba village, Barra, in Bahia state (10°48' S and 42°50' W). The study area is about 500 m away from the nearest village, that occupies mainly lowlands in the flooding plain of São Francisco River, near Icatu River. The dunes are apparently undisturbed by recent human action except for some extraction of wood for fire making. Indeed, the local human demographic density (less than 5 inhabitants.km⁻²) is one of the lowest for the State (Bahia-Septaltec 1978).

The studied area represents the third of the five geomorphologic dominia of the sandy seas in the middle São Francisco River, as classified by Barreto (1996). In this dominium of dunes with sharp morphology, dune summits stand about 40 m higher than the river level, and up to 20 m higher than the dune valleys. Vegetation physiognomy on the dunes differs from that on neighbor alluvial plain for in the first the trees and bushes are shorter and patchier in distribution and there is not a conspicuous herbaceous covering even in the raining season. Therefore, most of sandy soil rests exposed, except for the presence of patches covered by the terrestrial bromeliad *Bromelia antiacantha* Bertol., by the small cacti *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy and by litter.

Field procedures and data analysis – Six expeditions were accomplished. The first two took place in August-October/1988 and January-February/1989, and the last four in February-March/1996, September/1996, December/1996 and February-March/1997. The species list was obtained by collecting in a 10 ha sand dune area during 1988, 1989 and 1997 expeditions. Vernacular names of plant species were obtained by interviews with the local population. Vouchers of the botanical material obtained are housed in the herbaria HUEFS and SPF (acronyms according to Holmgreen *et al.* 1990).

Quantitative analyses were based on data obtained from sampling grids and included the following three items:

(1) Density estimate and distribution of height frequencies of woody species - (data collected in 1989) The point-quarter method described in Krebs (1999) was applied for 210 sampling points in two grids (11 columns × 10 lines) plotted 50 m apart. Distance between successive rows and between successive columns was 20 m. Woody individuals taller than 1.5 m were included in the sampling and their height and species recorded.

(2) Evaluation of phenologic state of woody species - In 1989 the phenologic state of the trees and shrubs, whose fruits and seeds were supposed to be consumed by the endemic rodent *Trinomys yonenagae* Rocha (*Eugenia* sp., *Copaifera coriacea* Mart., *Simaba ferruginea* A. St-Hil., *Byrsonima gardnerana* A. Juss., *Jatropha mutabilis* (Pohl) Baill., and *Bombacopsis retusa* (Mart. & Zucc.) A. Robyns), were evaluated. A total of 110 points per grid was used to sample the nearest individual (distance ≤ 10 m) taller than 1.0 m of each species in each quadrant. For each individual it was

recorded the presence or absence of leaves, flowers and fruits. In each one of the four field campaigns from 1996 to 1997 the phenology analysis was broadened to include all the woody species (individuals higher than 1.0 m), sampled by the quarter-point method based on four parallel transects with one sampling point every 25 m (10 points per transect). Each sampled specimen was identified and its phenologic state (presence and absence) related to leaves (budding and shedding), flowers (development and anthesis), and fruits (development and dispersion) was recorded.

Spectrum of the dispersal syndromes was determined by analyses of the morphological characters of the dispersal units and comparing them to the classes of dispersal syndromes proposed by Pijl (1972). For the present study, barochory was included in the class of autochory.

(3) Multivariate description of the habitat structure (performed for the 1989 data) – The microgeographic position of the sampling points in the dunes was recorded as a nominal variable with four levels: summit (SUM: horizontal area leading to at least two descending slopes), valley (VAL: horizontal area leading to at least two ascending slopes), slope (SLO), and plateau (PLA: horizontal area leading to at least one descending and one ascending slope). A 4 m diameter circle centered in each point was used to evaluate the relative contribution of horizontal projection of trees (TRE: woody individuals with a single main stem, undivided near the soil), of shrubs (SHR: woody individuals with multiple stems rising from the soil + sub-shrubs), of herbaceous plants (HER: almost exclusively *Bromelia antiacantha* Bertol. and *Tacinga inamoena* (K. Schum.) N.P. Taylor & Stuppy), and of exposed sand (SAN). In order to estimate these values, an integer value (0 to 10) was attributed to each variable in a way that the four values per circle summed 10. The proportion of exposed soil (without plants) in each circle was evaluated for amount of litter (LIT) by attributing a value from 1 to 3 (little litter, equal parts of litter and uncovered sand, much litter). Each circle was also evaluated for the amount of shade (SHA), depending on the amount of branches in trees and shrubs, by attributing a value from 1 to 3 (little shade, median shade, much shade). Finally, it was computed the main height of (HEI) and mean distance to (DIS) the four closest woody individuals sampled per point by the point-quarter method. The variables TRE, SHR, HER, LIT, SHA, HEI, and DIS plus three binary (*dummy*) variables derived from the microgeographic region (SUM, VAL, and SLO) were reduced by a Factor Analysis based on the PCA model (Statistica for Windows, release 5.1, 1997) in order to detect orthogonal sets of highly correlated variables. The variable SAN and fourth level of the nominal variable (PLA) were ignored in order to avoid the colinearity effect. The analysis was performed for the total data (two grids) extracting the factors associated to latent roots (eigenvalues) greater than 1.000 and applying the VARIMAX orthogonal rotation, which simplifies the structure related to the components (Kleibaun *et al.* 1988). When used for the sake of description of data,

and not for hypothesis testing, factor analyses can hold wide departures from the ideal conditions as data normality (Gauch 1982), as in the data presented here.

Additionally, three profiles of the local plant community were drawn in order to graphically represent the structure of plant covering in a strip 2 meter wide in the summit, slope and valley.

Results

The floristic survey has detected 86 species in 37 families (table 1). The richest families were Leguminosae (24 species), Euphorbiaceae (9), and Cactaceae (5). Bignoniaceae, Convolvulaceae, Sterculiaceae, and Turneraceae were represented by

three species each, while Cyperaceae, Loranthaceae, Malvaceae, Molluginaceae, Rubiaceae, and Sapindaceae by two species each. The remaining 24 families were represented by only one species each. Some of the species either are still undescribed (*Eugenia* sp., probably an undescribed species; M.L. Kawasaki, personal communication) or were described during and after the 1980's (e.g., *Mimosa xiquexiquensis*, Barneby 1991, and *Pterocarpus monophyllus*, Klitgaard *et al.* 2000). Until now, *Dioclea marginata* was known only by the type, collected during the XIX century (Maxwell 1969). More than half of all the sampled species are trees or shrubs (50.6%), and the herbaceous and subshrub strata contribute only with 29.4% of the sampled species. Succulents represent 5.9% the species in the

Table 1. List of plant species from the dunes of Ibiraba, Bahia, Brazil, habits, dispersal syndromes, and their vernacular names collected with the local population. Code refers to the plant numbers represented in the profiles (figure 5). Vouchers: Q = collection by L.P. Queiroz; R = collection by P.L.B. Rocha. Dispersal syndromes: ANEM = anemochory; AUTO = autochory + barochory; EPIZO = epizoochory; ZOOC = zoochory (fleshy fruits or with fleshy seed arils).

Family/Species	Code	Vernacular names	Habit	Dispersal syndrome	Voucher
ACANTHACEAE					
<i>Harpochilus neesianus</i> Mart. ex Nees	9	brinco	Shrub	AUTO	Q 4793, 4887; R 11, 48
AMARANTHACEAE					
<i>Alternanthera amabilis</i> Hort. ex Lem.	-	-	Herb	AUTO	Q 4828
ANNONACEAE					
<i>Annona spinescens</i> Mart.	-	araticum	Tree	ZOOC	Q 4833, 6418
APOCYNACEAE					
<i>Allamanda puberula</i> A.DC.	-	canela-de-ema	Shrub	ANEM	Q 4821; R 33
BIGNONIACEAE					
<i>Godmania dardanoi</i> (J.C. Gomes) A.H. Gentry	-	-	Tree	ANEM	Q 4800
<i>Proterantha glandulosa</i> A.H. Gentry <i>ined.</i>	-	-	Liana	ANEM	Q 6441
<i>Tabebuia heptaphylla</i> (Vell.) Toledo	-	ipê-roxo	Tree	ANEM	Q 4787; R 12
BOMBACACEAE					
<i>Bombacopsis retusa</i> (Mart. & Zucc.) A. Robyns	-	castanha	Tree	AUTO	Q 4812, 6448; R 7
BORAGINACEAE					
<i>Cordia globosa</i> (Jacq.) Humb., Bonpl. & Kunth	-	-	Shrub	AUTO	Q 4801, 4877
BROMELIACEAE					
<i>Bromelia antiacantha</i> Bertol.	13	macambira	Herb	ZOOC	Q 4891, 6446; R 9
BURSERACEAE					
<i>Commiphora leptophloeos</i> (Mart.) J.B. Gillett	-	imburana	Tree	ZOOC	Q 4881, R 41
CACTACEAE					
<i>Arrojadoa penicillata</i> Britton & Rose	-	rabo-de-cachorro	Succulent	ZOOC	R 13
<i>Cereus albicaulis</i> (Britton & Rose) Luetzelb.	-	rabo-de-raposa	Succulent	ZOOC	R 47
<i>Pilosocereus gounellei</i> (F.A.C. Weber) Byles & Rowley subsp. <i>gounellei</i>	-	xique-xique	Succulent	ZOOC	Q 4873; R 22
<i>Pilosocereus tuberculatus</i> (Werderm.) Byles & Rowley	10	mandacaru	Succulent	ZOOC	Q. 4813; R 23
<i>Tacinga inamoena</i> (K. Schum.) N.P. Taylor & Stuppy	14	quipá	Succulent	ZOOC	Q 4826; R 4

continue

continuation

Family/Species	Code	Vernacular names	Habit	Dispersal syndrome	Voucher
CELASTRACEAE					
<i>Maytenus rigida</i> Mart.	4	colher, pau-de-colher	Tree	ZOOC	Q 4782, 6435; R 11
COMPOSITAE					
<i>Vernonia lilacina</i> Mart. ex DC.	-	-	Sub-shrub	ANEM	Q 4816
CONVOLVULACEAE					
<i>Evolvulus anagalloides</i> Meisn.	-	rama-de-noiva	Sub-shrub	AUTO	Q 4827; R 28, 53
<i>Ipomoea asarifolia</i> (Desr.) Roem. & Schult.	-	-	Herb	AUTO	Q 4886
<i>Ipomoea setifera</i> Poir.	-	-	Vine	AUTO	Q 4888
CYPERACEAE					
<i>Cyperus</i> cf. <i>retrorsus</i> Chapm.	-	-	Herb	EPIZO	Q 4785; R 16
<i>Fimbristylis</i> sp.	-	-	Herb	?	R 26
EUPHORBIACEAE					
<i>Chamaesyce alsinifolia</i> Boiss.	-	quebra-pedra	Herb	AUTO	Q 4796; R 34
<i>Cnidoscolus quercifolius</i> Pohl ex Baill.	-	favela	Tree	AUTO	Q 6449
<i>Cnidoscolus urens</i> (L.) Arthur	-	cansansão	Shrub	AUTO	Q 4874
<i>Croton heliotroifolius</i> Kunth	-	velame-da-caatinga	Shrub	AUTO	Q 4765, 4824; R 36
<i>Croton sonderianus</i> Müll.Arg.	5	marmeleiro	Shrub	AUTO	Q 4829; R 51
<i>Dalechampia scandens</i> L.	-	urtiga	Vine	AUTO	Q 4768, 4862
<i>Jathropha mutabilis</i> (Pohl) Baill.	-	pinhão	Shrub	AUTO	Q 4788, 6434; R 39
<i>Manihot caerulescens</i> Pohl	-	maniçoba	Shrub	AUTO	R 37
<i>Manihot heptaphylla</i> Ule	-	-	Shrub	AUTO	Q 4772, 4865
LEGUMINOSAE					
Caesalpinioideae					
<i>Bauhinia pentandra</i> (Bong.) D.Dietr.	-	-	Shrub	AUTO	Q 4892
<i>Chamaecrista belemii</i> (H.S.Irwin & Barneby) H.S.Irwin & Barneby var. <i>belemii</i>	6	são-joão-da-caatinga	Shrub	AUTO	Q 4818; R 18
<i>Chamaecrista desvauxii</i> (Collad.) Killip	-	vassourinha	Herb	AUTO	Q 4783; R 15
<i>Chamaecrista flexuosa</i> (L.) Greene var. <i>flexuosa</i>	-	jurema	Sub-shrub	AUTO	R 29
<i>Copaifera coriacea</i> Mart.	2	sapucaia	Tree	ZOOC	Q 4789, 6457; R 5
<i>Hymenaea eriogyne</i> Benth.	-	jatobá	Tree	AUTO	Q 4804, 4834; R 50
<i>Peltogyne pauciflora</i> Benth.	-	resineiro	Tree	ZOOC	Q 4819, 4823; R 21A, 24
<i>Senna gardneri</i> (Benth.) H.S.Irwin & Barneby	-	são-joão-da-caatinga	Shrub	AUTO	Q 4803, 6432; R 18
<i>Senna macranthera</i> var. <i>pubibunda</i> (Benth.) H.S.Irwin & Barneby	-	pé-de-cabra	Shrub	AUTO	Q 4867
Mimosoideae					
<i>Acacia paniculata</i> Willd.	-	jurema	Tree	AUTO	R 46
<i>Calliandra macrocalyx</i> Harms	-	orelha-de-onça, sucupira	Tree	AUTO	Q 4879; R 40
<i>Mimosa adenophylla</i> Taub.	-	jurema-lisa	Sub-shrub	ANEM	Q 4798; R 45
<i>Mimosa invisa</i> Mart. ex Colla	-	sensitiva	Shrub	AUTO	Q 4882
<i>Mimosa xiquexiquensis</i> Barneby	11	melosa	Sub-shrub	EPIZO	Q 4784; R 2
<i>Piptadenia moniliformis</i> Benth.	-	rama-de-bezerro, folha-miúda	Tree	AUTO	Q 4878
Papilionoideae					
<i>Aeschynomene martii</i> Benth.	-	-	Shrub	ANEM	Q 4892A; R 55
<i>Bocoa mollis</i> (Benth.) Cowan	8	brinco	Shrub	ZOOC	Q 4811, 6439; R 30
<i>Centrosema brasilianum</i> (L.) Benth.	-	feijão-bravo	Vine	AUTO	Q 4871
<i>Chaetocalyx scandens</i> var. <i>pubescens</i> (DC.) Rudd.	-	-	Vine	EPIZO	Q 4869
<i>Cratylia mollis</i> Mart. ex Benth.	-	camarutuba	Shrub	AUTO	Q 4872
<i>Dioclea marginata</i> Benth.	-	mucunã	Liana	AUTO	Q 4790, 6440; R 20
<i>Galactia remansoana</i> Harms	-	-	Vine	AUTO	Q 4795

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Family/Species	Code	Vernacular names	Habit	Dispersal syndrome	Voucher
Papilionoideae (cont.)					
<i>Pterocarpus monophyllus</i> Klitg., L.P.Queiroz & G.P.Lewis	-	casaca	Tree	AUTO	Q 4825, 6438
<i>Zornia sericea</i> Moric.	-	-	Herb	EPIZO	Q 4792
LORANTHACEAE					
<i>Psittacanthus bicalyculatus</i> Mart.	-	são-joão-da-caatinga	Hemiparasite	ZOOC	Q 6417; R 43
<i>Strutanthus syringifolius</i> Mart.	-	enxerto	Hemiparasite	ZOOC	Q 4868
MALPIGHIACEAE					
<i>Byrsonima gardnerana</i> A.Juss.	7	murici	Shrub	ZOOC	Q 4798, 6445; R 32
MALVACEAE					
<i>Pavonia varians</i> Moric.	-	malva	Sub-shrub	ANEM	Q 4885
<i>Sida galheirensis</i> Ulbr.	-	malva	Sub-shrub	ANEM	Q 4889
MELASTOMATACEAE					
<i>Mouriri pusa</i> Gardn.	-	puçá	Tree	ZOOC	Q 4890, 6437; R 54
MOLLUGINACEAE					
<i>Glischrothamnus ulei</i> Pilg.	-	-	Sub-shrub	EPIZO	Q 4810
<i>Mollugo verticillata</i> L.	-	papaconha	Herb	EPIZO	Q 4809; R 35
MYRTACEAE					
<i>Eugenia</i> sp.	1	araçá-de-boi	Tree	ZOOC	Q 4799; R 6
OCHNACEAE					
<i>Ouratea glaucescens</i> Engl.	-	resineiro, araçá-de-veado	Tree	ZOOC	Q 4820; R 21, 38
OLACACEAE					
<i>Ximenia americana</i> L.	-	ameixa	Shrub	ZOOC	Q 4817; R 19
POLYGALACEAE					
<i>Polygala mollis</i> Kunth	-	-	Herb	ANEM	Q 4807; R 27
POLYGONACEAE					
<i>Ruprechtia ramiflora</i> (Jacq.) C.A.Mey.	-	vara-de-curral, pau-de-curral	Tree	ANEM	Q 4830, 4863, 4866; R 52
RHAMNACEAE					
<i>Ziziphus joazeiro</i> Mart.	-	juá	Tree	ZOOC	Q 4763, 4860
RUBIACEAE					
<i>Alibertia</i> sp.	-	marmelada	Shrub	ZOOC	R 17
<i>Borreria verticillata</i> (L.) G.F.W.Mey.	-	canelinha	Sub-shrub	AUTO	Q 4786; R 31
SAPINDACEAE					
<i>Cardiospermum corindum</i> L.	-	chumbinho	Liana	ANEM	Q 4802; R 10
<i>Serjania comata</i> Radlk.	-	-	Liana	ANEM	Q 6443
SAPOTACEAE					
<i>Sideroxylon obtusifolium</i> (Roem. & Schult.) T.D.Penn.	-	quixaba	Tree	ZOOC	Q 4837, 6427
SCROPHULARIACEAE					
<i>Angelonia blanchetii</i> Benth.	-	-	Herb	AUTO	Q 4805, 4815
SIMAROUBACEAE					
<i>Simaba ferruginea</i> A.St.-Hil.	3	pra-tudo	Tree	ZOOC	Q 4864, 6433; R 1
STERCULIACEAE					
<i>Melochia tomentosa</i> L.	-	vassourinha-preta	Sub-shrub	?	R 3
<i>Waltheria indica</i> L.	-	-	Sub-shrub	AUTO	Q 4884
<i>Waltheria brachypetala</i> Turcz.	-	-	Shrub	AUTO	Q 4883

continue

continuation

Family/Species	Code	Vernacular names	Habit	Dispersal syndrome	Voucher
TURNERACEAE					
<i>Piriqueta duarteana</i> (Cambess.) Urb. var. <i>duarteana</i>	12	malva	Sub-shrub	AUTO	Q 4791; R 42
<i>Turnera diffusa</i> Willd. ex Schult.	-	-	Sub-shrub	AUTO	Q 4806, 4822
<i>Turnera opifera</i> Mart.	-	-	Sub-shrub	AUTO	Q 4876
VERBENACEAE					
<i>Lantana caatingensis</i> Moldenke	-	-	Shrub	ZOOC	Q 4875
VISCACEAE					
<i>Phoradendron linearifolium</i> Eichl.	-	enxerto	Hemiparasite	ZOOC	Q 4880

area and all belong to the family Cactaceae. Epiphytes were absent, climbing species (vines + lianas) represent 10.6% of the sampled species and there was only 3.5% of hemiparasitic species.

The point-quarter method was able to sample 22 species in the area. The number of sampled individuals of the two most abundant species (*Eugenia* sp. and *Copaifera coriacea*) represented almost 50% of total individuals of all species ($n = 832$), whereas 14 other species represented together only about 10%. Total density of woody species in both grids was very similar (1089 ± 55 and 1074 ± 51 individuals.ha⁻¹). The densities per species calculated based on the summation of both grids are shown in table 2. Given their similarity, both grids were also summed in the other analyses.

The profile of woody plant community is low: two-thirds of all individuals higher than 1.5 meters is 2 meters high or shorter, and only 5% is taller than 4.5 meters (figure 1). Only three species (*Bombacopsis retusa*, *Mouriri pusa*, and *Pterocarpus monophyllus*) have height mode equal or higher than 5.0 meters but their total frequency represent less than 1% of total community.

Between 98% and 100% of the individuals of the six species analyzed in 1989 had leaves. Flowers were present in individuals of *Jatropha mutabilis* (13.5% of all individuals), *Copaifera coriacea* (5%) and, to a lesser degree, in *Eugenia* sp. (0.9%) and *Byrsonima gardnerana* (0.6%). Fruits were present for *B. gardnerana* (40.1%), *J. mutabilis* (24%) and *Eugenia* sp. (16.6%) and, to a lesser extent, for *C. coriacea* (1.4%). A non-quantitative evaluation of fruiting for the same species in 1988 detected that fruits were common only for *Simaba ferruginea* and *Bombacopsis retusa* and that fruits of *Eugenia* sp. were found mainly in the soil.

Results from the broader phenologic analysis carried on from 1996 to 1997 are presented in figure 2. The graphs show that the budding and shedding of leaves, development and anthesis of flowers, and production and dispersion of fruits were not synchronized among the most abundant species. The graphs based on total values of the community show that about 50% of the individuals were producing leaves all over the year, but this value rose to 74% by December. Shedding was the greatest in September (72%) and reduced progressively to about 25% in March. Occurrence of development and anthesis of flowers were evenly distributed by the year reaching the greatest values (16% and 14% respectively) in March/1997. *Eugenia* sp., *Simaba ferruginea* and *Byrsonima gardnerana* blossom and are in bloom during the dry season and in the beginning of the rainy season, while *Copaifera coriacea* and *Maytenus rigida* bloom in the climax of rainy season. Fruit development was the greatest (36%) during December, when dispersion was the lowest (6%).

The spectrum of dispersal syndromes is presented in figure 3. For the entire plant community, there is a predominance of autochorous species (43.37%) followed by zoochorous (31.11%), anemochorous (16.87%) and epizoochorous species (8.43%). However, these proportions are not homogeneously distributed among the different life forms. All of the hemiparasites and succulent species are zoochorous and all but one species of lianas are anemochorous. Epizoochory was almost restricted to herbs and sub-shrubs (6 species) except for one vine. Fleshy fruits or seed arils are absent among herbs and sub-shrubs except for the terrestrial bromeliad *Bromelia antiacantha*. On the other hand, among the phanerophytes (trees + shrubs), zoochory is the most important dispersal syndrome, accounting for 50% of the trees and 28.6% of the shrubs.

Table 2. Frequency of occurrence, accumulated percentage and density of the most abundant woody plant species in the dunes of Ibiraba, Bahia, Brazil, as estimated by the point-quarter method based on individuals taller than 1.5 meters sampled in two grids.

Rank	Species	Frequency	Accumulated percentage (%)	Density (ind.ha ⁻¹)
1	<i>Eugenia</i> sp.	284	34.1	370
2	<i>Copaifera coriacea</i>	123	48.9	160
3	<i>Simaba ferruginea</i>	80	58.5	104
4	<i>Maytenus rigida</i>	77	67.8	100
5	<i>Croton sonderianus</i>	68	76.0	89
6	<i>Chamaecrista belemii</i>	48	81.7	62
7	<i>Byrsonima gardnerana</i>	44	87.0	57
8	<i>Harpochilus neesianus</i>	29	90.5	38
9	<i>Bocoa mollis</i>	22	93.1	29
10	<i>Jatropha mutabilis</i>	19	95.4	25
11	<i>Pilosocereus tuberculatus</i>	12	96.9	16
12	<i>Bombacopsis retusa</i>	5	97.5	7
13	<i>Ruprechtia ramiflora</i>	5	98.1	7
14	<i>Peltogyne pauciflora</i>	4	98.6	5
15	<i>Ouratea glaucescens</i>	3	98.9	4
16	<i>Cratylia mollis</i>	2	99.2	3
17	<i>Mouriri pusa</i>	2	99.4	3
18	<i>Ximenia americana</i>	1	99.5	1
19	<i>Pterocarpus simplicifolius</i>	1	99.6	1
20	<i>Commiphora leptophloeos</i>	1	99.9	1
21	<i>Senna gardneri</i>	1	99.9	1
22	<i>Pilosocereus gounellei</i>	1	100.0	1
Total		832	100.0	1,083

When superimposing the dispersal syndromes on the phytosociological data, the highest importance of zoochory for the studied community is observed. Fourteen out of the 22 surveyed species are zoochorous accounting for 78.7% of the total frequency and 78.6% of the total density. Except for two succulent and one hemiparasite species, all of these species are trees and shrubs. The second class is represented by the autochorous species which contributes for 20.7% of the total frequency and 20.8% of the total density. Only one surveyed species is anemochorous, contributing for ca. 0.6% of both the total frequency and density.

After a preliminary analysis, the values of the contribution of trees and shrubs were summed and the variables TRE and SHR were replaced in PCA analysis by the variable T&S. The linearity of the relationship for every pair of variables is one of the conditions for performing the factor analysis. A visual inspection of the scatter graph matrix for the chosen variables shows that linearity is not evident in most of the cases. Based, however, in the suggestion that a straight line is always

a good approximation for a monotonic function, most of the variance of the original data must be explained by the loadings resulting from the factor analysis (Harman 1976) and it is still an useful instrument both for systematizing a great amount of data and to generate hypotheses (Gauch 1982). Three principal components representing 68.5% of the total variance of primary data were extracted in the PCA analysis. The first component (eigenvalue = 2.25) explains 25.1% of the total variance of the data. It is explained by the positive association among the variables SHA, T&S, LIT, HEI, and negative association with DIS and represents a gradient of increasing density of woody plants. The second component (eigenvalue = 2.24) explains as much of the total variance as the first one (24.9%). It is explained by positive association between VAL and HER and represents a topographic and plant gradient of increasing amount of *Bromelia antiacantha* and *Tacinga inamoena* in the direction of valleys. The third component (eigenvalue = 1.67) explains 18.6% of the variance and represents a topographic gradient, from

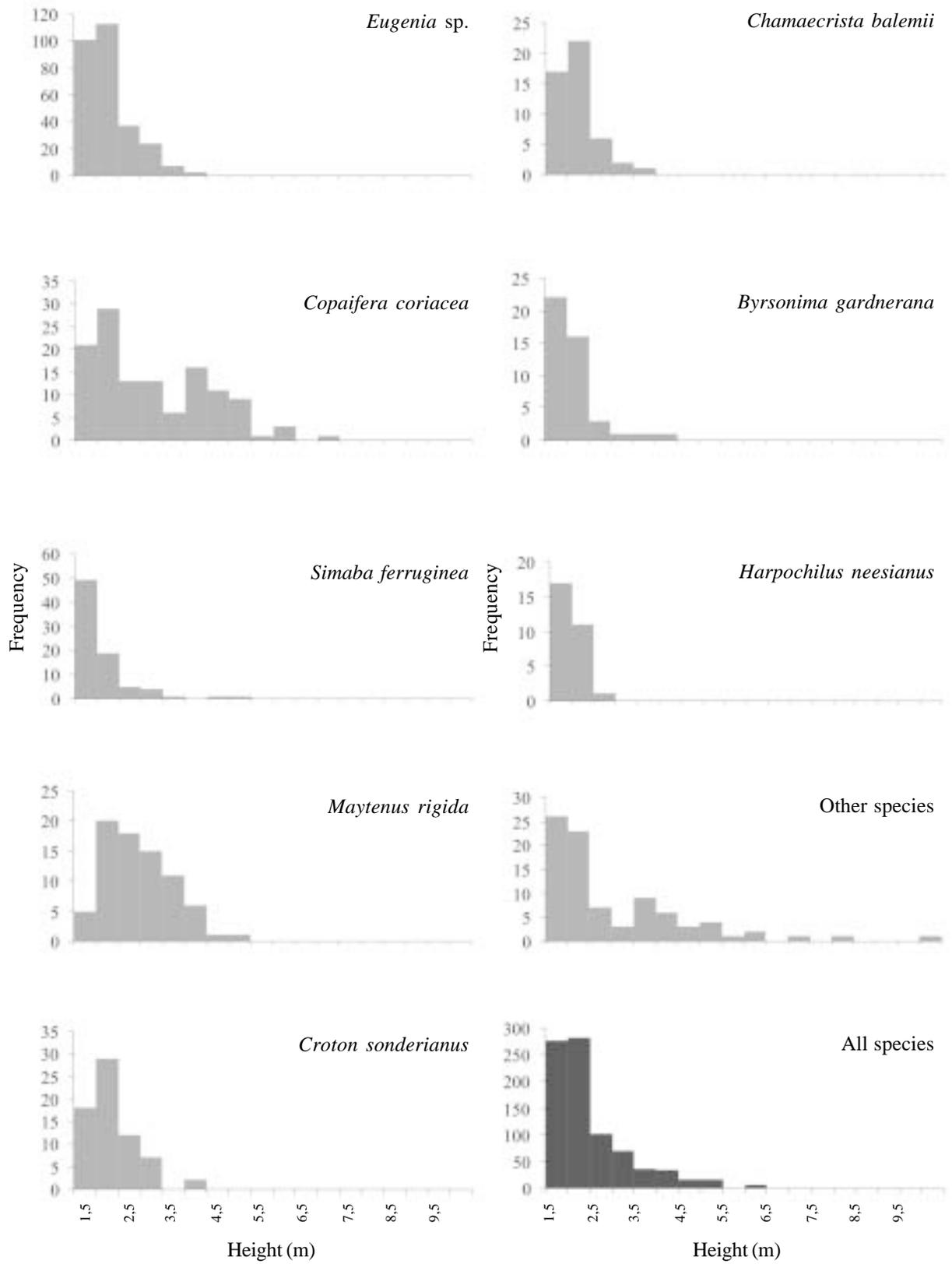


Figure 1. Height distribution of the main woody plants taller than 1.5 meters in the dunes of Ibiraba, Bahia.

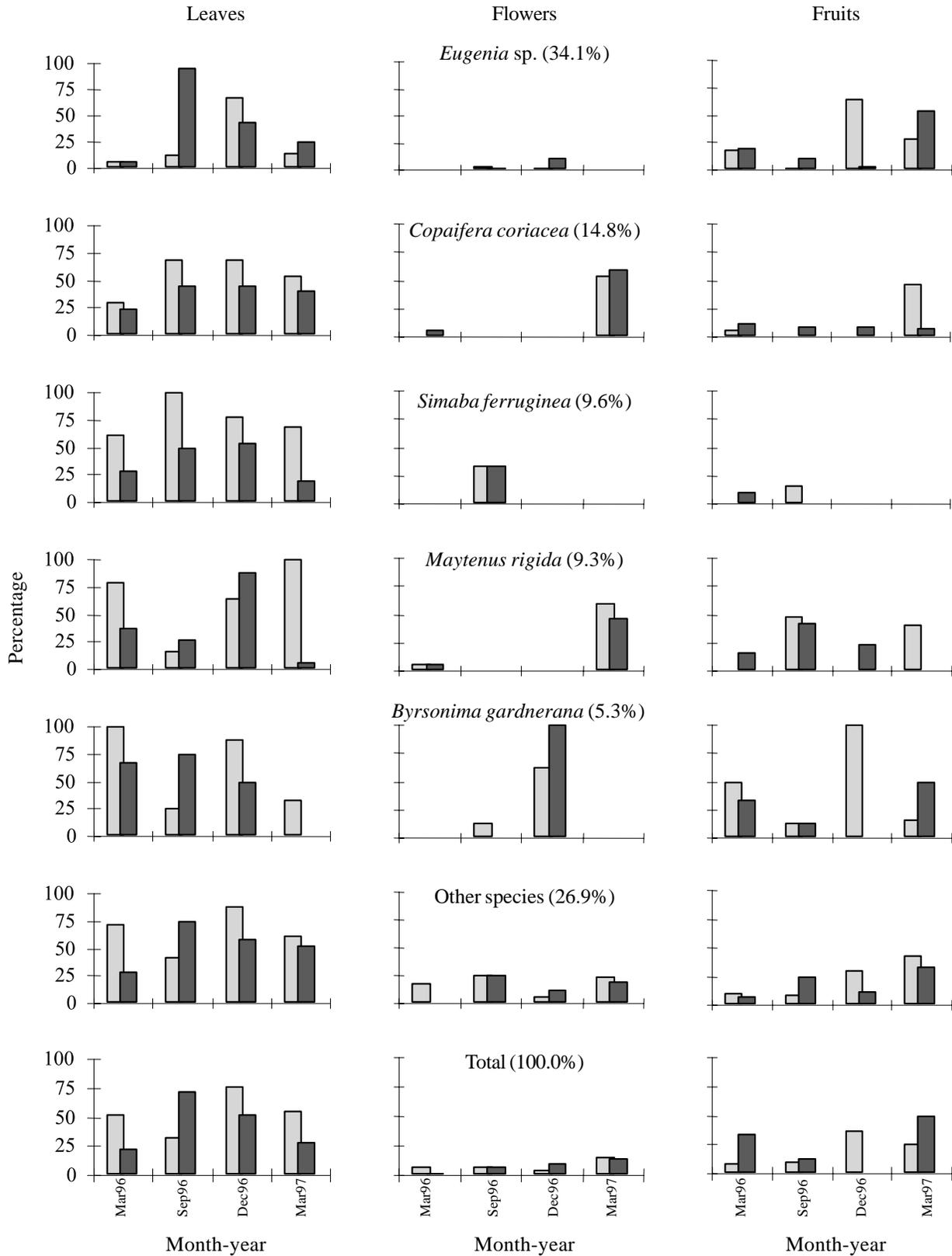


Figure 2. Phenologic state of the main woody plant species in the dunes of Ibiraba, Bahia, as quantified in four periods between 1996 and 1997. Clear bars represent budding (leaves), development (flowers), and production (fruits); dark bars represent shedding (leaves), anthesis (flowers), and dispersion (fruits). Values in parentheses refer to the relative abundance of the species.

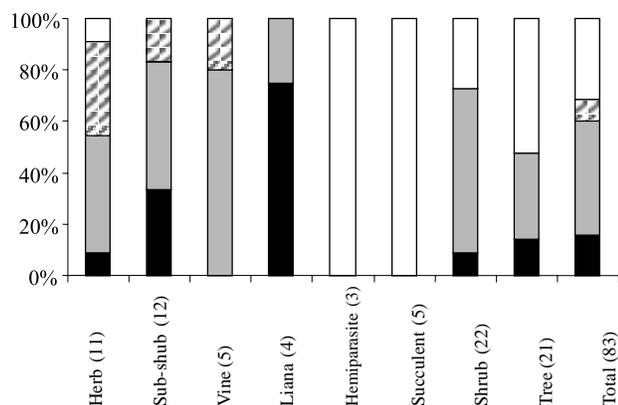


Figure 3. Spectrum of dispersal syndromes related to the life forms of the plant species in the dunes of Ibiraba, Bahia. Black bars = anemochory; gray bars = autochory + barochory; stripped bars = epizoochory; white bars = zoochory (fleshy fruits or with fleshy seed arils). Numbers in parentheses refer to number of species presenting the given life form.

summits to slopes. Figure 4 shows two-dimensional plots of component loadings. Figure 5 shows three profiles of the local plant community.

Discussion

Biogeography – The richness of plant species is low as compared to other Caatinga sites. We found 43 woody species and floristic surveys carried on other areas of Caatinga using similar methods as the presented here found 44 to 59 woody species (Lyra 1982, Araújo *et al.* 1995). The reduced number of species in the herbaceous/sub-shrub cover in the dunes is also found in other habitats in the bioma Caatinga: 31.7% of the species against 50.5% of trees and shrubs in Buíque, state of Pernambuco (Gomes 1999); 21.6% against 61.9% in Caruaru, state of Pernambuco (Alcoforado-Filho 2003); and 20.1% against 58.6% in Novo Oriente, state of Ceará (Araújo *et al.* 1998). Many of the species present in the dunes are typical from sandy soil areas in the Caatinga biome. They are present mainly in two wide areas: (a) the paleodunes of the São Francisco River between Ibiraba (ca. 10°48' S) and Casa Nova (ca. 09°20' S) in the State of Bahia extending North as far as the Gurguéia Valley, in the Southeast of the State of Piauí (ca. 09°00' S) and (b) the sedimentary deposits of Tucano-São Francisco, in the Moxotó Valley, State of Pernambuco (ca. 08°30' S), to the Raso da Catarina, State of Bahia (ca. 09°50' S). Examples of species ranging along the cited areas are *Bocoa mollis*, *Calliandra macrocalyx*, *Copaifera coriacea*, *Cratylia*

mollis, *Hymenaea eryogyne*, *Senna gardneri* (Leguminosae), *Harpochilus neesianus* (Acanthaceae), *Tacinga inamoena* (Cactaceae), *Byrsonima gardnerana* (Malpighiaceae), *Godmania dardanoi* (Bignoniaceae) and *Jatropha mutabilis* (Euphorbiaceae). Many of these species occur disjunctly in remote dry sandy areas in the Ibiapaba (ca. 04°00' S) and Araripe (ca. 07°30' S) regions (Araújo *et al.* 1998). Other species from the dunes have a very restricted geographic distribution and are probably endemic from the study area, as the Leguminosae *Dioclea marginata*, *Mimosa xiquexiquensis* (Barneby 1991), *Pterocarpus*

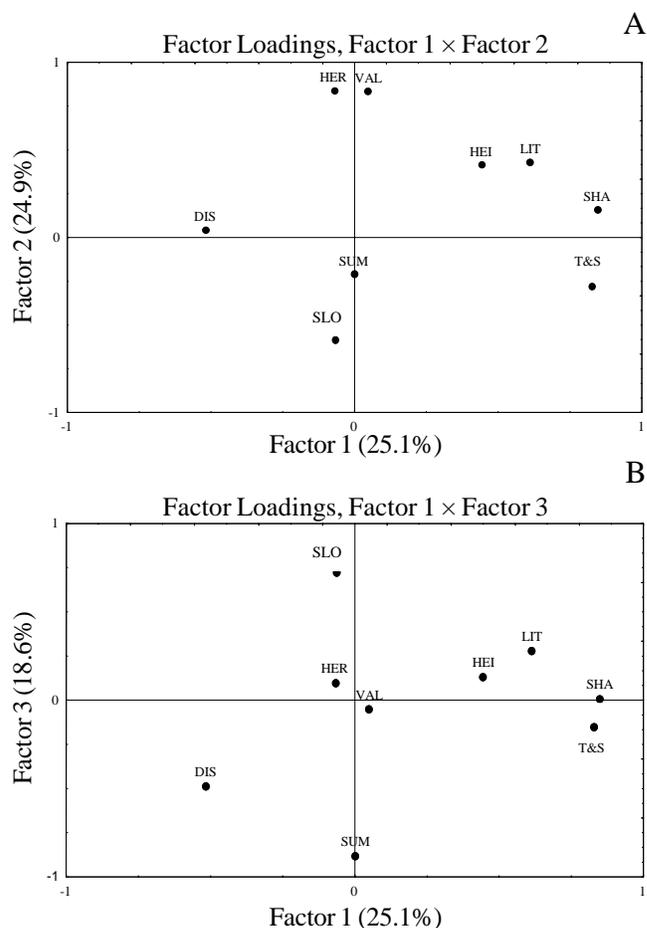


Figure 4. Results of PCA analysis for nine plant and microhabitat variables from the dunes of Ibiraba, Bahia. (A) Plot of nine microhabitat variables on first and second principal components. (B) Plot of nine microhabitat variables on first and third principal components. Values in parentheses refer to the percentage of the data variation explained by the factor. DIS = mean distance to the nearest woody plant; HEI = mean height of woody plants; HER = herbaceous cover; LIT = amount of litter; SHA = amount of shade; SLO = dune slope; SUM = dune summit; T&S = tree and shrub cover; VAL = dune valley. See text for details.

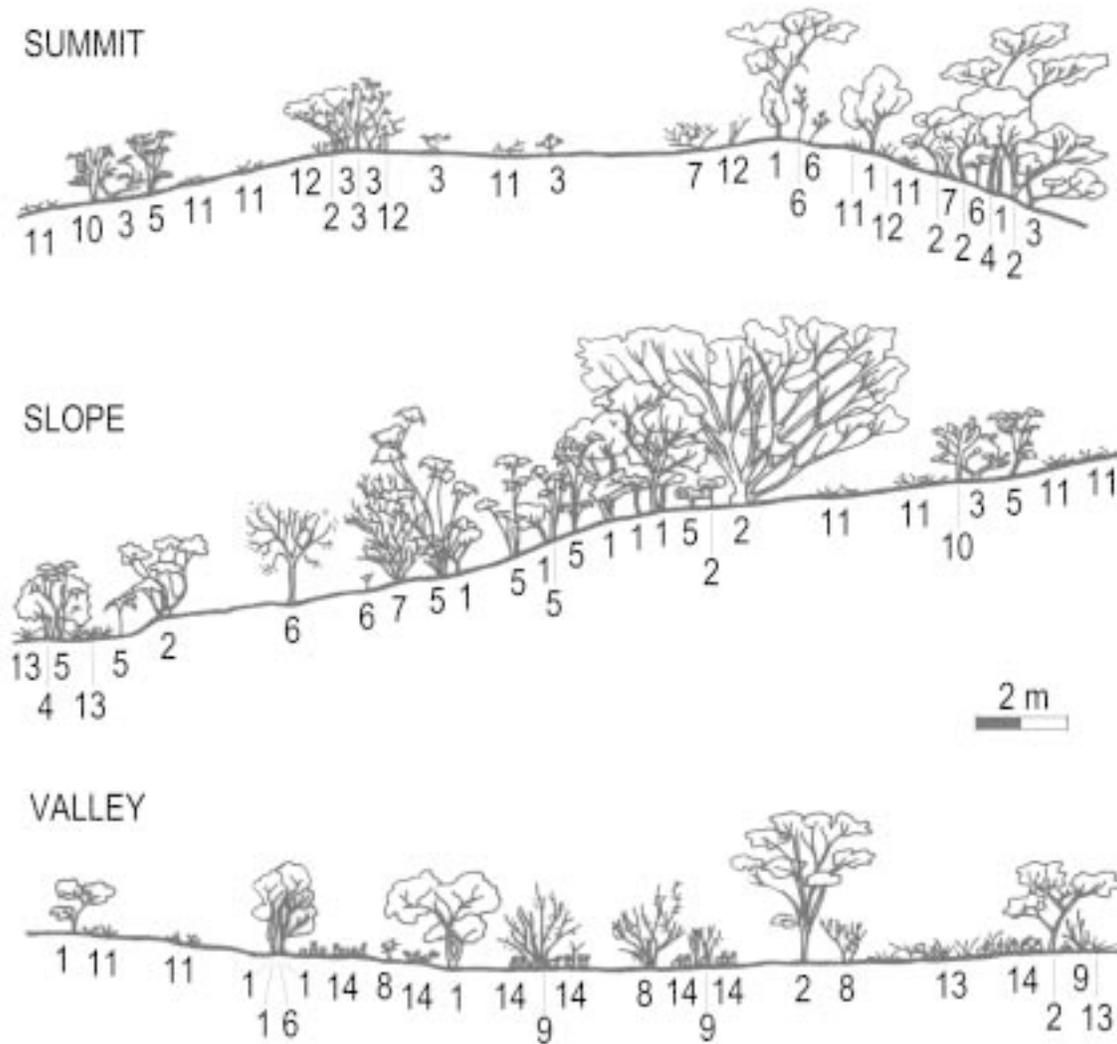


Figure 5. Three profiles of plant community on the dunes in Ibiraba, Bahia. The plants inside a strip 2 meter wide (perpendicular to dunes crests) are represented in different microgeographic positions (summit, slope, and valley). Numbers represent the codes of the species in the table 1.

monophyllus (Klitgaard *et al.* 2000), the Myrtaceae *Eugenia* sp., and the Molluginaceae *Glischrothamnus ulei* (Harley 1996).

Geographical distribution and paleoclimatic evidences (Prado & Gibbs 1993, Pennington *et al.* 2000, Prado 2000) suggest that the Neotropical seasonally dry forests must represent a phytogeographic unity, including the Caatinga in Northeastern Brazil. However, from the 57 Caatinga woody species used by Pennington and colleagues (Pennington *et al.* 2000) for the delimitation of the seasonally dry tropical forests, only *Commiphora leptophloeos* (Burseraceae) is found in the dunes, although other species cited by the authors occur in the Caatinga and gallery forests near the dunes, as *Couepia uiti* (Mart. & Zucc.) Benth. (Chrysobalanaceae), *Albizia inundata* (Mart.) Barneby

& J.W. Grimes, *Geoffroea spinosa* Jacq., and *Peltophorum dubium* (Spreng.) Taub. (Leguminosae). Moreover, species included in that phytogeographic unity are rarely found in other sandy areas in the Caatinga biome (see floristic checklists in Araújo *et al.* 1998, Figueirêdo *et al.* 2000). This suggests that the plants inhabiting the dunes in the middle São Francisco River (or even those inhabiting other sandy areas inside the limits of the biome Caatinga) may represent one phytogeographic unity different from the seasonally tropical dry forests (species inhabiting non-sandy areas in Caatinga). This hypothesis of distinct historical processes acting in the different phytogeographic unities seems to be corroborated by the analysis of the geographic distribution of some animals.

Regarding the fauna present in the dunes, all the most abundant terrestrial vertebrate species present there are endemic. In one ecological study focusing the lizard community in the area, 7 out of 11 lizard species captured in pitfall traps were endemic, corresponding to 98% of 879 collected individuals (Rocha 1998). Another study on terrestrial small mammals was based on 8,860 trapnights and resulted in 264 captured individuals, 263 representing a single endemic species of echimyid rodent (Rocha 1991, 1995, Rocha, unpublished data). Also new species of arthropods of the middle São Francisco have been described in the area (e.g., Xavier & Rocha 2001), although species of this group should not be regarded as endemic before further analysis of data from other Caatinga areas, which are still scanty. It seems that the evolution of the endemic species of both plants and animals in the dunes could be derived from the same biogeographical process. Regarding the sandy areas in Caatinga, disjunct geographical distribution is known also for populations of the sand-dweller lizards *Tropidurus cocorobensis* (Rodrigues 2003) and for species of the fossorial and saxicolous genus *Calyptommatus* (Rodrigues 2001). Rodrigues has suggested that the distribution of the first one can be understood only admitting that the sandy areas were much wider in past (Rodrigues 2003). This scenario coincides with that proposed here for the plants inhabiting sandy areas in the Caatinga, since present isolated sandy areas may have been wider and closer to each other in the past.

Phenology – One of the most striking features of the Caatinga is the deciduousness of the leaves in the dry season. The proportion of the species that keep their leaves in the dry season ranges from 26% (Machado *et al.* 1997) to almost zero, in areas where only *Ziziphus joazeiro* (Rhamnaceae) could be taken as evergreen (Oliveira *et al.* 1988). The studied site at Ibiraba is striking different from other caatinga areas since most species keep their leaves along the dry season and there is a continuous turnover of leaves during the year. In this respect, it is more similar to other sandy woodlands inside the Caatinga biome, as the carrasco vegetation of the Ibiapaba region (Araújo *et al.* 1998). The lower deciduousness in the dunes might reflect both different species composition and special adaptation of the plant species to this particular habitat. A definitive answer, however, should follow ecophysiological studies.

There is an almost complete absence of data about flowering and fruiting phenology of the plants of the caatinga. One of the most detailed study was presented by Machado *et al.* (1997) for a typical caatinga site in

the state of Pernambuco where most of the woody species flower at the beginning of the rainy season. This flowering pattern was observed in other seasonally dry forests and seems to be more common at the drier sites (Bullock 1995) where most of the woody species flower nearly simultaneously with leaf expansion (Bullock & Solís 1990, Guevara de Lampe *et al.* 1992). In the studied site, some species flower during the rainy season and others during the dry season, but at the community level it is not possible to correlate flowering activity with the rain distribution along the year, differently from other dry forests. Castro (1994) showed that there is a continuous action of pollinators (mainly eusocial bees) in some caatinga habitats along the year, and Viana (1999) showed that, in the dunes, bees are locally more abundant in rainy season but they do visit flowers also in the dry season. Therefore, the flowering pattern found could reflect this availability of pollinators. However, an unequivocal explanation to this pattern should rest on physiological analyses of the species based on a phylogenetic context.

Fruiting production starts at the beginning of the rainy season and dispersion occurs until the end of the dry season. Bullock (1995) concluded that, in tropical dry forests, fleshy fruits “are notoriously concentrated in wet season and scarce in the dry season” while anemochores and autochores are “absent or inconspicuous in the wet season and abundant in the dry season”. It is interesting to note that in the studied site, fleshy fruits (including species with fleshy arils) are dispersed along the year, mainly from the end of the wet season to the end of the next dry season.

Dispersion syndromes showed some unexpected figures when compared with other neotropical dry forests. Medina (1995) observed that these forests may be characterized by a higher proportion of wind dispersed species. In the studied site, typical anemochorous species accounted only for 16.5% of the species, mostly lianas and sub-shrubs. Among the phanerophytes (tree + shrubs), 11 tree and six shrub species are typically zoochorous (39.5%) and only six species of these two life forms (13.9%) are anemochorous. The predominance of the zoochory in the Ibiraba site is highlighted when the dispersal syndromes are analyzed in combination with the phytosociological data showing that zoochorous plants account for ca. 78.7% of the total plant density and frequency. These data show a higher proportion of zoochorous species and a lower proportion of anemochorous species among the woody plants. In contrast with the pattern observed at the Ibiraba site, a

typical dry forest site is reported to show higher proportions of anemochorous plants (Bullock 1995). For example, at Charallave (Venezuela), Wikander (1984) found 30.5% of the phanerophytes as typical anemochorous species.

Thus, both the phenological data of leaf deciduousness and flowering, as well as the dispersal syndromes data, reinforce the suggestions advanced by biogeographical data that the sandy dune vegetation of the São Francisco river may represent a phytogeographical unity different from the typical Caatinga or other neotropical dry forests. Similar studies in other sites could show if this inference could be generalized for the dry vegetation on sandy soil inside the Caatinga Dominion.

Habitat structure – The physiognomy of the plant community on the sand dunes in Ibiraba is quite different from the surrounding Caatinga formations. It lacks almost completely the herbaceous cover composed of annual or perennial species in the families Amaryllidaceae, Leguminosae, Graminae, Portulacaceae and Zygophyllaceae. Even during the rainy months, only 15% of the soil is covered by low, non-woody plants, most of which are mixed patches of *Bromelia antiacantha* and *Tacinga inamoena* (species until recently known in the literature as *Opuntia inamoena*). As the woody plants are sparse, 45.8% of the ground represents totally exposed sand.

Medina (1995) showed that the structure of the community changes along the rainfall gradient and noted that the most striking features changing in life forms along this gradient are related to tree height and degree of deciduousness. The long dry season could account for the low height of the trees observed in the studied site, agreeing with Medina (1995). On the other hand, many of the life forms expected for dry areas (Medina 1995) are absent or very rare at the Ibiraba site as, for example, sclerophyllous woody plants, non-succulent herbs, epiphytes, and lianas (woody vines). The life forms distribution observed in Ibiraba is more similar to those found in other sandy areas within the Caatinga biome, as in the Ibiabapa (Araújo *et al.* 1998) and the Buíque (Figueirêdo *et al.* 2000) regions. One striking feature of the physiognomy of the Ibiraba vegetation is the patchy distribution of the woody plants. It seems to be different from the physiognomy of any other vegetation described in the Caatinga biome and may result from the combined effect of the sandy substratum and sloped landscape.

The habitat of the dunes is also very simple and homogeneous in structure. The trees and shrubs have a

low profile and the topography is very repetitive, seemingly influencing the distribution of the patches of *Bromelia* and *Tacinga* (common in valleys). The woody plants do not seem to be influenced as a group by topography. However, as the mean distance to the closest trees and shrubs and their mean heights lie in different poles in the first axis of PCA, the taller plants tend also to form patches, which are very shaded and full of litter. As result for the small cursorial fauna, there are two main categories of protected patches: medium-sized predators protected areas (clusters of spiny plants at the level of the surface) and small-size predators and sun protected areas (clusters of litter in the shadow), and one category of exposed patches (exposed sand). Different groups of animals seem to explore differentially these microhabitat resources (Rocha 1991, 1998, Xavier & Rocha 2001, Xavier, unpublished data).

On the other hand, the dunes seem to offer to the local fauna a much more constant supply of resources than the Caatinga in the neighborhoods. *Eugenia* sp. is the most abundant woody species, representing 1/3 of all trees and shrubs taller than 1.5 m. Its seeds are the main source of food and water for the endemic rodents (Rocha 1991, Rocha, unpublished data). At least 50% of the woody plants retain the leaves even in the driest months and there are flowers of different species in anthesis all over the year. Fruits, on the other hand, are very few in the beginning of the rainy season. The ways these resources seem to modulate the abundance and diversity of the local fauna of vertebrates and arthropods has been explored recently (Rocha 1991, 1998, Neves & Viana 2002).

In spite of the apparent homogeneity of the habitat, the local diversity of lizards is high (17 syntopic species) compared to other open habitats in Brazil. In the Caatinga of Exu, Pernambuco, where habitat is highly heterogeneous due to the presence of granitic outcroppings, Vitt (1995) has found 18 species, a number considered by the author higher than most Caatinga habitats. Figures recorded for other open habitats are: 9 species in the Cerrados in Alto do Araguaia, Mato Grosso (Vitt 1991); 8 species in a “lavrado” area in Roraima (Vitt & Carvalho 1995); 5 species in a Cerrado area in Rondônia (Vitt & Caldwell 1993); 5 species in a Restinga (low coastal forest on sandy soil) area in Rio de Janeiro (Araujo 1991). In contrast, even much drier areas of Caatinga support a much more diversified small mammal fauna than the dunes (*e.g.*, six species in the Caatinga of Curaçá, BA – Rodrigues *et al.*, unpublished data).

The great amount of endemic taxa living on the dunes of Ibiraba (see also Rodrigues 1996) highlights

the relevance of the area for both conservation purposes and academic studies.

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References

- AB'SABER, A.N. 1974. O domínio morfoclimático semi-árido das caatingas brasileiras. *Geomorfologia* 43:1-39.
- ALCOFORADO FILHO, F.G., SAMPAIO, E.V.S.B. & RODAL, M.J.N. 2003. Florística e fitossociologia de um remanescente de vegetação espinhosa arbórea em Caruaru, Pernambuco. *Acta Botanica Brasilica* 17:287-303
- ANDRADE-LIMA, D. 1981. The caatingas dominium. *Revista Brasileira de Botânica* 4:149-153.
- ARAÚJO, A.F.B. 1991. Structure of a white sand-dune lizard community of coastal Brazil. *Revista Brasileira de Biologia* 51:857-865.
- ARAÚJO, E.L., SAMPAIO, E.V.S.B. & RODAL, M.J.N. 1995. Composição florística e fitossociologia de três áreas de caatinga. *Revista Brasileira de Biologia* 55: 595-607.
- ARAÚJO, F.S., SAMPAIO, E.V.S.B., FIGUEIREDO, M.A., RODAL, M.J.N. & FERNANDES, A.G. 1998. Composição florística da vegetação de carrasco, Novo Oriente - CE. *Revista Brasileira de Botânica* 21:15-26.
- BAHIA-SEPLANTEC. 1978. Atlas do estado da Bahia. Seplab, Salvador.
- BARNEBY, R. 1991. Sensitivae Censitae, a description of the genus *Mimosa* L. (Mimosaceae) in the New World. *Memoirs of the New York Botanical Garden* 65:1-835.
- BARRETO, A.M.F. 1996. Interpretação paleoambiental do sistema de dunas fixadas do médio rio São Francisco, Bahia. Tese de doutorado, Universidade de São Paulo, São Paulo.
- BARROS, R.C.H., OLIVEIRA, E.S., ROCHA, P.L.B. & BRANCO, L.L.G.S. 1998. Respiratory and metabolic responses of the spiny rats *P. yonenagae* and *P. iheringi* to CO₂. *Respiration Physiology* 111:223-231.
- BULLOCK, S.H. 1995. Plant reproduction in neotropical dry forests. *In* Seasonally dry tropical forests (S.H. Bullock, H.A. Mooney & E. Medina, eds). Cambridge University Press, New York, p.277-303.
- BULLOCK, S.H. & SOLÍS M., J.A. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22:22-35.
- CASTRO, M.S. 1994. Composição, fenologia e visita às flores pelas espécies de Apidae em um ecossistema de Caatinga (Nova Casa Nova - Bahia 9°26'S / 41°50'W). Dissertação de mestrado, Universidade de São Paulo, São Paulo.
- FERRI, M.G. 1955. Contribuição ao conhecimento da ecologia do cerrado e da caatinga. Estudo comparativo da economia d'água e de sua vegetação. Tese de doutorado, Universidade de São Paulo, São Paulo.
- FIGUEIRÊDO, L.S., RODAL, M.J.N. & MELO, A.L. 2000. Florística e fitossociologia de uma área de vegetação arbustiva caducifólia espinhosa no município de Buíque - Pernambuco. *Naturalia* 25:205-224.
- GAUCH, H.G. 1982. Multivariate analysis in ecology. Cambridge University Press, Cambridge.
- GIULIETTI, A.M., HARLEY, R.M., QUEIROZ, L.P., BARBOSA, M.R.V., BOCAGE NETA, A.L. & FIGUEIREDO, M.A. 2002. Espécies endêmicas da Caatinga. *In* Vegetação e Flora da Caatinga (E.V.S.B. Sampaio, A.M. Giuliatti, J. Virgínio & C.F.L. Gamarra-Rojas, eds.), Associação Plantas do Nordeste, Recife, p.103-118.
- GOMES, A.P.S. 1999. Florística e fitossociologia de uma vegetação arbustiva subcaducifólia no município de Buíque - Pernambuco. Dissertação de mestrado, Universidade Federal Rural de Pernambuco, Pernambuco.
- GUEVARA-DE-LAMPE, M., BERGERON, Y., MCNEIL, R. & LEDUC, A. 1992. Seasonal flowering and fruiting patterns in tropical semi-arid vegetation in northeastern Venezuela. *Biotropica* 24:64-76.
- HARLEY, R.M. 1996. Examples of endemism and phytogeographical elements in the caatinga flora. *In* Anais da Reunião Especial da Sociedade Brasileira para o Progresso da Ciência. SBPC, Feira de Santana, p.219-227.
- HARMAN, H.H. 1976. Modern factor analysis. Chicago University Press, Chicago.
- HOLBROOK, N.M., WHITBECK, J.L. & MOONEY, H.A. 1995. Drought responses of neotropical dry forest trees. *In* Seasonally dry tropical forests. (S.H. Bullock, H.A. Mooney & E. Medina, eds.), Cambridge University Press, New York, p.243-272.
- HOLMGREN, P.K., HOLMGREN, N.H. & BARNETT, L.C. 1990. Index Herbariorum. Ed. 8. The New York Botanical Garden, New York.

- KLEIBAUN, D.G., KUPPER, L.L. & MULLER, K.E. 1988. Applied regression analysis and other multivariate methods. PWS-KENT Publishing Company, Boston.
- KLITGAARD, B.B., QUEIROZ, L.P. & LEWIS, G.P. 2000. A new species of *Pterocarpus* (Leguminosae: Dalbergieae) from Bahia, Brazil. *Kew Bulletin* 55:732-735.
- KREBS, C.J. 1999. Ecological methodology. Addison Wesley Logman, California.
- LENCIONI NETO, F. 1994. Une nouvelle espèce de *Chordeiles* (Aves, Caprimulgidae) de Bahia (Brésil). *Alauda* 62:241-245.
- LYRA, A.L.R.T. 1982. A condição de 'brejo' e o efeito do relevo na vegetação de duas áreas no município de Brejo da Madre de Deus-PE. Dissertação de mestrado, Universidade Federal Rural de Pernambuco, Recife.
- MACHADO, I.C.S., BARROS, L.M. & SAMPAIO, E.V.S.B. 1997. Phenology of the caatinga species at Serra Talhada, PE, Northeastern Brazil. *Biotropica* 29:57-68.
- MARES, M.A., WILLIG, M.R. & LACHER JUNIOR, T.E. 1985. The Brazilian Caatinga in South American zoogeography: tropical mammals in a dry region. *Journal of Biogeography* 12:57-69.
- MAXWELL, R.H. 1969. The genus *Dioclea* in the New World. Doctoral thesis, University of Illinois, Carbondale.
- MEDINA, E. 1995. Diversity of life forms of higher plants in neotropical dry forests. In *Seasonally dry tropical forests* (S.H. Bullock, H.A. Mooney & E. Medina, eds.), Cambridge University Press, New York, p.221-242.
- NEVES, E.L. & VIANA, B.F. 2002. Abelhas eussociais (Hymenoptera, Apidae) visitantes florais em um ecossistema de dunas continentais no médio rio São Francisco, Bahia, Brasil. *Revista Brasileira de Entomologia* 46:573-580.
- NIMER, E. 1979. Climatologia do Brasil. IBGE, Rio de Janeiro.
- OLIVEIRA, J.G.B., QUSEADO, H.L.C., NUNES, E.P. & VIANA, F.A. 1988. Observações preliminares de fenologia de plantas de caatinga na Estação Ecológica de Aiuaba, Ceará, Esam, Mossoró. *Coleção Mossoroense, série B*, n. 538.
- OLIVEIRA, P.E., BARRETO, A.M.F. & SUGUIO, K. 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco River. *Palaeogeography, Palaeoclimatology, Palaeoecology* 152:319-337.
- OLIVEIRA, J.A., GONÇALVES, P.R. & BONVICINO, C.R. 2003. Mamíferos da caatinga. In *Ecologia e conservação da caatinga* (I.R. Leal, M. Tabarelli & J.M.C. Silva, eds.). Editora Universitária da UFPE, Recife, p.275-302.
- PENNINGTON, R.T., PRADO, D.E. & PENDRY, C.A. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27:261-273.
- PIJL, L. VAN DER. 1972. Principles of dispersal in higher plants. McGraw-Hill, New York.
- PRADO, D.E. 2000. Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. *Edinburgh Journal of Botany* 57:437-461.
- PRADO, D.E. & GIBBS, P.E. 1993. Patterns of species distribution in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* 80:902-927.
- RIBEIRO, M.F.S., ROCHA, P.L.B., MENDES, L.A.F., PERRY, S.F. & OLIVEIRA, E.S. 2004. Physiological effects of short-term water deprivation in the South American sigmodontine rice rat *Oligoryzomys nigripes* and water rat *Nectomys squamipes* within a phylogenetic context. *Canadian Journal of Zoology* 82:1326-1335.
- RIZZINI, C.T. 1979. Tratado de fitogeografia do Brasil. Editora de Humanismo e Tecnologia – Editora da Universidade de São Paulo, São Paulo, v.2.
- ROCHA, P.L.B. 1991. Ecologia e morfologia de uma nova espécie de *Proechimys* (Rodentia: Echimyidae) das dunas interiores do Rio São Francisco (BA). Dissertação de mestrado, Universidade de São Paulo, São Paulo.
- ROCHA, P.L.B. 1995. *Proechimys yonenagae*, a new species of spiny rat (Rodentia: Echimyidae) from fossil sand dunes in Brazilian Caatinga. *Mammalia* 59:537-550.
- ROCHA, P.L.B. 1998. Uso e partição de recursos pelas espécies de lagartos das dunas do rio São Francisco, Bahia (Squamata). Tese de doutorado, Universidade de São Paulo, São Paulo.
- RODAL, M.J.N. & SAMPAIO, E.V.S.B. 2002. A vegetação do bioma caatinga. In *Vegetação e Flora da Caatinga* (E.V.S.B. Sampaio, A.M. Giulietti, J. Virgínio & C.F.L. Gamarra-Rojas, eds.), Associação Plantas do Nordeste, Recife, p.11-24.
- RODRIGUES, M.T.U. 1996. Lizards, snakes and amphisbaenians of the palaeoquaternary sand dunes of the middle São Francisco River: Bahia: Brazil. *Herpetologica* 30:513-523.
- RODRIGUES, M.T.U. 2001. A new species of lizard, genus *Calyptommatus*, from the caatinga of the sate of Piauí, northeastern Brazil (Squamata, Gymnophthalmidae). *Papéis Avulsos de Zoologia* 41:529-546.
- RODRIGUES, M.T.U. 2003. Herpetofauna da Caatinga. In *Ecologia e conservação da caatinga* (I.R. Leal, M. Tabarelli & J.M.C. Silva, eds.). Editora Universitária da UFPE, Recife, p.181-236.
- SAMPAIO, E.V.S.B. 1995. Overview of the Brazilian Caatinga. In *Seasonally dry tropical forests* (S.H. Bullock, H.A. Mooney & E. Medina, eds.). Cambridge University Press, New York, p.35-63.
- STREILEIN, K.E. 1982a. Ecology of small mammals in the semiarid Brazilian caatinga. I. Climate and faunal composition. *Annals of the Carnegie Museum* 51:79-107.
- STREILEIN, K.E. 1982b. Ecology of small mammals in the semiarid Brazilian caatinga. II. Water relations. *Annals of the Carnegie Museum* 51:109-126.

- STREILEIN, K.E. 1982c. Ecology of small mammals in the semiarid Brazilian caatinga. IV. Habitat selection. *Annals of the Carnegie Museum* 51:331-343.
- VANZOLINI, P.E., RAMOS-COSTA, A.M.M & VITT, L.J. 1980. Répteis das caatingas. Academia Brasileira de Ciências, Rio de Janeiro.
- VIANA, B.F. 1999. A comunidade de abelhas (Hymenoptera: Apoidea) das dunas interiores do Rio São Francisco, Bahia, Brasil. *Anais da Sociedade Entomológica do Brasil* 28:635-645.
- VITT, L.J. 1991. An introduction to the ecology of cerrado lizards. *Journal of Herpetology* 25:79-80.
- VITT, L.J. 1995. The ecology of tropical lizards in the caatinga of Northeast Brazil. *Occasional Papers of the Oklahoma Museum of Natural History* 1:1-29.
- VITT, L.J. & CALDWELL, J.P. 1993. Ecological observations on cerrado lizards in Rondônia, Brazil. *Journal of Herpetology* 27:46-52.
- VITT, L.J. & CARVALHO, C.M. 1995. Niche partitioning in a tropical wet season: lizards in the lavrado area of northern Brazil. *Copeia* 195:305-329.
- WIKANDER, T. 1984. Mecanismos de dispersión de diásporas de una selva decídua en Venezuela. *Biotropica* 16:276-283.
- WILLIG, M.R. & MARES, M.A. 1989. Mammals from the caatinga: an updated list and summary of recent research. *Revista Brasileira de Biologia* 49:361-367.
- XAVIER, E. & ROCHA, L.S. 2001. Autoecology and description of *Mummucia mauryi* (Solifugae, Mummucidae), a new solifuge from Brazilian semi-arid Caatinga. *The Journal of Arachnology* 29:127-134.