THE ARBOREAL COMPONENT OF A DRY FOREST IN NORTHEASTERN BRAZIL*

RODAL, M. J. N. and NASCIMENTO, L. M.

Laboratório de Fitossociologia, Departamento de Biologia, Universidade Federal Rural de Pernambuco,
Rua Dom Manoel de Medeiros, s/n, Dois Irmãos, CEP 52171-900, Recife, PE, Brazil

Correspondence to: Maria Jesus Nogueira Rodal, Laboratório de Fitossociologia, Departamento de Biologia,
Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n, Dois Irmãos,
CEP 52171-900, Recife, PE, Brazil, e-mail: mrodal@terra.com.br

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ABSTRACT

The dry forests of northeastern Brazil are found near the coastal zone and on low, isolated mountains inland amid semi-arid vegetation. The floristic composition of these dry montane forests, as well as their relationship to humid forests (Atlantic forest *sensu stricto*) and to the deciduous thorn woodlands (*Caatinga sensu stricto*) of the Brazilian northeast are not yet well known. This paper sought to determine if the arboreal plants in a dry forest growing on a low mountain in the semi-arid inland region (Serra Negra, 8° 35' - 8° 38' S and 38° 02' - 38° 04' W) between the municipalities of Floresta and Inajá, state of Pernambuco have the same floristic composition and structure as that seen in other regional forests. In fifty 10 x 20 m plots all live and standing dead trees with trunk measuring ≥ 5 cm diameter at breast height were measured. Floristic similarities between the forest studied and other regional forests were assessed using multivariate analysis. The results demonstrate that the dry forest studied can be classified into two groups that represent two major vegetational transitions: (1) a humid forest/dry forest transition; and (2) a deciduous thorn-woodland/ dry forest transition.

Keywords: Brazil, dry forests, tree community, diversity, forest structure.

RESUMO

O Componente Arbóreo de uma Floresta Seca no Nordeste do Brasil

As florestas secas do Nordeste do Brasil são encontradas próximo à zona costeira, nos planaltos e em montanhas baixas e isoladas no interior do semi-árido nordestino. A composição dessas florestas secas e sua relação com as florestas úmidas (Floresta Atlântica *sensu stricto*) e a vegetação arbustivo-arbórea caducifólia espinhosa (Caatinga *sensu stricto*) do Nordeste do Brasil ainda não estão resolvidas. Este trabalho procura determinar se a flora arbórea da floresta seca que cresce em uma montanha baixa da região semi-árida localizada entre os municípios de Floresta e Inajá, Pernambuco (Serra Negra, 8° 35' - 8° 38' S e 38° 02' - 38° 04' W) apresenta a mesma composição florística e estrutura observada em outras florestas da região. Foram amostrados todos os indivíduos vivos ou mortos, ainda de pé, com diâmetro do tronco à altura do peito ≥ 5 cm, presentes em 50 parcelas (10 x 20 m). A similaridade florística entre Serra Negra e outras florestas da região foram avaliadas usando análises multivariadas. Os resultados demonstram que as florestas secas englobam dois conjuntos florísticos que representam duas transições: (1) transição florestas úmidas/ florestas secas; e (2) transição vegetação arbustivo-arbórea caducifólia espinhosa/floresta seca, onde está localizada Serra Negra.

Palavras-chave: Brasil, florestas secas, comunidade arbórea, diversidade, estrutura.

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INTRODUCTION

Tropical dry forests are found in areas having high year-round temperatures and a well-defined dry season that limits both plant growth and animal activity (Lüettge, 1997). Although climate is seasonally dry, enough moisture is available to support forest vegetation.

The concept of humid and dry tropical forests varies from author to author throughout the phytogeographical regions in which they occur (Richards, 1996). Gentry (1995), for example, using a floristic approach, classified neotropical dry forests as those occurring in areas receiving 700-1600 mm of rain per year, and having at least five months of less than 100 mm.

Although dry forests cover extensive areas throughout the world, most research efforts have focused on tropical humid forests (Gillespie *et al.*, 2000). Dry forest degradation has been similar to (and often greater than) that seen in humid tropical forests (Gentry, 1995; Mooney *et al.,* 1995; Janzen, 1997). In fact, Trejo & Dirzo (2000) argue that, for lack of non-disturbed study sites, few quantitative studies have been carried out on dry forests, which have a long history of human use, resulting in either their outright destruction or their conversion into sites with very different vegetation forms.

As the length of the dry season shows extreme variation throughout the tropics, no clear distinction exists between dry and humid tropical forests (Gentry, 1995), with one biome possibly changing into another over a distance of hundreds of miles (Sarmiento, 1972). In addition, although tropical forest researchers have determined that annual precipitation rates and seasonality are closely correlated with plant diversity, this relationship may not always be clear in dry neotropical forests (Gillespie *et al.,* 2000). Furthermore, Gentry (1995) attributed differences between dry forests mainly to biogeographical factors, since these forests show no significant increases in either species richness or diversity as rainfall increases.

Pennington *et al.* (2000) noted that in seasonally dry regions of Brazil the diverse forest and savanna types have been traditionally defined as belonging to the Amazonian forest, Atlantic forest, or *Cerrado* biomes. These same authors observed that the term "seasonally dry forest" includes several forest types (such as forests in more humid areas, and shrub vegetation in drier regions), and that the largest areas of seasonally dry forests in South America are found in northeastern Brazil (the *Caatinga* biome, which extends southward almost to the state of Minas Gerais). For these authors, the dry forests on the low hills in the semi-arid region of northeastern Brazil represent the most favorable end of a humidity gradient that trails off into the deciduous thorn woodland (DTW) (C*aatinga sensu stricto*).

However, other authors regard these same forests as part of the Atlantic coastal forest biome that extends all along the Brazilian seacoast, between the states of Rio Grande do Norte and Rio Grande do Sul. This biome is composed of a number of different vegetation types, ranging from humid forest (Atlantic forest *sensu stricto*) to seasonally dry forest (Atlantic forest *sensu lato*), within an area of high environmental heterogeneity (Coimbra-Filho & Câmara, 1996). While the bulk of the Atlantic coastal forest (ACF) hugs the coast, it can extend inland along rivers into the savanna region (*Cerrado*) (Oliveira-Filho & Ratter, 2000), and can cover the tops of low mountains in the Borborema Highlands or those scattered throughout the semi-arid region of northeastern Brazil (Joly *et al.,* 1999). The ACF has been intensely studied in southeastern Brazil (Scudeller *et al.,* 2001), while its floristic composition and physiognomy are much less studied in the northeastern part of the country, with the possible exception of the forests in southern Bahia (Thomas *et al*., 1998).

The majority of plant surveys in northeastern Brazil have concentrated on humid forests (Cavalcanti, 1985; Borges, 1992; Guedes, 1998; Tavares *et al*., 2000; Siqueira *et al*., 2001; Lins-e-Silva & Rodal, in press), although recent years have seen an increase in surveys of dry forests (Correia, 1996; Moura, 1997; Nascimento, 2001; Ferraz *et al.,* 2003; Andrade & Rodal, 2004) or in DTW (Araújo *et al.,* 1995; Figueirêdo *et al.,* 2000; Alcoforado-Filho *et al.,* 2003; Ferraz *et al.,* 2003). However, no studies have been published on the isolated dry forests on low mountains of northeastern Brazil's semi-arid areas nor have floristic composition and structure of these forest areas been compared with one another.

In the absence of sufficient data on this area, the present study sought to characterize the arboreal component of a dry forest community in the low mountains of Brazilian semi-arid northeastern region (Serra Negra) and to answer the following questions: (1) Are there floristic and structural differences among dry forests in northeastern Brazil? and (2) do the dry and humid forests in northeastern Brazil represent a single vegetation unit?

METHODS

Study area

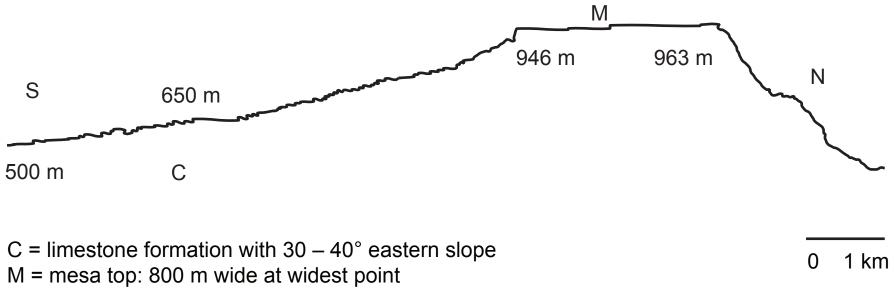
The Serra Negra Biological Reserve (8° 35' - 8° 38' S and 38° 02'- 38° 04' W), between the municipalities of Floresta and Inajá, Pernambuco state, is a low mountain located on a residual plain in the semi-arid region of northeastern Brazil. According to Andrade (1954) and Dantas (1980), the Serra Negra region, which originated in the Cretaceous, has a cuesta landform. The landscape is a relict plain derived from a larger sedimentary formation that was reworked throughout a series of paleo-environments under varying humidity conditions. The reserve itself contains 1,100 ha, and is located approximately 400 km from the Atlantic coast, between the municipalities of Floresta and Inajá, in Pernambuco state (IBAMA, 1989). The forest-covered summit measures 800-900 m in width, and is approximately 3,000 m long in an E/NE–W/SW direction. According to Andrade (1954), the maximum altitude is 963 m asl (Fig. 1).

Although no systematic rainfall records exist for the study area, estimates of precipitation based on regression (Rodal, 1983) show that the average annual rainfall on the summit is approximately 900 mm per year. Average annual temperature is 25.3 °C, with an absolute maximum of 38 °C, and an absolute minimum of 8 °C (IBAMA, 1989). Soils are deep and sandy (Jacomine *et al.,* 1973).

The altitude of Serra Negra, combined with its exposure to humid southeast winds from the São Francisco River valley, results in an amenable local climate in the midst of an otherwise semi-arid landscape. A dense forest, with trees such as *Manilkara salzmanii* (ADC.) Lam. (Sapotaceae) and *Trichilia emarginata* (Turcz.) C. DC (Meliaceae) reaching up to 35 m in height, covers the Serra Negra peak.

The main forested area in the eastern part of the Brazilian northeast (Alagoas, Pernambuco, and Paraíba states) is located principally between the coastal plain and the Borborema Highlands. The latter consists of a series of highly weathered massifs, composed mainly of metamorphosed rocks, such as gneisses and eruptive granites (Moreira, 1977). These massifs are the most outstanding regional geomorphological feature, the great diversity of which is paralleled by that of its vegetation, which includes deciduous thorn woodland (Alcoforado-Filho *et al.,* 2003), as well as both dry (Nascimento, 2001) and humid forests on the eastern slopes (Tavares *et al.*, 2000). Both of these forest types are known as *brejos de altitude*.

Down from these highlands and eastward to the sea, Precambrian rocks of the Borborema Highlands give way to the hills and coastal plains of the Barreiras Formation (Tertiary) whose vegetation ranges from humid (Atlantic forest *sensu stricto*) (Siqueira *et al.,* 2001) to dry forest (Atlantic forest *sensu lato*) (Andrade & Rodal, 2004). The western slopes, which are dominated by DTW vegetation (Rodal, 2001) of the Borborema, descend steeply towards the semi-arid inland region known as the *Depressão Sertaneja*. Scattered throughout this inland depression are a number of low mountains covered by dry forests, such as the Serra Negra.



C = limestone formation with 30 – 40° eastern slope
M = mesa top: 800 m wide at widest point
Source: Andrade (1954)

Fig. 1 — Schematic diagram of Serra Negra Mountain, Pernambuco state, Brazil.

According to Sampaio (1995) and Rodal (2001), the climate in Pernambuco state (where most of the quantitative surveys analyzed in this study were undertaken) is a complex combination of various climatic elements (precipitation, temperature, wind, etc.), which in turn are influenced by physiographic factors such as orography (Borborema Highlands) and continent effect. Precipitation diminishes inland (westward), decreasing from 2000 mm year^{-1} in the coastal plains to 500 mm year^{-1} in the semi-arid depression. Temperatures are generally much higher in these inland areas, although the Borborema Highlands are a local exception, having slightly lower temperatures than the surrounding areas, especially during the night.

Field methods

Fieldwork was carried out for 13 consecutive months, between January 1997 and January 1998. Fifty 10 x 20 m plots on the top of the mountain (930-940 m asl) were set along three parallel transects separated from one another by 100 m. The plots themselves were spaced 20 m apart from one another. All trunks (living and dead), except for lianas and palms, with a ≥ 5 cm diameter at breast height (DBH) were marked and identified to species; their diameters were recorded, and heights measured using an Abney Level.

Data analysis

Voucher specimens were processed, identified, and stored at the Professor Vasconcelos Sobrinho Herbarium (PEUFR) of the Universidade Federal Rural de Pernambuco (UFRPE). The classification system used follows Cronquist (1981).

To identify different height classes, a 4 m interval was used to evaluate the species, the number of trunks, and their basal areas (1.3-4 m, 4.1-8 m, ..., 32.1 + m). Density, frequency, and basal area (Kent & Coker, 1992) for all families and species were calculated using FITOPAC 2 software (Shepherd, 1995). The Cover Importance Index (Matteucci & Colma, 1982) and Shannon Diversity Index (Magurran, 1988) for families and species were also calculated.

In order to identify the similarities between the Serra Negra and the other forests in Pernambuco, multivariate analyses were performed using presence/absence of species in 12 surveys, including the study area. The surveys covered humid forests (Tavares *et al*., 2000; Siqueira *et al*., 2001; Lins-e-Silva & Rodal, in press); dry forests (the present survey; Correia, 1996; Moura, 1997; Nascimento, 2001; Andrade & Rodal, 2004), specifically at 900 m asl (Ferraz *et al*., 2003) and 700 m asl (Rodal *et al*., accepted); and DTW (Ferraz *et al.,* 2003), specifically at 500 m asl (Rodal *et al*., accepted). The Kendall correlation coefficient was used to test the relationship between altitude and basal area in these humid and dry forests (Ayres *et al*., 2000).

The terminology used to define montane (altitude > 600 m asl) and lowland forests (altitude < 100 m) followed Veloso *et al.* (1991). The authors that have worked in the northeastern forests differ with respect to nomenclature used in classifying ombrophylous (humid) and seasonal (dry) forests. For example, Andrade & Rodal (2004) employed definitions suggested by Veloso *et al*. (1991) while Tavares *et al*. (2000) used floristic composition to distinguish forest types. The quantitative surveys used in our comparative analyses classified forests as either humid or dry in accordance with the descriptions supplied by the various authors cited above. Table 1 presents the analyzed surveys listed by municipality and includes bibliographic references, geomorphology (Silva *et al*., 1993), altitude, and precipitation. Total annual rainfall at each survey site was obtained from either the studies themselves or SUDENE (1990).

All species present in more than one survey were taken into consideration, regardless of the number of individuals in each. Scientific names listed were synonymized according to the literature. Cluster analysis and principal component analysis (PCA) were performed using the same matrix. For the cluster analysis, the Sørensen index, and the weighted pair-group method using arithmetic averages (WUPGMA) were employed. For the PCA analysis, a variance-covariance matrix was used. Analyses were undertaken using FITOPAC 2 software (Shepherd, 1995).

RESULTS

Floristic composition and structure of the Serra Negra Forest

In 50 sample plots, a total of 1,525 stems (including dead ones) ha^{-1} were found, with a total

TABLE 1
Environmental variables and plant community attributes of the forests of Pernambuco state, Brazil. 1- 5 beside each municipality represents information about method applied. 1 = DBH > 5 cm; 2 = stem diameter at soil level > 3 cm; 3 = 1 ha; 4 = 0.3 ha; 5 = 0.1 ha; SN = species number; BA = basal area; TD = total density; AH = average height; and MXH = maximum height. Forests in sites at altitudes higher than 600 m asl are montane while those found at altitudes less than 100 m asl are lowland.

Municipality	Latitude	Longitude	Altitude (m asl)	Precip. (mm year^{-1})	Code area	Geomorphology	SN	BA (m2 ha^{-1})	TD (ind. ha^{-1})	AH (m)	MXH (m)	Reference
Humid forest												
Recife (1, 3)	8° 03’	34° 56’	30-50	2243	1	coastal plains	56	24.7	780	11.2	28	Lins-e-Silva & Rodal (in press)
Cabo de Santo Agostinho (1, 3)	8° 15’	35° 02’	20-80	2143	2	coastal plains	82	27.5	1.657	11.5	28	Siqueira *et al.* (2001)
Caruaru (1, 3)	8° 17’	35° 58’	900-1000	1020	3	eastern slopes of Borborema Highlands	93	44.4	1.561	12.0	35	Tavares *et al.* (2000)
Dry forest												
São Lourenço da Mata (1, 3)	8° 02’	35° 07’	900	1301	4	coastal plains to Borborema Highlands	88	23.9	1.145	10.7	32	Andrade & Rodal (2004)
Brejo da Madre de Deus (1, 3)	8° 21’	36° 28’	900 - 950	900	5	Borborema Highlands	62	50.3	1.527	10.3	30	Nascimento (2001)
Triunfo (2, 5)	7° 52’	38° 17’	900	1000	6	western slopes of Borborema Highlands	53	46.7	3.060	5.6	13	Ferraz *et al.* (2003)
Serra Negra (1,3)	8° 35’	38° 04’	930-940	900	7	Low mountain	52	50.3	1.525	8.9	35	this research
Betânia (2, 5)	8° 16’	30° 09’	690	510	8	semi-arid depression	33	23.4	4.230	4.0	8	Rodal *et al.* (accepted)
Jataúba (2, 4)	8° 10’	36° 40’	1020-1120	764	9	Borborema Highlands	106	67.2	4.919	4.6	15	Moura (1997)
Pesqueira (2, 4)	8° 22’	36° 42’	860-880	885	10	Borborema Highlands	65	49.6	4.406	5.8	16	Correia (1996)
Deciduous thorn woodland												
Serra Talhada (2, 5)	7° 59’	38°19’	700	639	11	semi-arid depression	23	52.4	3.590	4.0	8	Ferraz *et al.* (2003)
Betânia (2, 5)	8° 18’	30° 11’	500	510	12	semi-arid depression	21	18.7	2.530	3.5	8.5	Rodal *et al.* (accepted)

basal area of 50.32 m^2 ha^{-1}. Average tree height was 8.9 m (± 5.55 m), while the average maximum height per plot was 22.8 m. Average diameter was 14 cm (± 14.74 cm), with an average maximum diameter per plot of 64.2 cm. Fig. 2a shows that the majority of trunks were less than 10 m tall. Approximately 50% of the total basal area was accounted for by only 7% of the total number of stems (103), all of which were over 20 m tall. While taller trees accounted for most of the basal area (Fig. 2b), the largest number of species was found among trees less than 12 m tall (Fig. 2c).

Basal-area distribution and trunk number per height class indicate a double-layered stratification, with emergent trees between 28 and 35 m tall. The understory occupies the 4 to 12 m layer, with canopy beginning at 16 m.

Fifty-one species belonging to 30 families were found in the survey (Table 2). Shannon diversity index (H') for families was 2.06 nats ind.$^{-1}$ The most species-rich family was Myrtaceae (10 species), followed by Fabaceae and Sapotaceae (3 each). These three families accounted for 34% of all species recorded.

The families most heavily represented in the importance cover index (IC) were Myrtaceae, Mimosaceae, Meliaceae, Lauraceae and Urticaceae. All showed a reduced number of species, except Myrtaceae, which accounted for 49.38% of the total density and 18.19% of the total basal area.

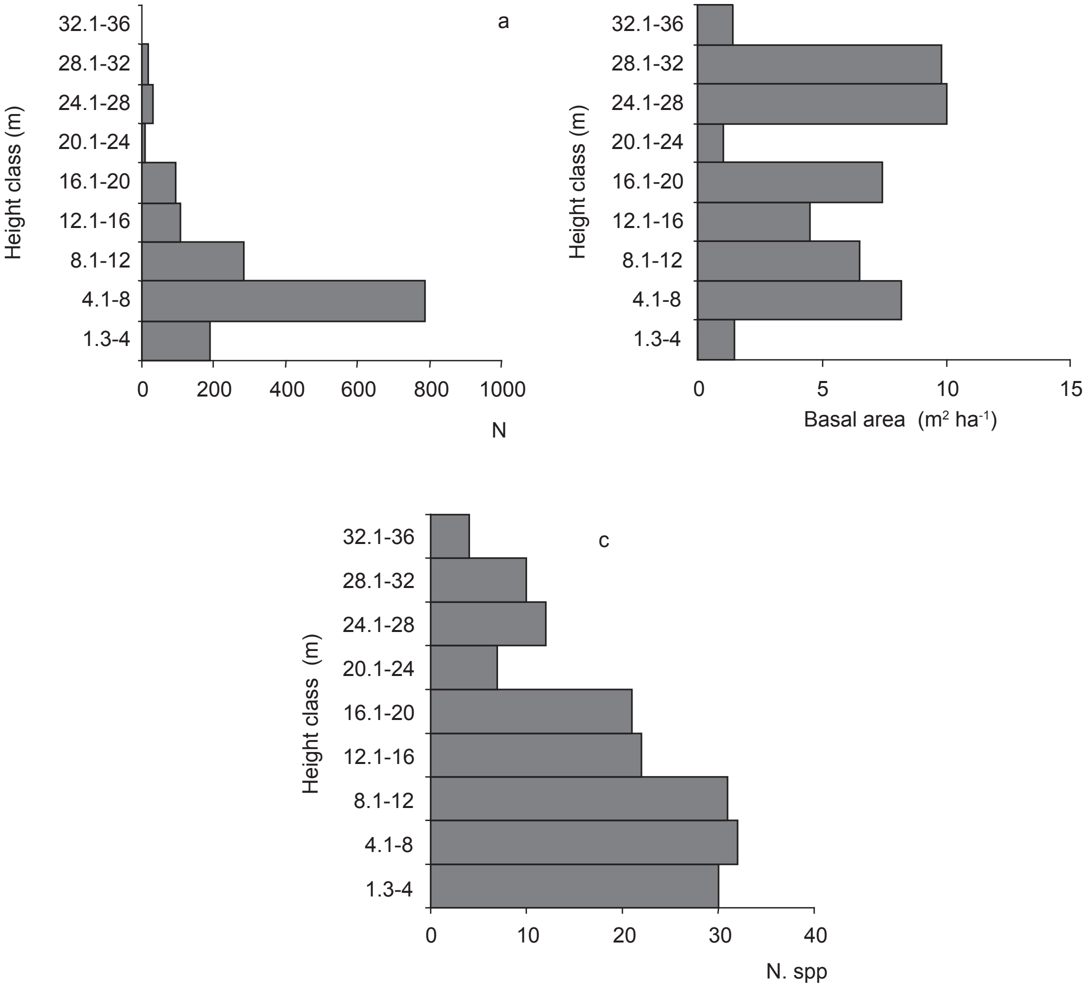


Fig. 2 — Distribution of number of stems (a); basal area (b); and number of species (c) per height class in montane dry forest of the Serra Negra Biological Reserve. N = number of stems, N. spp. = number of species.

TABLE 2

Tree species sampled in montane dry forest in the Serra Negra Biological Reserve, Pernambuco state, Brazil. NS = number of trunks; RD = relative density (%); RDo = relative dominance (%); RF = relative frequency (%); and IC = importance cover. Names after families indicate names of those who identified the plant species and their herbaria.

Families /Species	NS	RD	RDo	RF	IC	%IC
Myrtaceae (G.M.Barroso – RB)	**753**	**49.38**	**18.19**	**12.5**	**67.56**	**33.78**
1. *Myrcia fallax* (Rich.) DC	547	35.87	10.14	8.96	46.00	23.00
2. *Myrcia multiflora (*Lam.) DC.	67	4.39	1.92	4.69	6.31	3.16
3. *Myrciaria floribunda* (H.West ex Willd.) O.Berg	45	2.95	3.23	4.26	6.18	3.09
4. *Eugenia lambertiana* var. *hispidula* McVaugh	45	2.95	1.05	1.07	4.00	2.00
5. *Calyptranthes* cf *multiflora* Poepp. Ex O.Berg	17	1.11	0.53	1.49	1.64	0.82
6. *Campomanesia dichotoma* (O. Berg) Mattos	9	0.59	0.41	1.07	1.00	0.50
7. *Calyptranthes dardanoi* Mattos	6	0.39	0.60	1.07	1.00	0.50
8. *Myrcia caesia* O.Berg	8	0.52	0.21	1.49	0.73	0.37
9. *Psidium personii* McVaugh	5	0.33	0.04	0.85	0.37	0.19
10. *Eugenia hirta* O. Berg	4	0.26	0.05	0.43	0.31	0.16
Mimosaceae	**155**	**10.16**	**10.11**	**11.46**	**20.27**	**10.14**
11. *Inga thibaudiana* DC.	103	6.75	7.40	7.46	14.15	7.08
12. *Albizia polycephala* (Benth.) Killip ex Record	52	3.41	2.71	3.2	6.12	3.06
Sapotaceae (T.B.Pennington – K)	**29**	**1.90**	**17.73**	**3.39**	**19.63**	**9.82**
13. *Manilkara salzmanii* (ADC.) Lam.	25	1.64	17.40	2.35	19.04	9.52
14. *Pouteria ramiflora* (Mart.) Radlk.	2	0.13	0.29	0.43	0.42	0.21
15. *Sideroxylon obtusifolium* (Roem.& Schult) T.D. Penn.	2	0.13	0.04	0.21	0.17	0.09
Meliaceae	**82**	**5.38**	**9.88**	**7.03**	**15.26**	**7.63**
16. *Trichilia emarginata* (Turcz.) C. DC.	82	5.38	9.88	5.76	15.26	7.63
Combretaceae (I. B. Loyola – PEUFR)	**40**	**2.62**	**10.28**	**6.25**	**12.90**	**6.45**
17. *Terminalia brasiliensis* (Cambess ex A. St.-Hil.) Eichler	39	2.56	10.24	4.9	12.80	6.40
18. *Buchenavia capitata* (Vahl) Eichler	1	0.07	0.04	0.21	0.11	0.06
Phytolaccaceae	**7**	**0.46**	**9.32**	**1.56**	**9.78**	**4.89**
19. *Gallesia integrifolia* (Spreng.) Harms	7	0.46	9.32	1.28	9.78	4.89
Lauraceae (R.Roxana – UFP)	**68**	**4.46**	**3.99**	**6.51**	**8.45**	**4.22**
20. *Ocotea duckei* Vattimo	68	4.46	3.99	5.33	8.45	4.23
Nyctaginaceae (A.Furlan – HRCB)	**31**	**2.03**	**3.49**	**4.95**	**5.52**	**2.76**
21. *Guapira opposita* (Vell.) Reitz	31	2.03	3.49	4.05	5.52	2.76
Apocynaceae (M.F.Sales - PEUFR)	**34**	**2.23**	**2.91**	**4.69**	**5.14**	**2.57**
22. *Aspidosperma* cf. *illustre* (Vell.) Kuhlmann & Piraja	7	0.46	2.27	1.49	2.73	1.37
23. *Aspidosperma* sp.	27	1.77	0.64	2.77	2.41	1.21
Urticaceae	**58**	**3.80**	**0.85**	**4.43**	**4.65**	**2.33**
24. *Urera baccifera* Gaudich. Ex Wedd.	58	4.00	0.85	3.62	4.65	2.33
Euphorbiaceae (M. F. Araújo – PEUFR)	**46**	**3.02**	**0.67**	**4.95**	**3.69**	**1.84**
25. *Maprounea guianensis* var. *guianensis* Aubl.	37	2.00	0.36	2.99	2.79	1.40
26. *Sebastiania brasiliensis* Spreng.	9	0.59	0.31	1.28	0.90	0.45
Celastraceae (R. Okano – V)	**33**	**2.16**	**1.23**	**3.13**	**3.39**	**1.69**
27. *Maytenus obtusifolia* Mart.	28	1.84	1.10	2.35	2.94	1.47
28. *Maytenus* aff. *evonymoides* Reissek	5	0.33	0.12	0.85	0.45	0.23
Clusiaceae	**11**	**0.72**	**1.39**	**1.30**	**2.11**	**1.06**
29. *Garcinia gardneriana* (Planch. & Triana) Zappi	11	0.72	1.39	1.07	2.11	1.06

TABLE 2
Continued...

Families /Species	NS	RD	RDo	RF	IC	%IC
Erythroxylaceae	**13**	**0.85**	**0.58**	**3.13**	**1.44**	**0.72**
30. *Erythroxylum* sp.	8	0.52	0.52	1.71	1.04	0.52
31. *Erythroxylum macrochaetum* Miq.	5	0.33	0.06	0.85	0.39	0.20
Proteaceae	**9**	**0.59**	**0.36**	**1.56**	**0.95**	**0.48**
32. *Roupala paulensis* Sleumer	9	0.59	0.36	1.28	0.95	0.48
Moraceae	**6**	**0.39**	**0.52**	**1.56**	**0.91**	**0.46**
33. *Ficus* sp.	6	0.39	0.52	1.28	0.91	0.46
Rutaceae	**9**	**0.59**	**0.22**	**2.08**	**0.81**	**0.41**
34. *Zanthoxylum acutifolium* Engler	7	0.46	0.21	1.49	0.67	0.33
35. *Zanthoxylum rhoifolium* Lam.	2	0.13	0.01	0.21	0.14	0.07
Capparaceae (M. B. Costa e Silva – PEUFR)	**6**	**0.39**	**0.53**	**0.52**	**0.92**	**0.46**
36. *Capparis flexuosa* (L.) L.	6	0.39	0.53	0.43	0.92	0.46
Verbenaceae	**7**	**0.46**	**0.43**	**1.04**	**0.89**	**0.45**
37. *Vitex rufescens* A. Juss.	2	0.13	0.35	0.43	0.48	0.24
38. *Vitex* sp.	2	0.13	0.03	0.43	0.16	0.08
Sapindaceae	**8**	**0.52**	**0.12**	**2.08**	**0.64**	**0.32**
39. *Allophylus laevigatus* Radlk.	8	0.52	0.12	1.71	0.64	0.32
Myrsinaceae	**6**	**0.39**	**0.10**	**1.30**	**0.49**	**0.25**
40. *Myrsine guianensis* (Aubl.) Kuntze	6	0.39	0.10	1.07	0.49	0.25
Melastomataceae	**5**	**0.33**	**0.14**	**1.30**	**0.47**	**0.23**
41. *Miconia* cf. *minutiflora* Bonpl. DC.	5	0.33	0.14	1.07	0.47	0.24
Solanaceae (S.Knapp – BM)	**4**	**0.26**	**0.10**	**1.04**	**0.36**	**0.18**
42. *Solanum inaequale* Vell.	4	0.26	0.10	0.85	0.36	0.18
Bombacaceae (A.L. Bocage-Neta – IPA)	**1**	**0.07**	**0.26**	**0.26**	**0.32**	**0.16**
43. *Ceiba glaziovii* (Kuntze) K. Schum.	1	0.07	0.26	0.21	0.33	0.17
Fabaceae	**4**	**0.26**	**0.09**	**0.78**	**0.35**	**0.18**
44. *Machaerium angustifolium* Vogel	2	0.13	0.07	0.21	0.20	0.10
45. *Myroxylon peruiferum* L. f.	1	0.07	0.02	0.21	0.09	0.05
46. *Platymiscium floribundum* Vogel	1	0.07	0.01	0.21	0.08	0.04
Boraginaceae	**3**	**0.20**	**0.05**	**0.26**	**0.25**	**0.13**
47. *Cordia trichotoma* (Vell.) Arráb. ex Steud.	3	0.20	0.05	0.21	0.25	0.13
Rubiaceae	**2**	**0.13**	**0.05**	**0.26**	**0.18**	**0.09**
48. *Rudgea jacobinensis* Müll. Arg.	2	0.13	0.05	0.21	0.18	0.09
Asteraceae	**2**	**0.13**	**0.01**	**0.52**	**0.14**	**0.07**
49. *Verbesina macrophylla* (Cass.) S.F. Blake	2	0.13	0.01	0.43	0.14	0.07
Cactaceae	**1**	**0.07**	**0.05**	**0.26**	**0.11**	**0.06**
50. *Cereus jamacaru* DC.	1	0.07	0.05	0.21	0.12	0.06
Bignoniaceae	**1**	**0.07**	**0.01**	**0.26**	**0.07**	**0.03**
51. *Tabebuia* sp.	1	0.07	0.01	0.21	0.07	0.04
Dead trunks	**94**	**6.16**	**6.40**	**9.9**	**12.57**	**6.28**

If Sapotaceae and Combretaceae (families having less than 50 individuals per hectare, Table 2), are added to this group, the sum of the total basal area increases to 71%. Although Fabaceae contained more species in this survey than Mimosaceae (both families of the Order Fabales), this is not important within the forest structure.

The Shannon diversity index (H') for species was 2.72 nats ind^{-1}. Seven species accounted for approximately 72% of the total IC, whereas other 30 species represented less than 1% of the IC. *Myrcia fallax* (Myrtaceae) alone represented 35.87% of all trunks found in this survey. *Myrcia multiflora* (Myrtaceae), *Urera baccifera* (Urticaceae), and *Maprounea guianensis* (Euphorbiaceae) all showed high IC values, due in great part to their high relative densities and frequencies. *Manilkara salzmanii* (Sapotaceae), *Trichilia emarginata* (Meliaceae*), Terminalia brasiliensis* (Combretaceae), and *Gallesia integrifolia* (Phytolaccaceae) stood out for their high relative dominance (Table 2): these four species accounted for 46.8% of total dominance and 10.2% of total density.

Moving vertically from understory to canopy, Sapotaceae (mainly *Manilkara salzmanii*), Meliaceae (*Trichilia emarginata*), and Combretaceae (*Terminalia brasiliensis)* became increasingly important. Myrtaceae, with several species, mostly occupied the intermediate height classes, and *Myrcia fallax* was the most important species found in this study. It accounted for 39.4% of all individuals less than 12 m tall, and almost completely dominated the understory layer. Urticaceae (*Urera baccifera*) stood out in the < 4 m height class. Species such as *Manilkara salzmanii* and *Terminalia brasiliensis* were also represented in different height classes, while *Gallesia integrifolia* (Phytolaccaceae) was only present in the taller classes.

Floristic Similarities between the Serra Negra Forest and other Regional Forests

Cluster analysis of 155 species in 12 surveys allowed identification of three distinct groups, based primarily on their floristic composition (Fig. 3). The first group comprised all humid forests (1, 2, 3) and some dry forests (4, 5, 6). In the second group were two deciduous thorn woodlands (11, 12), and - in the third group - only dry forests (7, 8, 9, 10).

In the PCA, the first five ordination axes accounted for 65% of the variation. In Fig. 4 the first two axes suggest three groupings: one that includes

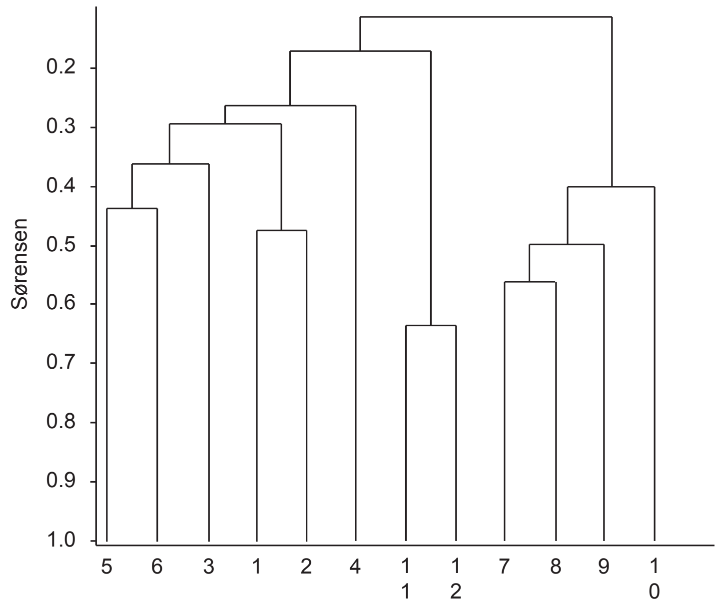


Fig. 3 — Floristic similarities between Serra Negra and other forest sites in Pernambuco state, Brazil. 1-2 = lowland humid forest; 3 = montane humid forest; 4 = lowland dry forest; 5-10 = montane dry forest; and 11-12 = deciduous thorn woodland. See information about the number of each area in Table 1.

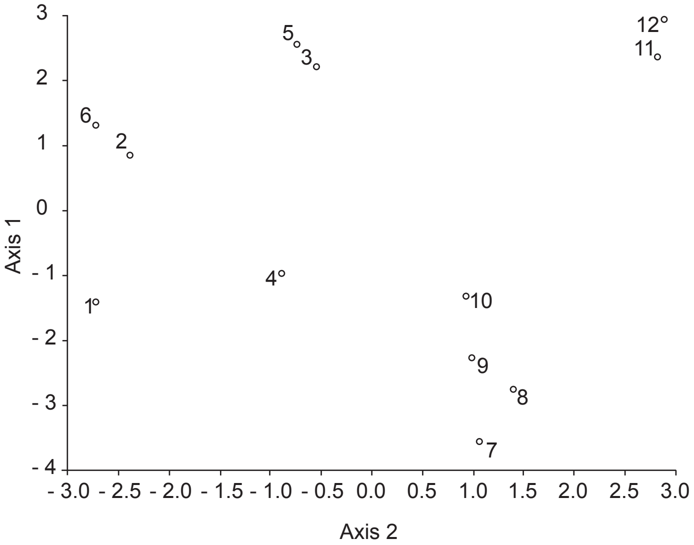


Fig. 4 — Principal component analysis between Serra Negra and other forests sites in Pernambuco state, Brazil. 1-2 = lowland humid forest; 3 = montane humid forest; 4 = lowland dry forest; 5-10 = montane dry forest; and 11-12 = deciduous thorn woodland. See information about the number of each area in Table 1.

most of the dry forests (7, 8, 9, 10); a second, deciduous thorn woodlands (11, 12); and a third comprising humid and dry forests (1, 2, 3, 5, 6).

DISCUSSION

Are there floristic and structural differences between different dry forests in northeastern Brazil?

In the first place, the basis for distinguishing montane dry forests that are more related with humid forest near the Atlantic coast, from others that are more closely associated with seasonal plant formations characteristic of the *Caatinga* biome, is the flora and structure of each florest area. Thus, Rodal (2001) argues that the dry montane forests studied by Ferraz (1994), Correia (1996), and Moura (1997) are more similar to the Caatinga biome, because of the absence of species characteristic of wet environments, and the presence of many species common to the northeastern Caatinga and other deciduous plant formations in South America. Our multivariate analysis results suggest that dry forests are quite heterogeneous. These dry forests are classifiable by either of two transitional states: one, related to the Atlantic Forest biome, that represents a transition from humid (1, 2, 3) to dry forest (4, 5, 6), and a second representing a transition from DTW (11, 12) to dry forests (7, 8, 9, 10).

A revision carried out by Siqueira *et al.* (2001) found that the most important families in the lowland humid forests (coastal forests) of Pernambuco, Paraíba, and Alagoas states, in terms of the number of individuals, are Anacardiaceae, Lecythidaceae, Moraceae, Sapotaceae, and Burseraceae. These families, while well represented in humid lowland (Siqueira *et al.*, 2001; Lins-e-Silva & Rodal, in press), dry lowland (Andrade & Rodal, 2004), and humid montane forests (Tavares *et al.*, 2000), are only moderately or poorly represented in dry montane forest of the semi-arid region (Correia, 1996; Moura, 1997; the present research); at 700 m asl (Ferraz *et al.*, 2003) and 500 m asl in DTW areas (Rodal *et al.*, accepted); and at 900 (Ferraz *et al.*, 2003) and 700 m asl in dry montane forest (Rodal *et al.*, accepted).

The surveys analyzed in this paper confirmed that the family Myrtaceae had the greatest cover importance value in the dry forest of Serra Negra as well as in the dry montane forest studied by Correia (1996) and Nascimento (2001). However, a study made by Andrade & Rodal (2004) in dry lowland forest showed that while Myrtaceae had the greatest number of species, this family had no structural importance. Surveys undertaken in DTW (Tavares *et al.,* 1969; Alcoforado-Filho *et al.,* 2003 and Ferraz *et al.,* 2003) registered the presence of Myrtaceae in areas of the *Caatinga* near the mountains and plateaus, as well as in the transitional zones between the humid forest and inland DTW. In these areas, again this family lacked structural importance.

Vegetation within the C*aatinga* (*sensu stricto*) at 700 (Ferraz *et al*., 2003) and 500 m asl (Rodal *et al*., accepted), and dry forest at 900 (Ferraz *et al.,* 2003) and 700 m asl (Rodal *et al*., accepted) changes with altitude increase in the eastern part of the *Caatinga* biome (Rodal & Sampaio, 2002). Increases in precipitation, humidity, plant size, and species number per area from the lowest in the center of the inland depression to the higher mountain areas result in the gradual substitution of DTW by dry forest.

In the lowest areas of the *Caatinga* biome (*ca.* 500 m asl) spiny, deciduous, and highly- branched plants typical of deciduous thorn woodland (DTW or *Caatinga sensu stricto)* and averaging between 3 and 4 m in height predominate. Anacardiaceae (*Schinopsis brasiliensis*, *Myracrodruon urundeuva*, and *Spondias tuberosa*), Cactaceae (*Pilosocereus* spp. and *Opuntia* spp.), Euphorbiaceae (*Cnidoscolu*s spp., *Croton* spp., and *Jatropha* spp.), Mimosaceae (*Mimosa* spp. and *Piptadenia* spp.), and Caesalpiniaceae (*Caesalpinia* spp.) are all typical of DTW (Rodal, 1992; Araújo *et al*., 1995).

Ferraz *et al.* (2003) observed that the DTW covering the surfaces of the semi-arid sedimentary plateaus (*ca.* 700 m asl) was generally taller than that seen at lower elevations (*ca.* 500 m asl). In addition to this difference, at higher altitudes other plant species became more common, *e.g*., *Rollinia leptopetala* (Annonaceae), *Syagrus oleracea* (Arecaceae), *Tabebuia impetiginosa* (Bignoniaceae), *Cordia trichotoma* (Boraginaceae), *Peltogyne pauciflora*, *Platysmicium floribundum* (Fabaceae), *Trichilia emarginata* (Meliaceae), *Campomanesia eugenioides* var. *desertorum*, *Eugenia flava*, *E. nigra*, *E. tapacunensis*, and *Psidium rivulare* (Myrtaceae), and *Allophylus quercifolius* (Sapindaceae).

Although in the *Caatinga* biome a strong relationship due to rising precipitation rates and decreasing temperatures is evident between altitude and plant height on a regional scale, this correlation may not be as noticeable on a local scale, at which plant height appears to be more strongly linked to soil water supply and local topography (Sampaio *et al*., 1981). At 900 m asl, for example, dry forest can be found that is dominated by tall trees and associated with only a few low, branched, thorny, deciduous species (typical of DTW - *Caatinga sensu stricto*), *e.g*., the Serra Negra, whereas other dry forest with tall trees exists at the same altitude but associated with a large number of those same deciduous species, as in an area studied by Ferraz *et al*. (2003).

Although Murphy & Lugo (1986) observed that seasonally dry forests have a smaller stature and a lower basal area than tropical rain (humid) forests, that pattern differs from the results of the present work on the Serra Negra forest and those of other dry and humid forests in studies by other authors using similar inclusion criteria (Table 1).

Half of the surveys, such as those of dry forests (5, 7) and humid forests (2, 3), showed a total density (TD) of approximately 1,500 trunks ha^{-1}. The occurrence of significantly lower TD values in other studies (*e.g*., 780 stems ha^{-1} in Lins-e-Silva & Rodal, in press) may be related to successional stages of regrowth, or to the degree of disturbance suffered in these areas. Considering all surveys using a 5 cm DBH, variation in basal area was positively associated only with increasing altitude (0.32 with $p \geq 0.09$), and not with subjective classification of forest areas as either dry or wet (Table 1).

Do dry and humid forests in northeastern Brazil represent a single vegetational unit?

Rodal & Sampaio (2002) observed that the biome concept is based on being able to identify "nuclear areas", in which a greater number of the characteristics considered basic to that biome can be found, as well as "marginal areas", in which these characteristics progressively decrease until arriving at the limits of another area where the vegetative and environmental features characterize another biome. These authors pointed out, however, that this approach has two basic requirements: identifying the basic features in each biome, and selecting the minimum number necessary to establish biome boundaries. However, no consensus about these criteria exists as yet among researchers studying the largest biomes in Brazil.

The separation of Serra Negra and other montane dry forests (Correia, 1996; Moura, 1997), specifically at 700 m asl Rodal *et al*., in press) from dry forests that are more related to coastal forests confirms the hypothesis proposed by Pennington *et al*. (2004) concerning the older, and now totally fragmented, seasonally dry neotropical forest biome, which includes that of the *Caatinga*. For these authors, the existence of strong floristic links between well-separated areas of seasonally dry forest in South America suggests that these areas are in fact fragments of an older and much larger forest formation. They argue that the drier conditions of the Pleistocene (coinciding with glacial periods) favored expansion of dry over wet forest. To support this theory, they cite data from molecular biogeographical studies suggesting that, in many cases, the speciation of trees and shrubs in dry forest of South America pre-dates the Pleistocene.

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