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GRADIENT ANALYSIS OF AN AREA OF COASTAL VEGETATION IN THE STATE OF PARAÍBA, NORTHEASTERN BRAZIL

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A transect of coastal vegetation was surveyed for its plant communities in the state of Paraíba, Northeastern Brazil. Two main plant formations are found in this region. The 'restinga' is the coastal sand dune vegetation and the 'tabuleiro' is the adjacent savanna-like formation. The ordination of sample units and species of the transect showed that these plant formations cannot be considered as discrete communities but they are actually a vegetational continuum made up of species adapted to sandy soils but with varying distributional patterns according to the exposure to maritime influences.

As comunidades vegetais de uma transeção de vegetação costeira foram inventariadas no litoral norte do estado da Paraíba, Brasil. Duas formações vegetais predominam nesta região: a restinga, que é a vegetação das dunas arenosas costeiras, e o tabuleiro, que é a formaçõo savânica (cerrado) adjacente. A ordenação de parcelas e espécies da transeção mostrou que estas duas formações vegetais não podem ser consideradas como comunidades discretas, mas sim como um contínuo vegetacional composto de espécies adaptadas a solos arenosos, mas com variados padrões distribucionais de acordo com a exposição às influências marinhas.

The mass of land at the junction of the east and north coasts of Brazil is made up of the northeastern states of Pernambuco, Paraíba, Rio Grande do Norte and Ceará. The vegetation of this region is roughly organized in belts of increasingly dry plant formations that run westwards following the sudden climatic changes, from the humid eastern coast to the vast semi-arid hinterland (the 'Sertão'). The plant formations fall into four broad phytogeographic zones defined by Andrade-Lima (1960a) as: (a) 'Littoral', that comprises the narrow strip of coastal vegetation along the whole seashore, including that of the sand dunes and mangrove formations; (b) 'Mata', consisting of the evergreen rainforests and seasonal semideciduous forests that occur mainly following the Atlantic coast, from the state of Paraíba to southern Brazil**, but also on some mountain chains within the semiarid interior (the 'brejos'); (c) 'Cerrado', which is found as disjunct patches of the great Central Brazilian savanna formation occurring on sandy soils close to the coast and on some isolated inner plateaux; and (d) 'Caatinga', the deciduous thorn forest or cactus-thorn scrub formation that covers the main part of the semi-arid hinterland of the region, approaching the seashore in the states of Rio Grande do Norte and Ceará. In many coastlands of this region, the Littoral Zone is followed by an adjacent inland Cerrado Zone. The predominant vegetation formations of these zones are regionally known as 'restinga' and 'tabuleiro', respectively.

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**Only sparse remnants of this forest, the 'Mata Atlântica', are still found in the region.

'Restinga' is a Portuguese word meaning sand bank that also became used, throughout Brazil, to refer to the vegetation of the coastal sand dunes. The physiognomy of the restinga formation varies considerably, comprising sparse beach grasslands and more or less closed scrubs and forests. Most studies on the floristic composition and plant community zonation of restinga vegetation in Brazil have been made in the southeastern states, particularly in the state of Rio de Janeiro (Ule, 1901; Schenk, 1903; Hemmendorf, 1912; Dansereau, 1947; Ruschi, 1950; Magnanini, 1954; Hueck, 1955; Dau, 1960; Ormond, 1960; Franco *et al.*, 1978a, b; Hay *et al.*, 1981; Grande & Lopes, 1981; Henriques *et al.*, 1984, 1986; Araújo & Henriques, 1984; Silva & Somner 1984a, b; Silva & Oliveira 1989). In Northeastern Brazil, floristic surveys and general descriptions are available for areas of restinga in the states of Pernambuco (Andrade-Lima, 1954, 1960a, b), Alagoas (Esteves, 1980; Rodicka 1980), Bahia (Seabra, 1949; IICA & CEPLAC, 1976; Morawetz, 1983) and Rio Grande do Norte (Tavares, 1960; Freire, 1990).

The cerrado (savanna) formation of Northeastern Brazil that occurs close to the coast on flat sandy plains is regionally called 'tabuleiro' (literally 'tray'), a name restricted by geologists to the local low plateaux formed on the surface of the Barreiras Geological Formation. The floristic and general ecology of 'tabuleiro' formations have been studied in the states of Pernambuco by Andrade-Lima (1954, 1960a, 1970), in Sergipe by Leite (1973, 1976) and Fonseca (1979), and in Paraíba and Pernambuco by Tavares (1988a, b).

These two types of vegetation formations, the restinga and the tabuleiro, are sometimes difficult to delimit in the field, since they both occur on sandy soils, have a wide variation in physiognomic types and can share a considerable number of species. Some authors believe that the restinga and the tabuleiro can intergrade to form a vegetational continuum (Andrade-Lima, 1960a; Leite, 1976).

The present communication is the first attempt to describe quantitatively the interface between the restinga and the tabuleiro formations. The study was carried out in the northernmost coastland of the state of Paraíba and was supported by the company Rutilo & Ilmenita do Brasil (RIB) which is engaged in sand dune mining. Knowledge of the natural vegetation of the area is useful for the company to facilitate the environmental rehabilitation of mined areas and of tailings dunes.

Description of the Study Area

The study area is situated in the municipality of Mataraca, at the northernmost coast of the state of Paraíba, Northeastern Brazil, where the Guaju river delimits the border with the state of Rio Grande do Norte (Fig. 1). This border is also considered as the transition between two types of geomorphological formations of the Brazilian Tertiary Littoral: the Super-humid, to the south, characterized by low cliffs, fixed sand dunes and reefs; and the Semi-arid, to the north, characterized by high and mobile sand dunes (Araújo & Lacerda, 1987). The climate is classified as Köppen's Am type, i.e. tropical and rainy with a short dry season. The mean annual temperature is 25.5°C and the monthly means range from 23.7°C in July to 26.8°C in February. The mean annual rainfall of 1725mm

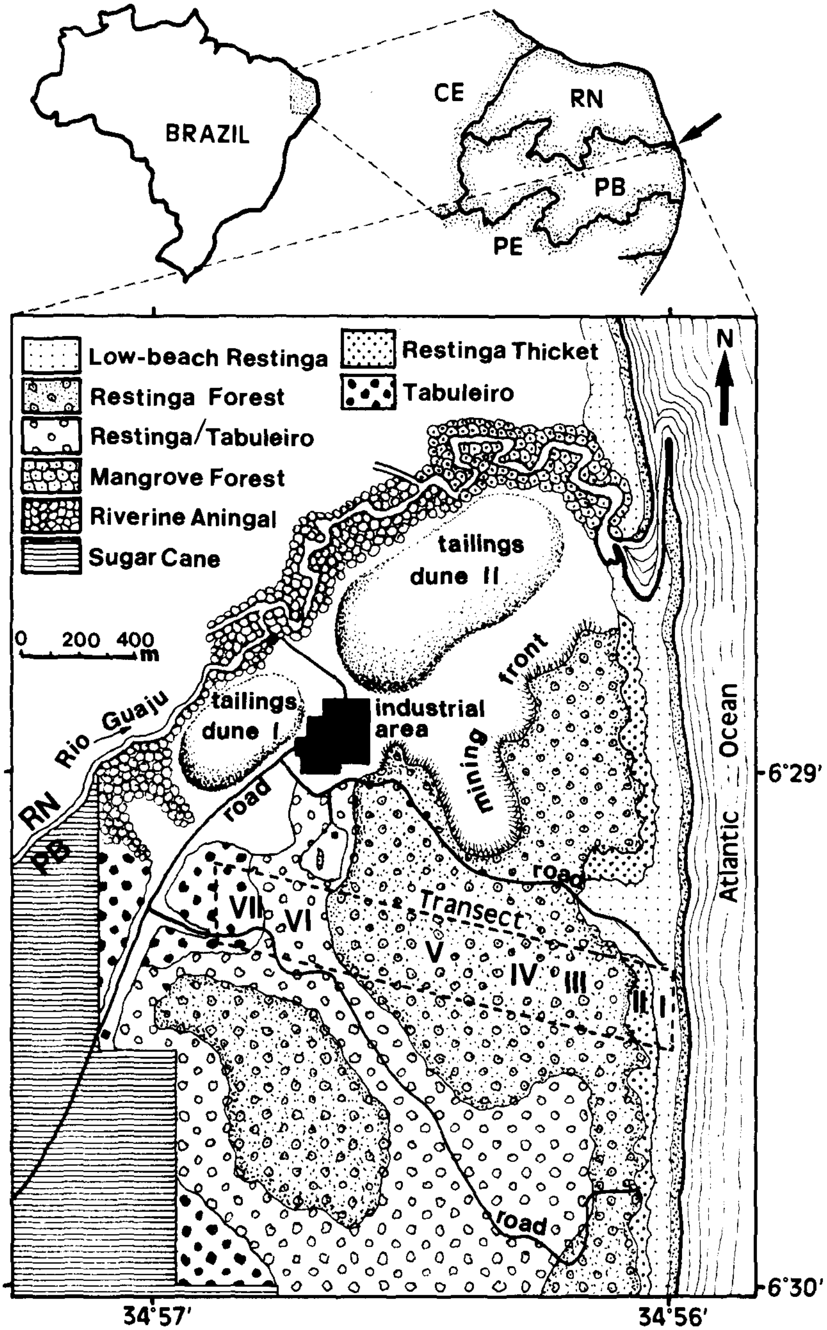

FIG. 1. Map of the study area showing the vegetation types and the transect with the situation of the seven blocks of plots (numbered with roman numerals). Brazilian states: CE – Ceará, RN – Rio Grande do Norte, PB – Paraíba, PE – Pernambuco. For the vegetation types outside the transect, reader is reported to Oliveira-Filho & Carvalho (1993).

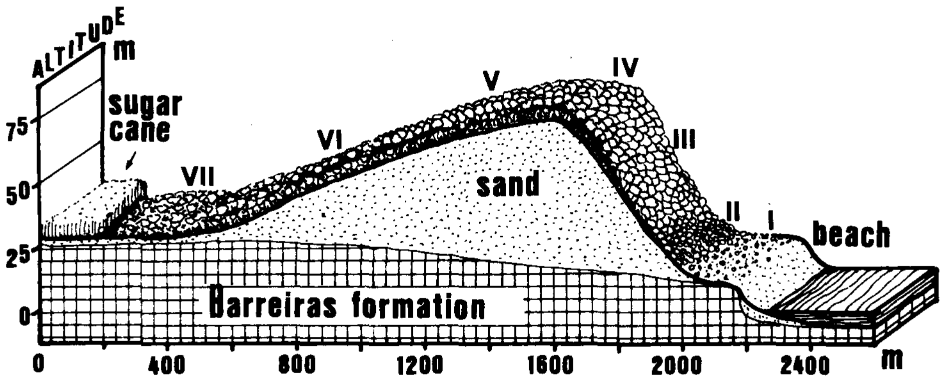

FIG. 2. Profile of the transect showing in relief the geological formations, the vegetation and the situation of the seven blocks of plots (numbered with roman numerals). Note: altitudinal exaggeration.

is concentrated (86.2 %) from February to August; the driest month is December, with a mean rainfall of 32mm, while two rainy peaks occur, May (289mm) and July (255mm).

The predominant geological formation of the region belongs to the Barreiras Group, which is mainly composed of clay-sandy sedimentary rocks from the Tertiary (Mabesoone & Castro, 1975). This formation is found covered, in most places, by sandy sediments that could have been wind-blown from the seashore (Bittencourt, 1975) and/or originated through weathering and redeposition of the sand portion of the rock (Beurlen, 1967).

As shown in Fig. 2, the Barreiras Formation outcrops in the study area only at the beach and is completely sand-covered inland. A narrow strip of sandy terrace at the beach is followed by the steep slope of a foredune. The terrace and the slope are both covered by restinga vegetation, the physiognomy varying from a herbaceous and sparse cover at the lower-beach, to a closed forest at the top of the dune. This dune has been formed from aeolian deposition of beach sand over the Barreiras Formation under the action of the trade winds that blow northwestwards during most of the year. This sand contains a low proportion of grains of heavy minerals (ilmenite, zirconite and rutile) that are extracted by the mining company.

Behind the crest of the foredune, that reaches 60–80m in altitude, the gentle inland slope leads to the wide tabuleiro plains where shallower sand layers lie over the Barreiras Formation (Fig. 2). The vegetation is characterized by a low grassy cover where many tortuous shrubs and trees are scattered or gathered in clumps. However, this vegetation has been replaced in most places by sugar cane plantations for at least the last 200 years. The foredunes, however, have not been used for agriculture because of poor soils, salt spray and aeolian erosion.

METHODS

A floristic survey was carried out in the study area from 1987 to 1991. Plant specimens were identified with the help of botanists of the herbaria of the Empresa Pernambucana de Pesquisa Agropecuária (IPA), Jardim Botânico do Rio de Janeiro (RB) Instituto de

Botânica de São Paulo (SP) and Universidade Estadual de Campinas (UEC). Voucher specimens are lodged in the herbarium of the Escola Superior de Agricultura de Lavras (ESAL) with duplicates at the Royal Botanic Garden, Edinburgh (E). The full results of this floristic survey is given by Oliveira-Filho & Carvalho (1993).

The quantitative survey of the vegetation was carried out on a 1700 x 290m transect beginning at the beach, crossing the foredune, and ending at an inland area of tabuleiro (Figs 1 and 2). Seven blocks of plots were set up within the transect and numbered with roman numerals. Each block was made up of ten circular plots, each with a radius of 10m (area = 314.16m^2). The plots of each block were placed in a straight line at right angles to the length of the transect. The centre of the plots were placed at 30m intervals to form a line of 290m, i.e. the total width of the transect. The seven blocks were sited along the transect to represent the physiognomic sub-types of vegetation recognized in the field:

Block I – Lower-beach restinga: This area is covered by a plant formation growing on the sandy and wind-beaten terraces beside the beach. The vegetation is characterized by a sparse grassy cover with scattered creeping plants, low herbs and cacti.

Block II – Upper-beach restinga thicket: This occurs at the base of the foredune and is characterized by low cushion-like thickets of woody plants strongly shaped by the wind. The height of the thickets commonly increases northwestwards following the predominant course of the trade winds. A sparse grassy cover or a bare sandy surface is found between these thickets.

Block III – Restinga forest of the maritime slope: The steep slope of the foredune facing the ocean is covered by a dense forest of low and tortuous trees (36m in height) with their crowns shaped by the trade winds so that the whole canopy shows deep 'scars' running upslope to the northwest. The forest floor is very shady and clean.

Block IV – Restinga forest of the crest of the foredune: The forest becomes taller at the top of the foredune with trees reaching 12m in height. Little or no effect of wind can be observed on the shape of the crowns. Lower trees and shrubs below the canopy form a shady understorey that can be easily penetrated on foot.

Block V – Restinga forest of the inland slope: The forest on this gentle slope is very similar in physiognomy to that of the top of the foredune. However, the tree density lowers gradually downslope.

Block VI – Restinga-tabuleiro transition: This area is covered by a forest with a very heterogeneous physiognomy. Many gaps and patches of scrub are found scattered within the forest. The height of trees varies widely and the shrubs make it difficult to walk through the forest.

Block VII – Tabuleiro woodland: The physiognomy is characterized by dense patches of trees and shrubs surrounded by a grassy cover with scattered low shrubs. The proportion of the woody and herbaceous components of the tabuleiro varies from place to place as is typical of the cerrado (savanna) formation.

Soil samples were collected at the centre of each plot and from the depth of 0–20 cm. The 10 soil samples of each block were mixed to form a bulk sample which was immediately placed within a sealed plastic bag in order to preserve soil moisture. The samples were all collected in a single day of the dry season. Chemical and physical analyses were carried out at the Soil Laboratory of the Escolá Superior de Agricultura de Lavras (ESAL), Lavras, Minas Gerais, following the procedures recommended by EMBRAPA (1979). Soil pH was measured with a potentiometer in a 1:25 soil to water suspension. Exchangeable phosphorus, potassium, sodium, zinc, iron, copper and manganese were extracted with Melish solution; the first three cations were measured in a photometer and the others were measured by atomic absorption. Exchangeable calcium, magnesium and aluminium were extracted with a 1N KCl solution; the aluminium was titrated with a 0.025N NaOH solution while calcium and magnesium were titrated with EDTA 0.025N. Organic carbon was determined by the Tiurim method and the percentage of organic matter was obtained with the Bremelen constant (1.724). Texture was obtained by the densimetric method of Bouyoucos and the moisture content by the relation between dry and moist weights.

The vegetation of the transect was surveyed for the percentage cover of each species of angiosperm present in the plots. Percentage cover was chosen because it allows quantification of species without the necessity of defining limits between individuals, greatly facilitating fieldwork with masses of subshrubs and herbs (Matteucci & Colma, 1982). Hence, estimation of percentage cover gave a common parameter for the various growth forms found along the transect, such as short grasses, creeping plants, cushion-like subshrubs, cacti, bromeliads, lianas, shrubs and trees. On the other hand, this method did not allow the quantitative description of particular vegetation strata.

Percentage cover was scored in classes with the following ranges:

1 – covering < 2.5% of the surface;
5 – covering from 2.5–7.5% of the surface;
10 – covering from 7.5–12.5% of the surface;
95 – covering from 92.5–97.5% of the surface;
99 – covering > 97.5% of the surface.

As it was difficult to assign accurately a score within a range of 5% to each species in a plot of 10m radius, the area was divided in quarters and each species was first given four scores per plot and the average used as its percentage cover for the whole plot. Values of mean percentage cover were also calculated for each species in each block of ten plots and for the whole set of 70 plots. The frequency of each species in the plots was also obtained for each block and for the whole transect.

An ordination by detrended correspondence analysis (DECORANA) was carried out with the computer program of Hill (1979). Using the percentage cover as abundance values, the program processed a matrix of 70 plots per 57 species. Less important species, with an overall average percentage cover < 0.5, were eliminated from the analysis. The results of the ordination of both plots and species were represented by scattergrams using the first four eigenvectors. The ordination of the species in the first two eigenvectors was used to help their arrangement in a table of species per block.

RESULTS

The 129 species of angiosperms recorded in the 70 plots are listed in Table 1 together with their frequency and mean percentage cover in the seven blocks of plots and in the whole transect. The arrangement of the species in this table is based mainly on the results of detrended correspondence analysis (DECORANA). These are summarized by Fig. 3, that shows the ordination of plots and species in the first two eigenvectors, represented by axes I and II. The third and fourth eigenvectors (axes III and IV), are not shown because they were responsible for a less expressive amount of variation and tended to repeat patterns that were already shown by axes I and II. The eigenvalues corresponding to axes I to IV were 0.773, 0.276, 0.169 and 0.113, respectively.

The first two eigenvectors show a high degree of coherence between plots of the same block, which appear mostly in cohesive clouds of points. Axis I shows, from right to left, a sequence that begins with the plots of block I (lower-beach restinga), continues with those of block II (upper-beach restinga thicket) and blocks III to V all together (restinga forest blocks), and ends with those of blocks VI and VII (tabuleiro blocks). Axis II separates the plots of the three blocks of restinga forest one from another (especially the inland slope ones, block V), and also the plots of the tabuleiro blocks one from another.

Each block of the restinga-tabuleiro continuum shows a characteristic group of dominant species, although these same species may also occur in other blocks with lower values of percentage cover. The lower-beach restinga (block I) is characterized by two ecological dominants, the short grass *Sporobolus virginicus* and the creeping *Ipomoea pes-caprae*, and by several other species with much lower percentage cover, such as *Fimbristylis glomerata*, *Cereus pernambucensis*, *Chrysobalanus icaco*, *Canavalia rosea* and *Eugenia ovalifolia*.

The species with highest values of percentage cover in the neighbouring upper-beach restinga thicket (block II) are *Syagrus schisophylla*, *Anacardium occidentale*, *Byrsonima gardneriana*, *Guapira pernambucensis*, *Pilosocereus hapalacanthus* and *Eugenia ovalifolia*. Many species typical of the lowerbeach restinga are found between the thickets while others that can grow as tall trees in the restinga forest are found as dwarfish subshrubs in the thickets, e.g. *Manilkara salzmannii*, *Tocoyena sellowiana*, *Pouteria venosa* and *Ocotea gardneri*.

The three blocks of restinga forest show particular ecological dominants. In the maritime slope (block III), they are *Tabebuia roseo-alba*, *Manilkara salzmannii*, *Ziziphus joazeiro* and *Syagrus schisophylla*. In the top of the dune (block IV) they are *Maytenus distichophylla*, *Myrcia sylvatica*, *Psidium decussatum*, *Cupania revoluta*, *Manilkara salzmannii* and *Xylopia nitida*. In the inland slope (block V) they are *Buchenavia capitata*, *Chamaecrista bahiae*, *Andira nitida*, *Protium heptaphyllum* and *Psidium decussatum*. However, several species with relatively high values of percentage cover are shared by these blocks, such as *Manilkara salzmannii*, *Pouteria venosa*, *Coccoloba cordifolia*, *Duguetia gardneriana*, *Maytenus distichophylla*, *Psidium decussatum*, *Pradosia lactescens* and *Simaba ferruginea*.

Table 1. Percentage cover and frequency of plant species along the transect of coastal vegetation.
The mean percentage cover (PC) together with the frequency (F = number of plots where the species is present) are given for each species in each block of plots (I to VII) and for the whole transect (T). The species were arranged according to their ordination by DECORANA (see Fig. 3).

Species	Family	I PC-F	II PC-F	III PC-F	IV PC-F	V PC-F	VI PC-F	VII PC-F	Totals PC-F
01. *Sporobolus virginicus* (L.) Kunth	Poaceae	21.5(10)	0.2(2)	–	–	–	–	–	3.10(12)
02. *Ipomoea pes-caprae* (L.) Sweet	Convolvulaceae	19.5(10)	0.2(2)	–	–	–	–	–	2.81(12)
03. *Fimbristylis glomerata* (Retz.) Nees	Cyperaceae	5.5(9)	0.1(1)	–	–	–	–	–	0.80(10)
04. *Cereus pernambucensis* Lem.	Cactaceae	3.2(7)	1.0(6)	0.2(2)	–	–	–	–	0.63(15)
05. *Chrysobalanus icaco* L.	Chrysobalanaceae	1.5(3)	0.2(2)	–	–	–	–	–	0.24(5)
06. *Sida ciliaris* L.	Malvaceae	1.4(6)	–	–	–	–	–	–	0.20(6)
07. *Canavalia rosea* (Sw.) DC.	Fabaceae	1.4(6)	–	–	–	–	–	–	0.20(6)
08. *Remirea maritima* Aublet	Cyperaceae	0.7(7)	0.1(1)	–	–	–	–	–	0.11(8)
09. *Turnera ulmifolia* L.	Turneraceae	0.6(6)	–	–	–	–	–	–	0.09(6)
10. *Capparis flexuosa* Vell.	Capparaceae	0.4(4)	–	–	–	–	–	–	0.06(4)
11. *Paspalum maritimum* Trin.	Poaceae	0.3(3)	0.1(1)	–	–	–	–	–	0.06(4)
12. *Gaylussacia brasiliensis* (Spr.) Meissner	Ericaceae	0.3(3)	–	–	–	–	–	–	0.04(3)
13. *Periandra mediterranica* (Vell.) Taub.	Fabaceae	0.3(3)	–	–	–	–	–	–	0.04(3)
14. *Commelina virginica* L.	Commelinaceae	0.3(3)	–	–	–	–	–	–	0.04(3)
15. *Stenotaphrum secundatum* (Walt.) Kuntze	Poaceae	0.3(3)	–	–	–	–	–	–	0.04(3)
16. *Alternanthera maritima* A.St.-Hil.	Amaranthaceae	0.2(2)	–	–	–	–	–	–	0.03(2)
17. *Crotalaria unifoliolata* Benth.	Fabaceae	0.2(2)	–	–	–	–	–	–	0.03(2)
18. *Cassia uniflora* Sprengel	Caesalpiniaceae	0.1(1)	–	–	–	–	–	–	0.01(1)
19. *Philoxerus portulacoides* A.St.-Hil.	Amaranthaceae	0.1(1)	–	–	–	–	–	–	0.01(1)
20. *Cuphea flava* Sprengel	Lythraceae	0.1(1)	–	–	–	–	–	–	0.01(1)
21. *Jacquinia brasiliensis* Mez	Theophrastaceae	0.5(1)	1.6(4)	–	–	–	–	–	0.30(5)
22. *Eugenia ovalifolia* Cambess.	Myrtaceae	2.5(5)	8.6(8)	–	–	–	–	–	1.59(13)
23. *Pilosocereus hapalacanthus* Werd.	Cactaceae	2.2(6)	6.5(10)	2.0(4)	0.1(1)	–	–	–	1.54(21)
24. *Guapira pernambucensis* (Casar) Lundell	Nyctaginaceae	1.3(5)	9.5(6)	–	–	–	0.5(1)	0.3(3)	1.66(15)
25. *Tocoyena sellowiana* (Cham. & Schltr.) Schum.	Rubiaceae	0.4(4)	2.5(9)	0.2(2)	0.2(2)	0.5(1)	–	–	0.54(18)
26. *Byrsonima gardneriana* Juss.	Malpighiaceae	–	10.7(9)	–	–	1.7(4)	–	0.1(1)	1.79(14)
27. *Syagrus schisophylla* (Mart.) Glassman	Arecaceae	0.2(2)	15.0(9)	12.0(10)	2.1(5)	–	–	–	4.19(26)
28. *Anacardium occidentale* L.	Anacardiaceae	–	11.0(5)	5.5(3)	4.5(1)	–	8.0(4)	8.5(6)	5.36(19)
29. *Cenchrus echinatus* Schrader	Poaceae	0.1(1)	0.2(2)	0.1(1)	–	0.1(1)	–	–	0.07(5)
30. *Cnidoscolus urens* (L.) Arthur	Euphorbiaceae	–	0.2(2)	–	0.1(1)	0.1(1)	–	–	0.06(4)
31. *Aechmaea stephanophora* E.Morr. ex Baker	Bromeliaceae	–	0.1(1)	0.1(1)	–	–	–	–	0.01(2)
32. *Humiria floribunda* Mart.	Humiriaceae	–	0.1(1)	–	–	–	–	–	0.01(1)

Species	Family	I PC-F	II PC-F	III PC-F	IV PC-F	V PC-F	VI PC-F	VII PC-F	Totals PC-F
33. *Maytenus erythroxylum* Reisseck	Celastraceae	3.5(5)	2.1(4)	3.8(8)	0.1(1)	3.2(7)	1.9(6)	3.2(5)	2.54(36)
34. *Ximenia americana* L.	Olacaceae	–	3.2(5)	3.5(4)	4.1(4)	–	–	–	1.54(13)
35. *Tabebuia roseo-alba* (Ridl.) Sandw.	Bignoniaceae	–	3.6(4)	19.5(8)	5.0(4)	–	–	–	4.01(16)
36. *Manilkara salzmannii* (A.DC.) Lam.	Sapotaceae	–	8.0(6)	18.5(9)	7.0(3)	4.0(3)	–	–	5.36(21)
37. *Pouteria venosa* (Mart.) Baehni	Sapotaceae	–	5.0(5)	6.0(5)	0.1(1)	6.0(4)	–	–	2.44(15)
38. *Ziziphus joazeiro* Mart.	Rhamnaceae	–	–	12.0(7)	2.5(2)	–	–	–	2.07(9)
39. *Coccoloba cordifolia* Meissner	Polygonaceae	–	0.3(3)	6.5(7)	2.7(6)	1.4(5)	0.6(2)	–	1.64(23)
40. *Talisia acutifolia* Radlk.	Sapindaceae	–	0.3(3)	0.5(1)	–	–	–	–	0.11(4)
41. *Eugenia cassinoides* Berg	Myrtaceae	–	–	1.6(2)	0.1(1)	–	–	–	0.24(3)
42. *Casearia sylvestris* Sw.	Flacourtiaceae	–	–	1.1(2)	0.1(1)	–	–	–	0.17(3)
43. *Eugenia punicifolia* (Kunth) DC.	Myrtaceae	–	–	0.2(2)	0.1(1)	–	1.4(6)	–	0.24(9)
44. *Licania littoralis* Warm.	Chrysobalanaceae	–	–	0.1(1)	–	–	–	–	0.01(1)
45. *Hohenbergia ridleyi* (Baker) Mez	Bromeliaceae	–	–	0.1(1)	0.1(1)	–	–	–	0.01(2)
46. *Inga capitata* Desv.	Mimosaceae	–	–	1.6(2)	4.1(4)	–	–	–	0.81(6)
47. *Sorocea ilicifolia* Miq.	Moraceae	–	–	1.3(5)	3.0(4)	–	–	–	0.61(9)
48. *Eugenia uvalha* Cambess.	Myrtaceae	–	–	0.5(1)	3.9(7)	–	0.5(1)	–	0.70(9)
49. *Campomanesia dichotoma* (Berg) Mattos	Myrtaceae	–	–	3.5(4)	6.0(5)	–	0.5(1)	0.7(3)	1.53(13)
50. *Eugenia flava* Berg	Myrtaceae	–	–	1.6(3)	2.7(6)	1.1(3)	–	–	0.77(12)
51. *Duguetia gardneriana* Mart.	Annonaceae	–	–	1.5(3)	5.0(6)	3.2(6)	0.1(1)	–	1.40(16)
52. *Erythroxylum andrei* Plowman	Erythroxylaceae	–	–	1.5(2)	4.2(6)	0.6(2)	0.3(3)	0.3(3)	0.99(16)
53. *Myrcia sylvatica* (Mey) DC.	Myrtaceae	–	–	–	13.0(9)	2.8(8)	0.2(2)	0.7(3)	2.39(22)
54. *Maytenus distichophylla* Mart. ex Reisseck	Celastraceae	–	–	6.6(7)	13.5(10)	6.6(8)	8.0(7)	2.4(5)	5.30(37)
55. *Guettarda platypoda* DC.	Rubiaceae	–	4.2(8)	1.6(8)	5.7(8)	2.4(7)	7.1(9)	7.0(8)	4.00(48)
56. *Ocotea gardneri* (Meissner) Mez	Lauraceae	–	0.2(2)	0.6(2)	6.1(6)	3.5(3)	–	–	1.49(13)
57. *Hymenaea courbaril* L.	Caesalpiniaceae	–	–	–	2.6(4)	0.1(1)	–	–	0.39(5)
58. *Calycorectes sellowianus* Berg	Myrtaceae	–	–	–	1.6(4)	–	–	–	0.23(4)
59. *Pithecellobium foliolosum* Benth.	Mimosaceae	–	–	–	2.5(2)	–	–	–	0.36(2)
60. *Brosimum gaudichaudii* Trécul	Moraceae	–	–	–	1.5(3)	–	–	–	0.21(3)
61. *Apuleia leiocarpa* (Vogel) Macbr.	Caesalpiniaceae	–	–	–	1.6(1)	–	–	–	0.14(1)
62. *Copaifera cearensis* Huber ex Ducke	Caesalpiniaceae	–	–	–	1.5(1)	–	–	–	0.21(1)
63. *Hymenaea rubriflora* Ducke	Caesalpiniaceae	–	–	–	1.0(2)	–	–	–	0.14(2)
64. *Astronium fraxinifolium* Schott.	Anacardiaceae	–	–	–	0.1(1)	–	–	–	0.01(1)
65. *Pogonophora schomburgkiana* Meiss.	Euphorbiaceae	–	–	–	0.5(1)	–	–	–	0.07(1)
66. *Coccoloba vellosiana* Casar	Polygonaceae	–	0.5(1)	6.2(7)	0.5(1)	2.3(6)	2.7(6)	3.6(5)	2.26(26)
67. *Solanum paludosum* Moric.	Solanaceae	–	–	0.4(4)	–	0.3(3)	–	1.3(5)	0.29(12)
68. *Tetracera breyniana* Schltr.	Dilleniaceae	–	0.1(1)	0.2(2)	0.1(1)	0.3(3)	–	1.4(6)	0.30(13)

Species	Family	I PC-F	II PC-F	III PC-F	IV PC-F	V PC-F	VI PC-F	VII PC-F	Totals PC-F
69. *Xylopia nitida* Dun.	Annonaceae	–	–	1.1(2)	6.1(9)	6.6(7)	–	–	1.97(18)
70. *Pradosia lactescens* (Berg) Mattos	Sapotaceae	–	–	4.2(6)	0.2(2)	6.5(6)	–	–	1.56(14)
71. *Simaba ferruginea* A.St.-Hil.	Simaroubaceae	–	–	2.5(1)	2.0(1)	9.5(6)	1.0(2)	–	2.14(10)
72. *Psidium decussatum* DC.	Myrtaceae	–	–	7.0(7)	10.0(10)	11.1(8)	–	1.0(2)	4.19(27)
73. *Protium heptaphyllum* (Aublet) Marchand	Burseraceae	–	–	0.6(2)	5.1(5)	14.5(9)	–	–	2.89(16)
74. *Buchenavia capitata* (Vahl.) Eichl.	Combretaceae	–	–	–	–	26.0(7)	–	1.0(1)	3.86(8)
75. *Chamaecrista bahiae* (Irwin) Irwin & Bar.	Caesalpiniaceae	–	–	–	–	13.5(8)	–	0.5(1)	2.00(9)
76. *Andira nitida* Mart. ex Benth.	Fabaceae	–	–	–	–	12.0(4)	–	0.1(1)	1.72(5)
77. *Guapira opposita* Lundell	Nyctaginaceae	–	–	–	–	7.0(4)	–	0.1(1)	1.01(5)
78. *Vitex triflora* Vahl.	Verbenaceae	–	–	–	2.0(2)	5.0(3)	–	–	1.00(5)
79. *Talisia obovata* A.C.Sm.	Sapindaceae	–	–	–	0.2(2)	3.0(2)	–	–	0.46(4)
80. *Peltogyne recifensis* Ducke	Caesalpiniaceae	–	–	–	–	1.5(1)	–	–	0.21(1)
81. *Cecropia obtusa* Trécul	Cecropiaceae	–	–	–	–	1.3(5)	1.1(2)	–	0.34(7)
82. *Apeiba tibourbou* Aublet	Tiliaceae	–	–	–	–	1.1(2)	–	–	0.16(2)
83. *Andira fraxinifolia* Benth.	Fabaceae	–	–	–	–	1.0(1)	–	–	0.14(1)
84. *Didymopanax morototoni* Decne & Planchon	Araliaceae	–	–	–	–	1.0(1)	–	–	0.14(1)
85. *Clusia burchellii* Engler	Clusiaceae	–	–	–	–	0.5(1)	–	–	0.07(1)
86. *Bauhinia rubiginosa* Bong.	Caesalpiniaceae	–	–	–	–	0.5(1)	–	–	0.07(1)
87. *Tabebuia chrysotricha* (Mart.) Standl.	Bignoniaceae	–	–	–	–	0.5(1)	–	–	0.07(1)
88. *Pterocarpus violaceus* Vogel	Fabaceae	–	–	–	–	0.5(1)	–	–	0.07(1)
89. *Licania octandra* (Hoffmgg.) Kuntze	Chrysobalanaceae	–	–	–	–	0.2(2)	0.1(1)	–	0.04(3)
90. *Pithecellobium saman* (Jacquin) Benth.	Mimosaceae	–	–	–	–	0.1(1)	0.1(1)	–	0.03(2)
91. *Inga fagifolia* (L.) Willd.	Mimosaceae	–	–	–	–	0.2(2)	–	–	0.03(2)
92. *Faramea* sp.	Rubiaceae	–	–	–	–	0.1(1)	–	–	0.01(1)
93. *Coccoloba latifolia* Lam.	Polygonaceae	–	–	–	–	0.1(1)	–	–	0.01(1)
94. *Cordia exaltata* Lam.	Boraginaceae	–	–	–	–	–	6.5(7)	0.1(1)	0.94(8)
95. *Cupania revoluta* Radlk.	Sapindaceae	–	–	2.6(3)	10.0(5)	6.5(4)	13.5(10)	3.3(8)	5.13(3)
96. *Bowdichia virgilioides* Kunth	Fabaceae	–	–	–	–	–	16.5(8)	4.6(5)	3.01(13)
97. *Pithecellobium cochliocarpum* (Gomes) Mcbr.	Mimosaceae	–	–	–	–	–	14.5(8)	7.1(8)	3.09(16)
98. *Tapirira guianensis* Aublet	Anacardiaceae	–	–	–	–	2.7(4)	23.0(9)	6.1(6)	4.54(19)
99. *Sacoglottis mattogrossensis* Malme	Humiriaceae	–	–	–	–	–	20.5(10)	12.0(10)	4.64(20)
100. *Hancornia speciosa* Gomez	Apocynaceae	–	–	–	–	–	11.0(8)	18.5(10)	4.21(18)
101. *Thyrsodium schomburgkianum* Benth.	Anacardiaceae	–	–	–	–	–	2.5(3)	1.5(2)	0.57(5)
102. *Lecythis pisonis* Cambess.	Lecythidaceae	–	–	–	–	1.0(1)	2.5(3)	–	0.50(4)
103. *Eschweilera ovata* (Cambess.) Miers.	Lecythidaceae	–	–	–	–	–	1.5(1)	–	0.21(1)
104. *Guazuma ulmifolia* Lam.	Sterculiaceae	–	–	–	–	0.1(1)	1.0(2)	–	0.16(3)

Species	Family	I PC-F	II PC-F	III PC-F	IV PC-F	V PC-F	VI PC-F	VII PC-F	Totals PC-F
105. *Ouratea cearensis* (V.Thiegem) Sastre	Ochnaceae	–	–	–	–	–	1.0(1)	–	0.14(1)
106. *Syagrus oleracea* (Mart.) Becc.	Arecaceae	–	–	–	–	–	1.0(1)	–	0.14(1)
107. *Trema micrantha* Blume	Ulmaceae	–	–	–	–	–	0.5(1)	–	0.07(1)
108. *Allophylus puberulus* Radlk.	Sapindaceae	–	–	–	–	–	0.5(1)	–	0.07(1)
109. *Luehea paniculata* Mart.	Tiliaceae	–	–	–	–	–	0.1(1)	–	0.01(1)
110. *Eugenia uniflora* L.	Myrtaceae	–	–	–	–	–	0.1(1)	–	0.01(1)
111. *Zollernia latifolia* Benth.	Caesalpiniaceae	–	–	–	–	–	0.1(1)	–	0.01(1)
112. *Astrocaryum fraxinifolium* Mart.	Arecaceae	–	–	–	–	–	0.1(1)	–	0.01(1)
113. *Hirtella ciliata* Mart. & Zucc.	Chrysobalanaceae	–	–	–	–	–	1.7(4)	5.1(9)	0.97(13)
114. *Hirtella racemosa* Lam.	Chrysobalanaceae	–	–	–	–	–	0.2(2)	1.9(7)	0.30(9)
115. *Vismia guianensis* (Aublet) Choisy	Clusiaceae	–	–	–	–	1.2(4)	1.2(4)	4.2(6)	0.94(14)
116. *Byrsonima cydoniifolia* Juss.	Malpighiaceae	–	–	–	–	–	–	7.6(9)	1.09(9)
117. *Echinolaena inflexa* (Poir.) Chase	Poaceae	–	–	–	–	–	–	5.2(8)	0.74(8)
118. *Bulbostylis paradoxa* (Sprengel) C.B.Clark	Cyperaceae	–	–	–	–	–	–	5.2(8)	0.74(8)
119. *Ouratea fieldingiana* Engler	Ochnaceae	–	–	–	–	–	–	3.2(7)	0.46(7)
120. *Eragrostis compacta* Steud.	Poaceae	–	–	–	–	–	–	2.0(7)	0.29(7)
121. *Curatella americana* L.	Dilleniaceae	–	–	–	–	–	–	2.7(5)	0.39(5)
122. *Panicum rostellatum* Trin.	Poaceae	–	–	–	–	–	–	2.1(5)	0.30(5)
123. *Andira laurifolia* Benth.	Fabaceae	–	–	–	–	–	–	0.8(4)	0.11(4)
124. *Byrsonima sericea* DC.	Malpighiaceae	–	–	–	–	–	–	0.7(3)	0.10(3)
125. *Rapanea guianensis* Aublet	Myrsinaceae	–	–	–	–	–	–	0.3(3)	0.04(3)
126. *Chaetocarpus myrsinites* Baill.	Euphorbiaceae	–	–	–	–	–	–	0.5(1)	0.07(1)
127. *Aegiphila pernambucensis* Moldenke	Verbenaceae	–	–	–	–	–	–	0.1(1)	0.01(1)
128. *Humiria balsamifera* (Aublet) A.St.-Hil.	Humiriaceae	–	–	–	–	–	–	0.1(1)	0.01(1)
129. *Pera ferruginea* Schott.	Euphorbiaceae	–	–	–	–	–	–	0.1(1)	0.01(1)

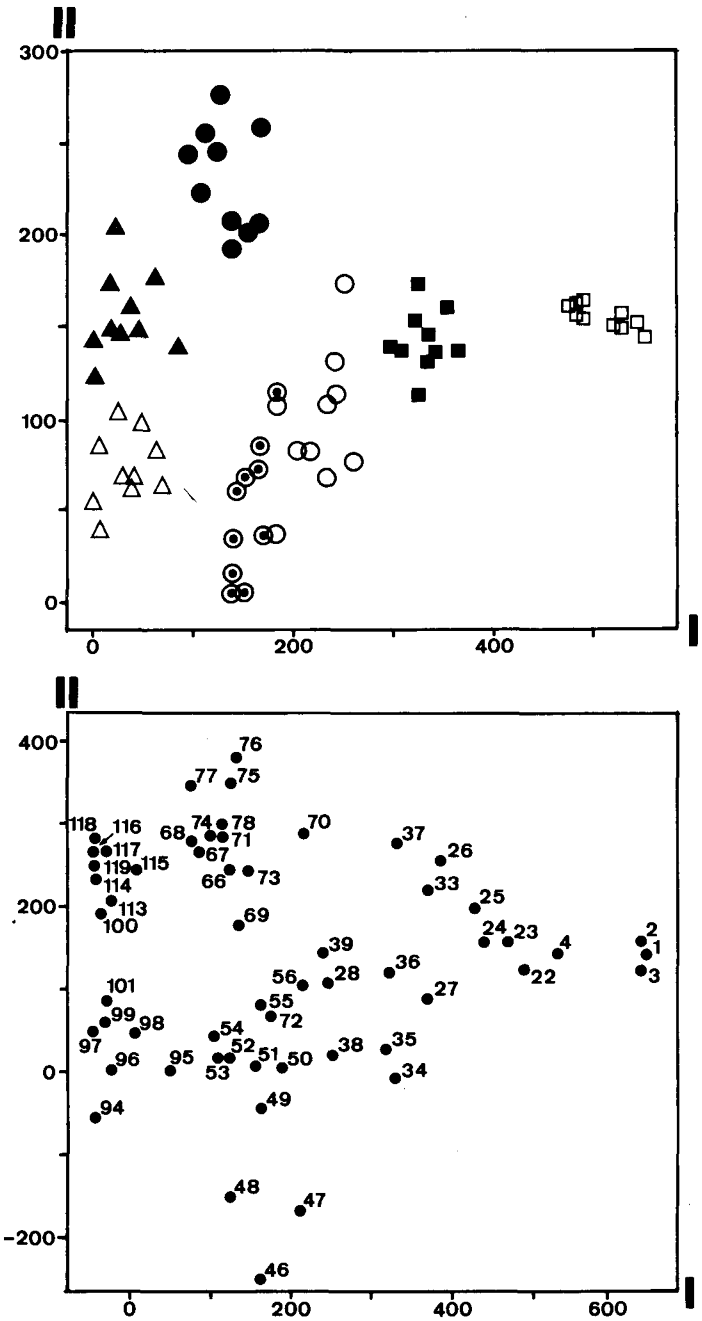

FIG. 3. Results of ordination by detrended correspondence analysis of plots (upper diagram) and species (bottom diagram). The symbols in the plot ordination represent the blocks of the transect: I, II, III, IV, V, VI, VII. The numbers in the species ordination correspond to the species numbers in Table 1.

The dominant species of the restinga-tabuleiro transition (block VI) are *Tapirira guianensis, Sacoglottis mattogrossensis, Bowdichia virgilioides, Pithecellobium cochliocarpum* and *Cupania revoluta* while in the tabuleiro woodland (block VII) they are *Hancornia speciosa, Sacoglottis mattogrossensis, Anacardium occidentale* and *Byrsonima cydoniifolia.* Many species that are abundant in these two blocks are also common in the restinga blocks, e.g. *Anacardium occidentale, Guettarda platypoda, Coccoloba vellosiana, Cupania revoluta, Maytenus erythroxylum* and *Maytenus distichophylla.*

The results of soil analyses for the seven blocks of the transect are given in Table 2. Some general trends can be observed in these data. Soil pH is lower and levels of K, Mn, H+Al, C and organic matter are higher from the top of the dune to the tabuleiro (blocks IV to VII). The amounts of K, Ca, Mg and Fe are much higher while Zn and Na are virtually absent in the tabuleiro blocks (VI and VII). The total amount of exchangeable cations, the cation exchange capacity and the levels of organic matter all increase from the seashore to the tabuleiro. The soils are all coarse-textured although the percentage of sand is slightly lower in the tabuleiro. Soil moisture was lower in the seashore and in the maritime slope; the highest value is found at the top of the dune after which soil moisture decreases progressively downslope to the tabuleiro.

DISCUSSION

The restinga and the tabuleiro cannot be considered as discrete communities since, at least in the study area, they form a vegetational continuum in which the species are found in narrow to wide distribution patterns. There is greater dissimilarity in community structure between some subtypes of the restinga vegetation, such as the beach and the forest, than between the latter and the tabuleiro woodland. The restinga-tabuleiro continuum is certainly made up of a set of plant species capable of growing on sandy and nutrientpoor soils, which, however, vary widely in their ability to survive exposure to maritime conditions.

The correlation between maritime influences and zonation of coastal vegetation has been widely studied in temperate regions and the most important factors indicated as responsible for the distribution of plant species are salt spray, soil salinity, soil stability, microclimate (temperature, humidity and desiccation by wind) and interactions between species (e.g. Oosting, 1945; van der Valk, 1974; Goldsmith, 1978; Barbour, 1978; Silander & Antonovics, 1982). These same effects have been identified as causing plant zonation in sand dune coastal vegetation in tropical regions, including the Brazilian restinga (Dansereau, 1947; Gooding, 1947; Magnanini, 1954; Ormond, 1960; Jenick & Lawson, 1968; Randall, 1970; Messana *et al.* 1977; Franco *et al.* 1978a, b; Morawetz, 1983; Henriques *et al.* 1984, 1986). The effect of wind on the vegetation of the study area is evidenced by the shape of thickets and tree-crowns in all sites facing the ocean. The environmental harshness increases with the proximity of the ocean as shown by the vegetation, which becomes lower and sparser as one approaches the foreshore.

The plant communities of the lower-beach restinga and of the upper-beach restinga thicket are probably composed of the species most resistant to salt spray, desiccation by

Table 2. Soil properties at the study area.
Results of chemical and physical analyses of samples of superficial soil (0–20cm of depth) taken from the seven blocks (I to VII) of the transect of coastal vegetation.

Blocks	pH in water	P	K	Zn	Cu	Fe	Mn	Ca	Mg	Na	Al	H+Al	EC	t	T	C	O.M.	sand	silt	clay	moisture
		ppm						meq.100g^{-1}								%					
I	6.6	3	5	0.4	–	41.7	2.7	0.4	0.2	0.2	0.1	0.7	0.8	0.7	1.3	0.1	0.1	95	1	4	2.0
II	6.4	4	6	0.6	0.3	55.5	3.0	0.6	0.1	0.2	0.1	0.7	0.9	0.8	1.4	0.1	0.1	95	1	4	1.8
III	6.5	4	8	0.4	0.3	34.4	3.0	0.6	0.2	0.1	0.1	0.7	0.9	0.9	1.5	0.1	0.1	95	1	4	1.6
IV	5.3	2	16	–	1.6	31.0	64.8	0.4	0.4	0.1	0.1	1.7	0.9	1.9	3.5	1.2	2.1	97	1	2	4.5
V	5.4	2	16	0.3	0.3	18.5	63.5	0.5	0.4	0.1	1.1	2.7	1.0	2.0	4.0	1.8	3.2	93	3	4	3.8
VI	5.8	5	48	–	0.6	235.5	61.5	4.7	0.9	–	0.1	2.6	5.7	5.8	8.3	2.1	3.6	82	7	11	3.2
VII	5.7	4	45	–	0.5	187.3	63.4	5.0	0.8	–	0.1	2.5	5.9	5.5	8.6	2.0	3.5	83	6	11	3.1

EC = Total exchangeable cations
t = Effective cation exchange capacity
T = Cation exchange capacity at pH 7
O.M. = Organic matter

wind, soil instability and soil salinity (shown to be higher in these sites by the levels of Na). These plant species are ecological dominants of a very harsh and continuous environment, so most of them have also a wide geographical distribution along the Brazilian coast, e.g. as *Remiria maritima, Cereus pernambucensis, Philoxerus portulacoides* and *Alternanthera maritima*, while some of them are cosmopolitan, such as *Ipomoea pes-caprae, Canavalia rosea and Sporobolus virginicus* (Araújo & Lacerda, 1987). Hay *et al.* (1981) have calculated an average similarity of 60 % between the dune and foredune plant communities occurring from the southern to the northeastern coast of Brazil. However, as might be expected, geographical proximity increases the floristic similarities between restinga formations. In the present case, the highest similarity was found with the restingas of Natal, surveyed in the neighbouring state of Rio Grande do Norte by Freire (1990) with 58 species in common (45% of the species in Table 1).

The restinga forest grows on the foredune slopes where environmental harshness is reduced with increasing distance from the seashore, especially on the inland slope which is more protected against the sea winds. In addition to this, the vegetation itself probably improves the environment because it protects the soil from wind erosion and from superficial drying, enriches the soil with organic matter and reduces nutrient losses by leaching. The differences in soil properties found between the sites of restinga at the seashore and at the foredune forest are probably brought about to a large extent by these effects of the vegetation.

Unlike the seashore restinga formation, the restinga forest are known to vary widely in floristic composition throughout Brazil, especially when comparing the northeastern and the southeastern areas (Eiten, 1970; Rizzini, 1979; Henriques *et al.* 1986). Some species occurring as dominants in the restinga forest of the study area are also reported by Andrade-Lima (1960a) as typical of these same formations in Pernambuco, e.g. *Manilkara salzmannii, Tabebuia roseo-alba* and *Anacardium occidentale*. However, when compared with a restinga forest of the northeastern state of Bahia described by IICA & CEPLAC (1976), only one species was found in common with the present study: the very widespread *Didymopanax morototoni*. Surprisingly, the restinga forest studied had also many species that are typical of other vegetation formations of dry climates as well as of humid climates. *Ziziphus joazeiro, Capparis flexuosa* and *Psidium decussatum*, for instance, are characteristic species of the thorn forest of the dry hinterlands (Andrade-Lima, 1960a). Many other species are regarded by Andrade-Lima (1960a) as typical of the coastal rainforest (Mata Atlântica), such as *Pithecelobium saman, Pterocarpus violaceus, Sacoglottis mattogrossensis, Pogonophora schomburgkiana, Lecythis pisonis, Buchenavia capitata, Apeiba tibourbou* and *Hymenaea rubriflora*. In fact, except for the latter, all these species are of wide ecological amplitude, being found in various types of forests throughout Brazil (J. Ratter, pers. comm.). Some other species were also found in common with a hinterland orogenic forest ('brejo') studied in the state of Paraíba by Mayo & Fevereiro (1982), such as *Myrcia sylvatica, Tapirira guianensis, Byrsonima sericea, Hymenaea courbaril, Cupania revoluta* and *Thyrsodium schomburgkianum*. Here again, these are widespread species, except for the latter. The restinga forest in northern Paraíba is actually composed of a mixture of species that are shared with other formations, and only a few species can be considered as typical of this formation. This feature, however, has been also recognized as peculiar of the restinga flora as a whole (Araújo & Lacerda, 1987).

The tabuleiro can be certainly considered as a type of cerrado, as evidenced by its physiognomy, with the typical woody/grassy plants ratio, and by the presence of many species characteristic of this savanna-like formation in Central Brazil. From 59 woody species sampled in blocks VI and VII, 29 (49.15%) were also found in a list produced by Ratter & Dargie (1992) containing 485 species of shrubs and trees occurring in 26 cerrado areas surveyed in central and northern Brazil. Besides this, the abundant species of Gramineae of those blocks, *Echinolaena inflexa, Eragrostis compacta* and *Panicum rostellatum*, are also typical of the core region of the cerrado (Heringer *et al.*, 1977). However, there was still a considerable number of species that do not occur in the core region, including the abundant *Ouratea cearensis, Campomanesia dichotoma* (= *Britoa triflora*) and *Hirtella racemosa*, demonstrating that the tabuleiros of this region are to a certain extent a floristically differentiated type of cerrado.

The relatively high similarity in community structure with the neighbouring restinga vegetation certainly contributes to the distinctive nature of the tabuleiro vegetation within the cerrado formation. Some species that are abundant in both formations, such as *Anacardium occidentale, Guettarda platypoda* and *Maytenus distichophylla*, are probably more influenced by light availability than by maritime effects, since they occur in the study area mostly in relatively open vegetation, such as the tabuleiro woodland and the restinga thicket. However, the tabuleiro formation occurs normally on areas that are well protected against the sea wind. Moreover, the soil texture is less coarse and the levels of most mineral nutrients and organic matter are higher than in the restinga soils, although the changes in soil properties from the restinga to the tabuleiro are as gradual as the changes in plant community structure. Nevertheless, it must be added that the soils and the climate cannot be regarded as the only factors determining occurrence of this savanna-like formation outside its core area. The influence of fire and grazing, associated with (or independent of) man-made disturbances, which are marked in the study area, can never be neglected as key-factors determining savanna landscapes worldwide (Werner, 1991).

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