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The coastal *restinga* vegetation of Pará, Brazilian Amazon: a synthesis

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ABSTRACT – (The coastal *restinga* vegetation of Pará, Brazilian Amazon: a synthesis) The present article reviews studies (some unpublished) of the vegetation of coastal sandy soils (*restinga*) along the coast of Pará State, northern Brazil. A total of 411 higher plant species are reported; Fabaceae, Poaceae, Cyperaceae, Rubiaceae and Myrtaceae are the most species-rich families. Nearly half of the *restinga* species (48%) are terrestrial herbs; palms, trees and shrubs account for 39% of the species, the remainder being lianas and epiphytes. Species are frequently wide-spread and occur in coastal areas of Southeastern Brazil as well as at inland sites in the Amazon region. Only two species appear to be exclusively coastal; whereas other species appear to exhibit a preference for sandy soils. Plant assemblages are commonly classified by means of "formations" associated with certain habitats but current data do not allow the description of well-defined plant associations. The species composition at different sites along the Pará coast does not show any clear regional grouping pattern. Seasonal changes in the composition of *restinga* vegetation are most probably linked to variation in ground water level. *Restinga* forest is mostly low and open; among the dominant tree species are *Humiria balsamifera* Aubl., *Pouteria ramiflora* (Mart.) Radlk., *Anacardium occidentale* L., *Byrsonima crassifolia* (L.) Kunth, and *Tapirira guianensis* Aubl.

Key words - coastal forest, dune vegetation, sandy coastal plain

RESUMO – (Vegetação de restinga do Estado do Pará, Amazônia Brasileira: uma síntese). Este artigo apresenta uma revisão dos estudos (alguns não publicados) da vegetação de restinga da costa do Estado do Pará, na região norte do Brasil. Ao todo foram registradas 411 espécies de plantas vasculares, sendo as famílias Fabaceae, Poaceae, Cyperaceae, Rubiaceae e Myrtaceae as mais ricas em espécies. Dentre as espécies da restinga, 48% são ervas terrestres, 39% são palmeiras, árvores e arbustos, sendo o restante constituído por lianas e epífitas. As espécies são amplamente distribuídas ocorrendo inclusive em ambientes costeiros de outras regiões brasileiras, como a região sudeste, assim como em ambientes não costeiros da Amazônia. Apenas duas espécies parecem ser exclusivamente costeiras, já outras espécies parecem ter preferência por ambientes de solo arenoso em geral. Diferentes associações de plantas são descritas e agrupadas em diferentes tipos de "formações vegetais" associadas à certos habitats, mas os dados da literatura não permitem identificar com precisão tais associações em toda a costa. Análises estatísticas mostraram que a distribuição das espécies ao longo da costa não apresentam nenhum padrão de agrupamento. Mudanças na composição da vegetação de restinga nas estações seca e chuvosa são mais provavelmente ligadas à variação do nível do lençol freático. As florestas de restinga são, em sua maioria, abertas e de pequeno porte. Entre as espécies arbóreas dominantes estão: *Humiria balsamifera* Aubl., *Pouteria ramiflora* (Mart.) Radlk., *Anacardium occidentale* L., *Byrsonima crassifolia* (L.) Kunth e *Tapirira guianensis* Aubl.

Palavras-chave - floresta costeira, planície arenosa costeira, vegetação de dunas

Introduction

The term *restinga* is commonly used in Brazil to describe the landscape forming on coastal sandy soils as well as the associated vegetation. More specifically, it is applied to sand bars forming between coastal lagoons and the ocean (Suguio 1992). For our discussion of northern Brazilian coastal vegetation, we follow Araújo & Henriques (1984), who characterize *restinga* vegetation as the complex of plant communities occurring on the quaternary sandy coastal plains of Brazil. *Restinga* vegetation includes herbaceous plant communities as well as assemblages dominated by shrubs or trees, with widely varying canopy coverage. *Restinga* vegetation colonizes *chêniers*, active or fixed dunes and dune valleys and is usually distinct from the neighbouring mangroves thriving on muddy sediments regularly inundated by the tides. Variety and composition of plant assemblages along the coastal plain depend on the local setting of marine and terrestrial environmental parameters (Alves *et al.* 2007). *Restinga* vegetation plays an ecologically important role in stabilizing active dunes by reducing the movement of sand (Pfadenhauer 1978, Tsoar & Arens 2003).

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Restingas occur along approximately 70% of the Brazilian coastline (Guedes *et al.* 2006), which exceeds 8,000 km in length (Tessler & Goya 2005). However, distribution of *restinga* areas is not continuous; they reach their greatest extensions (up to 700 km) in Rio Grande do Sul State in southern Brazil (Villwock 1987 *fide* Araujo 2000).

Large areas of coastal vegetation suffer from human impacts, leading to degradation of beaches and dunes along the entire coast of Brazil (Scarano *et al.* 2004). Disorderly occupation of beaches along the Brazilian coast has caused loss of *restinga* vegetation cover (Scherer *et al.* 2005).

About 40% of the 1,500 km-long coastline of the Amazon region belongs to the state of Pará (Suguio & Tessler 1984). Amazonian *restingas* are found sporadically on dune ridges and beaches between Marajó Bay (Pará) and São Marcos Bay (Maranhão) (Seeliger 1992). In Pará State, the greatest increase in human population has been recorded for the north-eastern coastal region (Szlafsztein 2003), where *restinga* areas are located. The state government of Pará is encouraging tourism as an additional source of income for the local population (Szlafstein & Stern 2007). In this context, road infrastructure has been improved to facilitate tourist access to beach areas. Tourism is, however, restricted to a few sites (namely Marudá, Algodoal, Salinópolis and Ajuruteua) within the so-called *Salgado Paraense* (Prost & Rabelo 1996). Here and elsewhere, uncontrolled urban expansion as well as exploitation of illegal extraction sites for building materials (sand, loam) or unauthorized establishment of landfills has led to serious environmental problems within the protected coastal areas (Souza Filho 2001). In addition, wood cutting (Glaser *et al.* 2003, focussing on mangroves) and hunting (Pereira & Alvez 2006) impose further threats to coastal vegetation and the associated fauna.

As destruction of this fragile ecosystem through human impacts increases at an accelerating pace (Bastos *et al.* 2001), gathering the existing information about *restingas* and intensifying corresponding research efforts are crucial steps towards their conservation and recovery. As a contribution towards this, we review the currently available literature on *restinga* vegetation of the coast of Pará and present an analysis of the current state of knowledge.

Material and methods

Data collection was based on articles published in scientific journals and books, conference proceedings with abstract collections, technical reports as well as graduate monographs, master's dissertations and doctoral studies. Studies were included if the respective study sites were located along the coast of the Brazilian state of Pará (between 0°42' N, 50°06' W and 1°00' S, 46°00' W). In this region, the climate is warm throughout the year (annual mean air temperature about 26 °C, with minimum temperatures above 18 °C). Precipitation is seasonal with a perhumid rainy season between January and June. During the driest months (September to November), monthly precipitation is below 50 mm. The annual precipitation average is about 2,500 mm (INMET 1992).

Plant species lists were checked for synonyms using taxonomic databases (IPNI 2008, Tropicos 2008) and checklists (Peterson *et al.* 2001, Zuloaga *et al.* 2003, Funk *et al.* 2007); taxonomic names from the analysed *restinga* articles were updated if necessary. The assignment of genera to angiosperm families follows APG II (Stevens 2001, APG 2003).

Based on the species lists obtained from the literature, the distribution and habitat preferences of selected woody species were investigated by analysing the respective information from the data base of the João Murça Pires Herbarium (MG) at the Emilio Goeldi Museum of Pará, Belém. To detect possible groupings among study sites, a dissimilarity matrix based on site-wise presence/absence lists of fully identified plant species was calculated. The applied dissimilarity measure was the Raup-Crick index (Raup & Crick 1979) which is not sensitive to the number of species recorded at each site, thus reducing the influence of site-specific differences in sampling effort on the grouping procedure (*e.g.* Vellent *et al.* 2007). Grouping was then analysed by non-metric multidimensional scaling (NMDS). All calculations were performed with GNU R 2.8.1 (R Development Core Team 2008) with packages "vegan" (Oksanen *et al.* 2008) and "MASS" (Venables & Ripley 2002).

Results and discussion

Study sites are shown in figure 1. The majority of the reviewed studies are abstracts published in conference proceedings (42% of the total number of studies, $n = 62$). Articles published in scientific journals account for 26%, book chapters for 4% and doctoral, master's and graduate studies for 5, 10 and 10%, respectively; technical reports account for another 8% of the reviewed studies. All consulted sources are in the Portuguese language.

The first to mention *restinga* vegetation in Pará was Pires (1973), who described it as "the vegetation growing on the white sand of the beaches and likewise on the dunes". He further mentions *Anacardium occidentale* L., *Byrsonima crassifolia* (L.) Kunth and *Chrysobalanus icaco* L. as typical constituents of *restinga* vegetation.

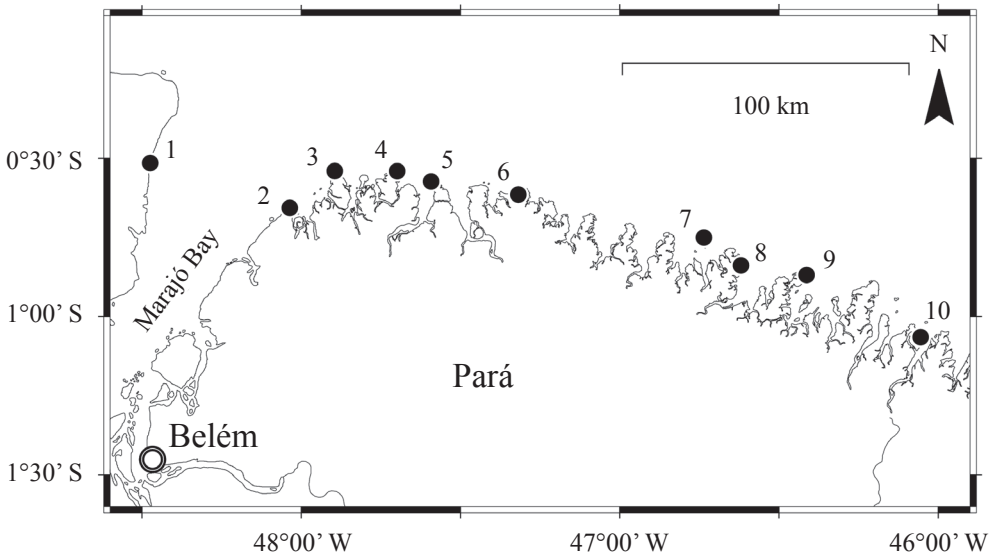

Figure 1. *Restinga* study sites along the coast of Pará State, Brazil (name of the corresponding administrative district in parentheses): 1. Bacurizal (Salvaterra). 2. Ilha Nova (São Caetano de Odivelas). 3. Ilha Romana (Curuça). 4. Crispim Beach (Marapanim). 5. Algodoal (Maracanã). 6. Atalaia (Salinópolis). 7. Ilha Canela (Bragança). 8. Vila Bonifácio (Bragança). 9. Urumajó (Augusto Corrêa). 10. Jabotitiua – Jatium (Viseu). Map based on the GMT coastline database (Wessel & Smith 1996).

Later, Braga (1979) suggested a phytogeographical subdivision of the Amazon region, where he considered the *restingas* of Pará as poorly developed vegetation with low diversity. Studies specifically targeting *restinga* vegetation were first conducted in the 1980s around Algodoal beach (site 5 in figure 1; Bastos 1988, Santos & Rosário 1988).

From the 90s onward, the number of studies focussing on *restinga* vegetation has increased but the more extensive studies concentrate on Algodoal, Crispim beach (site 4, figure 1) and Vila Bonifácio (site 8, figure 1). Studies conducted at these sites considered mainly floristic and phytosociological aspects of vascular plant formations (Algodoal: Bastos 1996, Crispim: Costa-Neto *et al.* 1995, 2000, Amaral 1997, Costa-Neto 1999, Bonifácio: Silva *et al.* 2007, Santos 2008, Silva 2008). The species assemblages at the remaining sites within the study area were characterized by "rapid assessment"-type surveys (Lisboa *et al.* 1993, Amaral *et al.* 2001, Santos *et al.* 2001, Bastos *et al.* 2002). Amaral *et al.* (2008) present a check-list of species reported at 10 sites along the Brazilian Amazon coast but do not consider the more recent studies at Vila Bonifácio (Silva *et al.* 2007, Santos 2008, Silva 2008). A small number of studies provide local taxonomic keys for certain groups (Turneraceae: Vicente *et al.* 1999; Poaceae: Rocha *et al.* 2001a, b; Eriocaulaceae: Rocha & Bastos 2004; Myrtaceae: Rosário *et al.* 2005; Fabaceae-Caesalpinioideae: Sousa 2008; Rubiaceae: Margalho 2008) or for all woody or herbaceous species found at a specific site (Amaral 1997, Costa-Neto 1999, Silva 2008).

Within the *restinga* landscape, authors differentiate between several plant formations; we use "formation" in the sense of an assemblage of plants visibly discernible from other assemblages by forming a distinctive structural pattern. Formations are associated with certain habitat types and may be characterized by a distinctive set of plant species. In denominating formations, the literature mainly follows Araújo & Henriques (1984). The formations distinguished are: (1) halophile herbaceous salt-marsh vegetation subject to occasional tidal inundation (HSM); (2) psammophile herbaceous-rhizomatous vegetation of active dunes, possibly involved in dune build-up and fixation (HAD); (3) herbaceous dune valley vegetation (HDV; *campo de dunas*); (4) patches of woody vegetation within marshland (PWM; *moitas*, *formação arbustiva aberta*); (5) *restinga* forest (RF) of non-inundated areas such as paleodunes. It is assumed that the influence of tidal inundation and salt spray from the sea decreases from (1) to (5) but data on inundation frequency and soil pore water salinities are not available. Bastos (1996) and Amaral (1997) further identify a (salt-)marsh formation established behind fore-dunes next to the beach (*brejo herbáceo*, herbaceous swamp: HS). HSM is described for Crispim Beach only (Costa-Neto 1999) but it is possible that this formation was not clearly separated from other

types of marsh vegetation by other authors. Occurrence of PWM was documented for Crispim and Algodoal (Amaral *et al.* 2008); the remaining formations have been observed along the entire coastline.

The total number of species reported for *restingas* from the coast of Pará amounts to 411, from 90 plant families (Amaral *et al.* 2008); the most intensively studied sites yielded the greatest number of species (273/77, 205/67 and 126/58 species/families at Algodoal, Crispim and Bonifácio, respectively; Bastos 1996, Amaral 1997, Amaral *et al.* 2008, Santos 2008, Silva 2008). The highest species richness was found in the Fabaceae family (53 species), followed by Poaceae (39), Cyperaceae (35), Rubiaceae (20) and Myrtaceae (19). Fabaceae (20) and Myrtaceae (≥ 17) featured the highest number of woody species (Bastos 1996, Amaral 1997, Silva 2008). Myrtaceae were important constituents of woody *restinga* vegetation, as in other parts of the country (Lemos *et al.* 2001, Araujo *et al.* 2004, Assis *et al.* 2004a; Assis *et al.* 2004b; Dornelles & Waechter 2004, Scherer *et al.* 2005, Pimentel *et al.* 2007, Sacramento *et al.* 2007, Martins *et al.* 2008). Dominating genera in Myrtaceae are *Eugenia* (≥ 7 species) and *Myrcia* (8). A special adaptation to *restinga* soils is attributed for example to *Myrcia cuprea* (O. Berg) Kiaersk. (Ferreira 2006).

Almost one half (48%) of the plant species are predominantly herbaceous, whereas 1, 17 and 21% are palms, trees and shrubs, respectively; the remaining species are lianas (11%) and epiphytes (2%).

Amaral (1997) was able to show that the number of tree and shrub species forming patches of woody vegetation within marsh (PWM) at Crispim increases with patch size (between 0.7 and 339 m^2) from 4 to 39, and that certain species do not occur when patch size is too small.

Overall species richness is low when compared to the southern Brazilian *restinga* flora (Rio de Janeiro State: 1005 species, Araújo 2000, Bertioga/São Paulo State: 611 species, Martins *et al.* 2008). High species richness of southern Brazilian *restingas* has been explained by their proximity (both in space and species composition) to the Atlantic rainforest (Araújo 2000, Scarano 2002). The relationship between *restinga* species from the Pará coast and the corresponding Amazonian rainforest species has not been analysed so far. Large variation in diversity can be expected, considering the differences in size and habitat diversity between the extensive *restingas* of southern Brazil and those considered here. Furthermore, both extension and habitat diversity may not be comparable among studies due to the individual researcher's decisions regarding the delimitation of the respective study area.

Table 1 shows a selection of those species reported from at least 50% of the reviewed sites with their respective habitats (Costa-Neto *et al.* 1995, 2000, Bastos 1996, Amaral 1997, Costa-Neto 1999, Amaral *et al.* 2008). It is evident that there is plenty of overlap between species assemblages assigned to the different habitat types. The occurrence of woody species within HS and HDV refers mostly to seedlings, which are usually unable to establish themselves permanently within the respective habitat (Bastos 1996), but may, within HDV, succeed to form patches of woody vegetation (PWM; Amaral 1997). Similarly, seedlings of mangrove tree species (*Avicennia germinans* (L.) L.,

Table 1. Herbaceous and woody *restinga* plant species from the coast of Pará and their respective habitat types. Listed are only species present at least in 5 of 10 reviewed study sites. (HSM = herbaceous salt marsh; HAD = herbaceous vegetation of active dunes; HS = herbaceous swamp; HDV = herbaceous dune valley vegetation; PWM = patches of woody vegetation within marshland; RF = restinga forest.) Species are listed in sequence of supposed ability to thrive under marine influence, derived from occupied habitat types and the corresponding distance to the sea.

Species		HSM	HAD	HS	HDV	PWM	RF	Sites %
Herbaceous								
Sesuvium portulacastrum (L.) L.	Aizoaceae	•		•				90
Blutaparon portulacoides (A. St.-Hil.) Mears	Amaranthaceae	•	•	•				50
Sporobolus virginicus (L.) Kunth	Poaceae	•	•	•	•			80
Fimbristylis cymosa (Lam.) R. Br.	Cyperaceae			•				70
Alternanthera tenella Colla	Amaranthaceae			•				70
Blutaparon vermiculare (L.) Mears	Amaranthaceae			•				60
Canavalia rosea (Sw.) DC.	Fabaceae-Faboideae		•					60

continue

continuation

Species		HSM	HAD	HS	HDV	PWM	RF	Sites %
Fimbristylis spadicea (L.) Vahl	Cyperaceae		•	•				90
Ipomoea pes-caprae (L.) R. Br.	Convolvulaceae		•	•				100
Ipomoea imperati (Vahl) Griseb.	Convolvulaceae		•	•				90
Vigna luteola (Jacq.) Benth.	Fabaceae-Faboideae		•	•				60
Cassytha filiformis L.	Lauraceae		•	•	•			80
Cyperus ligularis L.	Cyperaceae		•	•	•			80
Paspalum vaginatum Sw.	Poaceae		•	•	•			70
Ambrosia microcephala DC.	Asteraceae		•	•	•			70
Eclipta prostrata (L.) L.	Asteraceae		•	•	•			60
Sarcostemma clausum (Jacq.) Schult.	Apocynaceae-Asclepiadoideae		•	•	•			50
Centrosema brasilianum (L.) Benth.	Fabaceae-Faboideae		•	•	•	•	•	60
Eleocharis geniculata (L.) Roem. & Schult.	Cyperaceae			•	•		•	80
Rhynchospora riparia (Nees) Boeck.	Cyperaceae			•	•			70
Cyperus polystachyos Rottb.	Cyperaceae			•	•			50
Scoparia dulcis L.	Plantaginaceae			•	•			50
Stylosanthes angustifolia Vogel	Fabaceae-Faboideae			•	•	•		50
Ludwigia hyssopifolia (G. Don) Exell	Onagraceae			•	•	•		70
Desmodium barbatum (L.) Benth. & Oerst.	Fabaceae-Faboideae			•	•	•		50
Comolia villosa (Aubl.) Triana	Melastomataceae			•	•	•		50
Chamaecrista ramosa (Vogel) H.S. Irwin & Barneby	Fabaceae-"Caesalpinoideae"				•	•		50
Crotalaria retusa L.	Fabaceae-Faboideae				•		•	60
Turnera melochioides A. St.-Hill. & Camb.	Turneraceae				•			70
Cissus biformifolia Standl.	Vitaceae				•			70
Cissus verticillata (L.) Nicolson & C.E. Jarvis	Vitaceae				•			70
Woody								
Chrysobalanus icaco L.	Chrysobalanaceae		•	•	•	•	•	90
Entada polystachya (L.) DC.	Fabaceae-Mimosoideae			•	•			60
Rhabdadenia biflora (Jacq.) Müll. Arg.	Apocynaceae			•	•			50
Dalbergia ecastaphyllum (L.) Taub.	Fabaceae-Faboideae			•				90
Rhizophora mangle L.	Rhizophoraceae			•		•		50
Laguncularia racemosa (L.) C.F. Gaertn.	Combretaceae			•		•		50
Conocarpus erectus L.	Combretaceae			•		•		50
Byrsonima crassifolia L.	Malpighiaceae			•		•	•	50
Annona glabra L.	Annonaceae			•			•	70
Guettarda angelica Mart. ex Müll. Arg.	Rubiaceae				•		•	60
Tapirira guianensis Aubl.	Anacardiaceae				•	•	•	70
Anacardium occidentale L.	Anacardiaceae				•	•	•	90
Cassipourea guianensis Aubl.	Rhizophoraceae				•	•	•	50
Myrcia cuprea (O. Berg) Kiaersk.	Myrtaceae				•	•	•	70
Eugenia biflora (L.) DC.	Myrtaceae				•	•	•	50
Himatanthus articulatus (Vahl) Woodson	Apocynaceae				•	•	•	70
Vismia guianensis (Aubl.) Choisy	Clusiaceae				•	•	•	70
Clusia grandiflora Splitg.	Clusiaceae				•	•	•	60
Licania octandra (Hoffmanns. ex Roem. & Schult.) Kuntze	Chrysobalanaceae				•	•	•	50
Copaifera martii Hayne	Fabaceae-"Caesalpinoideae"				•	•	•	60
Protium heptaphyllum (Aubl.) Marchand	Burseraceae				•	•	•	70
Pouteria ramiflora (Mart.) Radlk.	Sapotaceae					•	•	50
Humiria balsamifera Aubl.	Humiriaceae					•	•	50
Astrocaryum vulgare Mart.	Arecaceae					•	•	60

Acanthaceae-Avicennioideae; *Laguncularia racemosa* (L.) C. F. Gaertn., Combretaceae; *Rhizophora mangle* L., Rhizophoraceae) are reported in HS and PWM but do not develop to full size (Bastos 1996, Santos *et al.* 2001, Bastos *et al.* 2002).

A number of species are widespread and occur also in southern Brazilian *restingas*, for example the trees *Anacardium occidentale* (Anacardiaceae; Silva & Oliveira 1989, Freire 1990, Freire & Monteiro 1993, Matias & Nunes 2001, Pereira & Alvez 2006, Queiroz 2007), *Guapira opposita* (Vell.) Reitz (Nyctaginaceae; Silva & Oliveira 1989, Danilevicz *et al.* 1990, Rossoni & Batista 1994, Menezes & Araujo 1999, Lemos *et al.* 2001, Moreto & Mondin 2002, Sá 2002, Sztutman & Rodrigues 2002, Dornelles & Waechter 2004, Batista *et al.* 2005, Neto *et al.* 2005, Scherer *et al.* 2005, Sonehara 2005, Klein *et al.* 2007, Pimentel *et al.* 2007, Martins *et al.* 2008) and *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae; Silva & Oliveira 1989, Assumpção & Nascimento 2000, Pereira & Alvez 2006, Leite *et al.* 2007, Pimentel *et al.* 2007, Sacramento *et al.* 2007). These species are, however, not restricted to *restinga* habitats. Other common woody *restinga* species in Pará are *Chrysobalanus icaco* (Chrysobalanaceae), *Humiria balsamifera* Aubl. (Humiriaceae) and *Byrsonima crassifolia* (Malpighiaceae). *B. crassifolia* is not reported from southeast and southern Brazil, where *B. sericea* DC. is common (Assumpção & Nascimento 2000, Menezes & Araujo 2004, Matallana *et al.* 2005, Pereira & Alvez 2006, Sacramento *et al.* 2007).

An analysis of the João Murça Pires Herbarium specimen data base shows that in Pará the only woody *restinga* species restricted to the coastal zone are *Coccoloba ramosissima* Wedd. (Polygonaceae), the aforementioned *Myrcia cuprea* (Myrtaceae) and the Sapindaceae *Dodonaea viscosa* Jacq. The latter species is, however, widespread and not restricted to the coastal region elsewhere. *D. viscosa* is not a typical lowland rainforest tree, and it may be that collectors in Pará so far neglected, *e.g.*, open and anthropogenically influenced areas, resulting in a biased view of *D. viscosa*'s distribution in this region. It proved difficult to ascertain whether species were restricted to inland sites *e.g.* to sandy soils, as such information is often omitted from herbarium labels. However, occurrence on sandy soils and in *campina* or *campinarana* (open shrub on poor sandy soils and white sand forest, respectively) environments was mentioned for a number of species (3-23% of non-*restinga* vouchers for the woody species listed in table 1).

Among the herbaceous plants, *Ambrosia microcephala* DC. (Asteraceae) is cited as the only species restricted to *restinga* vegetation of northern Brazil (Freire & Monteiro 1993, Costa-Neto 1999). Widespread along the coast of Brazil (and other tropical coasts) are the HAD/HSM species *Sesuvium portulacastrum* (L.) L. (Aizoaceae), *Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae), *Sporobolus virginicus* (L.) Kunth (Poaceae) and *Blutaparon portulacoides* (A. St.-Hil.) Mears (Amaranthaceae), which are considered to be an important stabilizer of active dunes (Pfadenhauer 1978, Cordazzo 1985, Costa-Neto 1999).

It was not possible within the scope of this review, to verify the identification of species by consulting all original collections deposited in the local herbaria MG and IAN (both in Belém, Brazil). A small number of corrections of previous misidentifications discussed by Rocha *et al.* (2001a, b) and Margalho (2008) are silently applied in table 1. Due to the less taxonomically motivated character of most studies, there may be more cases of overlooked or incorrectly identified species. For example, *Clusia palmicida* Rich. ex Planch. & Triana (Clusiaceae) has so far been reported only from Bonifácio (Silva 2008); it is probably more widespread but may not have been noted as it is easily mistaken for *C. grandiflora* Splitg. (J. B. F. Silva, unpublished data).

Non-metric multidimensional scaling with presence-absence data of plant species did not yield a distinct grouping of sites (figure 2); possible divisions exist among sites of the Bragança-Viseu basin (sites 7-10 in figure 1) on one hand, localities around Marajó Bay (sites 1-3 in figure 1) on the other and then the remaining, loosely associated sites Salinópolis, Crispim and Algodoal (4-6 in figure 1). Additional field work is needed to confirm the existence of such a regional pattern. Hierarchical clustering based on a Bray-Curtis (= Czekanowski/Sørensen) dissimilarity matrix for a similar data set presented by Amaral *et al.* (2008) shows a close association between the well-sampled sites Algodoal and Crispim and non-conclusive grouping of the other localities.

It can be expected that the seasonal precipitation regime of the study region induces dominance shifts in plant communities. Bastos (1996) documented by means of wells that the ground water table at Algodoal sunk during the dry season by 2.6, 2.9, 1.5 and 1.4 m in comparison to the local wet season maximum in HAD, PWM, HDV and HS formations, respectively; her HDV and HS wells were covered by 0.1 and 0.7 m of surface water during the rainy season, respectively (included in the figures given above). Bastos (1996) noted corresponding changes in the composition of the

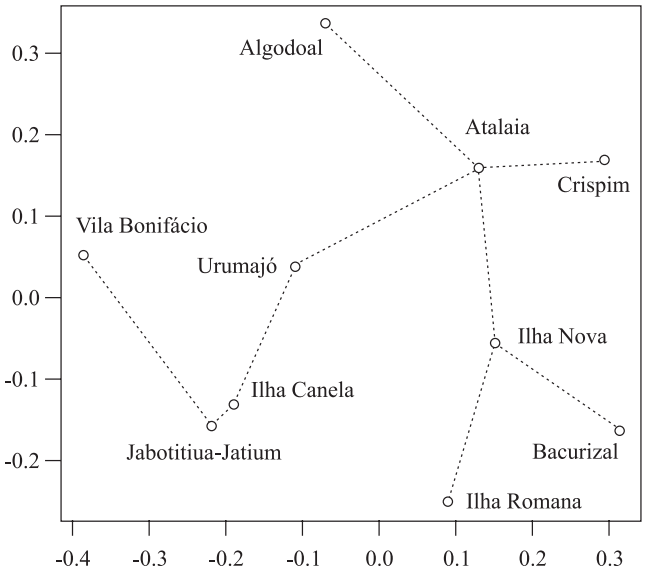

Figure 2. Non-metric multidimensional scaling (NMDS) of *restinga* sites along the coast of Pará (Raup-Crick dissimilarity matrix based on occurrence of plant species; R^2 for non-metric fit between observed rank dissimilarities and ordination distance: 0.99). Dotted lines show the minimum spanning tree among sites derived from NMDS results.

herbaceous vegetation, resulting in a reduced number of species during the dry season. The same author observed a reduction of vegetation cover during the dry season along with leaf fall in the persisting plants, both indicators of reduced water availability. Elevation profiles for Algodoal and Bonifácio (Bastos 1996, Silva 2008) show that most woody constituents of *restinga* vegetation were restricted to stabilised, elevated dune regions not reached by tidal inundation; structural development and species richness increased with distance from the sea (Bastos 1996).

Bastos (1996), Amaral (1997) and Silva (2008) provided data on structural properties of woody vegetation at Algodoal, Crispim and Bonifácio, respectively. Bastos (1996) considered trees and shrubs with breast height stem diameters ≥ 1.6 cm. Amaral (1997) and Silva (2008) measured the stem diameter at ground level, Amaral (1997) including all woody plants and Silva (2008) only those ≥ 2.5 cm (measured within the cylindrical stem section next to the soil surface). Coverage/basal area of woody vegetation was reported by all authors as projected stem area (at breast height or basal) per unit of ground area. Amaral (1997) and Silva (2008) observed that a great number of stems show prostrate growth, and that, as a consequence, stem length often exceeds actual crown height. *Pouteria ramiflora*, *Anacardium occidentale* and *Humiria balsamifera* were among the largest trees at Bonifácio, with maximum/average basal stem diameters of 32/8, 25/12 and 29/16 cm, respectively (Silva 2008); even larger specimens of *H. balsamifera* with basal diameter > 80 cm were observed at Bonifácio outside Silva's sampling plots (R. M. Silva, U. Mehlig and L. O. Santos, unpublished data). However, the latter species lagged behind the more abundant *P. ramiflora*, *A. occidentale* and *Byrsonima crassifolia* in terms of average basal area (3.3, 1.8, 1.2 and 1.1 $m^2\,ha^{-1}$, respectively; Silva 2008). Amaral (1997) and Bastos (1996) do not report average and maximum diameters of single species; at Crispim, *H. balsamifera* is the species with the highest basal area (5.7 $m^2\,ha^{-1}$) within the larger patches of woody vegetation. Interestingly, *H. balsamifera* was not found by Bastos (1996) at Algodoal, where *Byrsonima crassifolia* (in PWM) and *Tapirira guianensis* (in RF) reach the highest basal areas (0.9 and 2.0 $m^2\,ha^{-1}$, respectively). A summary of forest structure data is given in table 2.

Table 2. Forest structure data from Algodoal, Crispim, and Bonifácio, coast of Pará State, Brazil. Sampling area refers only to the plots where forest structure data were collected; floristic data were also recorded outside of these plots. Bastos (1996) used a minimum breast height diameter of 1.6 cm, Silva (2008) a minimum ground level diameter of 2.5 cm; to facilitate comparison, data of Amaral (1997; no minimum diameter) are presented for basal diameters ≥ 2.5 cm (obtained by interpolation from his histograms).

Site	Sampling área (ha)	Density (indiv. ha^{-1})	Basal área ($m^2\,ha^{-1}$)	Height max. (m)	Diameter max. (cm)	Diameter mean (cm)
Algodoal (Bastos 1996)	0.50	1,669*	16.2	10	24.5	4.6
	0.05	6,060**				
Crispim (Amaral 1997)	0.32	1,581* to 6,023	15.4	8	> 45.3	–
Bonifácio (Silva 2008)	0.46	2,293**	9.9	8	25	5.5

* = calculated for patches of woody vegetation, excluding open areas; ** = *restinga* forest.

The *restinga* vegetation of Pará is, as far as is known, rather poor compared to the more abundant flora of the sandy coastal plains of southeastern Brazil. This is probably due to the less extensive *restinga* areas in Amazonia. While a few species are specialists for coastal environments, the majority of taxa also occurs at sites distant from the sea; however, a number of species seem to prefer sandy soils in the hinterland, as well. No endemic species are known and no clear pattern emerges in respect to the grouping of *restinga* plant communities along the coast of Pará. The currently applied terminology for plant formations is not satisfactory; transitions between the different environments have to be analysed ever more carefully, and drastic seasonal changes in the species composition of herbaceous communities are not covered by the superficial classification "formations" provide. A more precise description of plant communities is necessary as a starting point for further ecological studies as well as for specifying conservation and management strategies. Future research should not only try to identify the plant associations and their set of characteristic species within the different *restinga* habitats, but also focus on the environmental parameters that may determine the occurrence of each plant association.

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