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PLANT DIVERSITY, INTERSPECIFIC ASSOCIATIONS, AND POSTFIRE RESPROUTING ON A SANDY SPIT IN A BRAZILIAN COASTAL PLAIN

Paulo Cirne, Henrique Leão Teixeira Zaluar & Fabio Rubio Scarano[1]

Universidade Federal do Rio de Janeiro, CCS, IB, Departamento de Ecologia, Laboratório de Ecologia Vegetal, Caixa Postal 68020, cep 21941-970, Rio de Janeiro, RJ, Brazil

Abstract. Diversity, phytosociology, interspecific associations, and postfire resprouting patterns were studied on a sandy spit in a Brazilian coastal plain. The spit is geologically more recent than the surrounding vegetation. It resembles a sandy bridge over a contiguous marsh that almost links a dry, sandy forest on the land side of the marsh to a palm scrub on the ocean side of the marsh. The species colonizing the exposed sand of the spit originated partly in the neighboring dry forest and partly in the palm scrub on the seashore. The vegetation of the spit was oligarchic, since only three species accounted for more than 75% of the value coverage of the area. These dominant species were the geophyte palm *Allagoptera arenaria*, and the legume shrubs *Andira legalis* and *Swartzia apetala*. Therefore the Shannon diversity index (H′) was low (0.8), despite the comparatively high species richness (25) of the 0.3-ha area sampled. Two man-made fires have also burnt the spit vegetation in the past ten years. The most recent fire (seven months before this survey) did not favor new invasions via seed germination but favored resprouting from established species. The three dominant species were negatively associated with each other. The general trend of species association was also negative. We propose that this negative overall trend results from competition for space at an early successional stage. This negative association is unlike that for late successional open *restinga* vegetation, where positive interactions reportedly play a major role in community structure. *Accepted 30 January 2003.*

Key words: Allagoptera arenaria, Andira legalis, *disturbance*, *fire persistence*, *interspecific associations*, *plant invasion*, *resprouting*, *restinga*, *succession*, Swartzia apetala.

INTRODUCTION

Coastal areas often exhibit rapid changes in the dynamics of their habitats that may be caused by the formation and/or depletion of new sites, such as foredunes and sandy spits. These new sites are potential habitats for invasion by terrestrial plants (Crawford 1989). Large-scale spatial and temporal processes may lead to the formation of coastal sandy plains. In Brazil, sandy plains are found on 5000 km of the Atlantic coastline, and in places stretch inward as far as 30 km (Lacerda *et al.* 1993). They are locally called *restingas* and result from Quaternary marine transgressions and regressions. The ages of various *restingas* range from 8,000 to 100,000 years BP (Martin *et al.* 1993).

Once *restingas* were formed, plants from the neighboring Atlantic rainforest invaded and colonized the new areas (Scarano 2002). These plants must have had a high ecological plasticity, as often reported for cases of successful invasions (Weber & D'Antonio 1999, Baruch *et al.* 2000), since *restinga* and rainforest habitats are extremely different (Scarano 2002). The high species richness of several *restingas* (Araujo 2000, Pereira & Araujo 2000) is a clear measure of this colonization success.

At a smaller spatial and temporal scale, new habitats form in the dune system because of sand movement and accretion (Crawford 1989). Such local movements of sand present an opportunity to study invasion by native species. Moreover, human disturbances such as fire may also contribute to plant invasion (Harper 1977, Bellingham 1998). We focused on a sandy spit (*ca.* 0.5 ha in area), formed as a fixed sand dune developed on a freshwater marsh at a *restinga* in southeastern Brazil. Locals periodically burn the vegetation on the spit to reduce plant cover. We aimed to find out 1) which plant species have successfully colonized this spit; 2) which, and by which mechanisms, plant species persisted after two fires occurred in the past decade; and finally 3) whether the domi-

[1] e-mail: fscarano@biologia.ufrj.br

nant species in the landscape were associated with patches of species richness and abundance on the spit.

MATERIALS AND METHODS

Study site. The study site is located in the Jacarepiá State Ecological Reserve, Saquarema municipality, on the northern coast of Rio de Janeiro state, southeastern Brazil (22°47'–22°57'S; 42°20'–42°43'W). Mean annual temperature ranges from 24 to 26°C and mean annual rainfall is 1000 mm (Sá 1992). This site protects one of the last remnants of fixed-dune forest in the state (see Sá 1992 for a detailed description of the local plant communities). The swale between dune forest and strand line is covered by marsh vegetation. A spit of sandy soil, some 200 m long by 70 m wide (maximum) extends into the marsh, almost forming a "bridge" from the forest edge to a palm scrub by the ocean. The legume shrub *Andira legalis* and the geophyte palm *Allagoptera arenaria* are visually predominant in the vegetation of the spit. *Allagoptera arenaria* is also dominant in the vegetation of the palm scrub. In the last ten years, the spit vegetation was twice burnt (January 1995 and July 2000). These fires were man-made and spread to other parts of the marsh and adjacent forest.

Field survey. In February 2001, seven months after a fire, we established twenty 30 m-long line-transects on the spit within the 0.3 ha permanent plot pre-

TABLE 1. Phytosociological dominance assessed as cover value (CoV) of species on a sandy spit seven months after a man-made fire. CoV is the sum of relative frequency (F%) and percent cover (C%). Fn = absolute frequency.

Species	Families	Fn	F%	C%	CoV
Allagoptera arenaria (Gomes) Kuntze	Arecaceae	227	49.67	64.20	113.87
Andira legalis (Vell.) Toledo	Leg. Faboideae	47	10.28	13.18	23.47
Swartzia apetala Raddi	Leg. Caesalpinoideae	72	15.75	5.23	20.99
Ocotea notata Mez	Lauraceae	21	4.60	5.00	9.60
Tibouchina trichopoda Baill.	Melastomataceae	11	2.41	3.15	5.53
Eugenia ovalifolia Cambess.	Myrtaceae	15	3.28	1.01	4.30
Aechmea bromeliifolia (Rudge) Baker	Bromeliaceae	7	1.53	1.40	2.93
Tapirira guianensis Aubl.	Anacardiaceae	6	1.31	1.03	2.35
Inga maritima Benth.	Leg. Mimosoideae	8	1.75	0.51	2.26
Coccoloba alnifolia Casar.	Polygonaceae	8	1.75	0.44	2.19
Cereus fernambucensis Lem.	Cactaceae	5	1.09	0.93	2.03
Neoregelia cruenta (Grah.) L.B. Smith	Bromeliaceae	4	0.88	0.71	1.59
Guapira opposita (Vell.) Reitz	Nyctaginaceae	4	0.88	0.39	1.27
Sideroxylon obtusifolium (Roemer & Schultes) T.D. Pennington	Sapotaceae	2	0.44	0.52	0.95
Tocoyena bullata Mart.	Rubiaceae	3	0.66	0.29	0.95
Eugenia nitida Cambess.	Myrtaceae	3	0.66	0.28	0.94
Myrsine umbellata Mart.	Myrsinaceae	3	0.66	0.27	0.90
Manilkara subsericea Dubard	Sapotaceae	2	0.44	0.38	0.82
Cupania emarginata Cambess.	Sapindaceae	2	0.44	0.23	0.67
Maytenus obtusifolia Mart.	Celastraceae	2	0.44	0.17	0.61
Vitex poligama Cham.	Verbenaceae	1	0.22	0.33	0.54
Schinus terebinthifolius Raddi	Anacardiaceae	1	0.22	0.23	0.45
Myrtaceae	Myrtaceae	1	0.22	0.08	0.30
Cyrtopodium polyphyllum (Vell.) Pabst ex F. Barros	Orchidaceae	1	0.22	0.03	0.25
Pilosocereus arrabidae (Lem.) Byles & Rowley	Cactaceae	1	0.22	0.03	0.24

TABLE 2. Proportion of individuals that resprouted (A = aerial; U = underground; A+U = aerial + underground), died after the fire of July 2000, or occurred in patches unaffected by this fire (NF).

Species	Resprouting %			Dead %	NF %
	A	U	A+U		
Allagoptera arenaria	0	95.6	0	0	4.4
Andira legalis	17	66	6.4	0	10.6
Swartzia apetala	0	94.4	0	0	5.6
Ocotea notata	0	90.5	0	0	9.5
Tibouchina trichopoda	18.2	63.6	0	0	18.2
Eugenia ovalifolia	0	86.7	0	0	13.3
Aechmea bromeliifolia	0	71.4	0	28.6	0
Tapirira guianensis	0	100	0	0	0
Inga maritima	0	100	0	0	0
Coccoloba alnifolia	0	87.5	0	0	12.5
Cereus fernambucensis	0	60	40	0	0
Neoregelia cruenta	0	75	0	0	25
Guapira opposita	0	75	0	0	25
Sydероroxylon obtusifolium	0	100	0	0	0
Tocoyena bullata	0	66.7	0	0	33.3
Eugenia nitida	0	100	0	0	0
Myrsine umbellata	0	100	0	0	0
Manilkara subsericea	0	100	0	0	0
Cupania emarginata	0	100	0	0	0
Maytenus obtusifolia	0	50	50	0	0
Vitex poligama	0	0	0	0	100
Schinus terebinthifolius	0	100	0	0	0
Myrtaceae	0	100	0	0	0
Cyrtopodium polyphyllum	0	100	0	0	0
Pilosocereus arrabidae	0	100	0	0	0

viously surveyed by Cirne & Scarano (2001). Plants sampled according to the line-intercept method (Mueller-Dombois & Ellenberg 1974) included woody plants, bromeliads, orchids, palms, and cacti of all sizes but excluded climbers and ruderals, due to their reduced biomass locally. This method allowed us to calculate the relative frequency (number of line-transects in which a given species occurred divided by 20, i.e., the total number of line-transects) and cover (number of meters covered by the canopy of a given species divided by 600, i.e., the total number of meters of the line-transects) of each species. The sum of these two values is the Cover Value (CoV). We classified as dominants species with CoV equal or higher than 20 out of a possible total of 200, i.e., 10% of total CoV. Species with CoV < 2 (1% of the total) were considered locally rare. We also estimated species richness and diversity (Shannon-Wiener H', Magurran 1988) of the sandy spit.

This method also allowed us to list the species underneath the canopy of the dominant plants. When canopy superposition was observed, we treated the plants as co-occurring, as assessed by the values for canopy cover along a given line-intercept. We tested the significance of interspecific associations between dominant plants by chi square ($P < 0.05$; Kent & Coker 1992), by counting the number of co-occurrences of each species pair. Additionally, we applied a variance test to determine the prevalent pattern of species association within the community, using data regarding presence/absence of species in vegetation patches (Schluter 1984). For each species found in the phytosociological survey, we also noted whether there were any visual signs of aerial and/or underground resprouting in response to the previous fire.

RESULTS

We found 457 individuals, comprising 25 plant species and 17 families. Plants covered 306.74 m (51.1%) of the total 20 line-intercepts. Table 1 shows that 79.2% of the total CoV was accounted for by *Allagoptera arenaria* (56.9%), *Andira legalis* (11.7%), and *Swartzia apetala* (10.5%). Fourteen (56%) species were locally rare (CoV < 2) and made up only 5.3% of the total CoV. Arecaceae and Leguminosae were the two dominant families (80.3 % of the total CoV). The diversity index (0.8) was very low.

All species resprouted after the fire (Table 2). Only two individuals were found dead (both *Aechmea bromeliifolia*) and only two new individuals (*Vitex poligama* and *Guapira opposita*) recruited from seed after burning. Most resprouting occurred from underground organs, although *Andira legalis*, *Cereus fernambucensis*, *Maytenus obtusifolia*, and *Tibouchina trichopoda* also showed aerial resprouting (Table 2).

Allagoptera arenaria had higher co-occurrence and associated diversity values than *Andira legalis* and *Swartzia apetala* (Table 3). However, *S. apetala* had fewer isolated individuals than the other two species. We also found a total of 241 isolated plants (52.7% of the total number of individuals): the three dominant species plus individuals belonging to 21 other species (15 families). Excluding the three dominants, 45 plants were found isolated (40.5% of the total individuals of the non-dominant species).

The association tests between dominant species indicated that all three were significantly associated with each other ($P < 0.05$), and that the association patterns were always negative. Chi square values for interspecific association were: *Andira legalis* vs. *Allagoptera arenaria* = 36.09; *A. legalis* vs. *Swartzia apetala* = 11.24; *S. apetala* vs. *A. arenaria* = 9.86. At the community level, the variance test showed a significant trend of negative association between species (V = 0.49, $P < 0.05$).

DISCUSSION

The vegetation of the sandy spit showed a diversity index (H') much lower (0.8) than other open *restinga* vegetation types on older terrain (H' > 2.0; see Liebig *et al.* 2001). This low diversity is due to an oligarchic structure in which the three dominant species (*Allagoptera arenaria*, *Andira legalis*, and *Swartzia apetala*) account for more than 75% of the coverage value of the vegetation. Open *restingas* are often oligarchic (Scarano 2002), however the dominance of a few species is not as marked in other *restingas* as the dominance of the three species of this sandy spit. The low diversity index of the spit contrasts with a considerable species richness (25 species in 0.3 ha). These species are habitat generalists, possibly from the neighboring dry forest and the palm scrub by the ocean, and are often found in both exposed/shaded, wet/dry *restinga* (for plant geographic distribution and habitat preference, see Sá 1992, Araujo *et al.* 1998, Araujo 2000, Cirne & Scarano 2001, Scarano *et al.* 2002).

These species withstand the environmental pressures common to open *restinga* vegetation (high temperatures, high light intensity, oligotrophy, drought, and wind), and are also fire-resistant since they resprouted after a recent fire event. This is rather surprising because fire is neither a recurrent event in the

TABLE 3. Frequency of species co-occurrence in patches (canopy superposition) for the three dominant plants, species diversity (H' = Shannon-Wiener diversity index) in patches dominated by the given species, and number of isolated occurrences and the specific proportion of area covered by isolated individuals. Different letters in H' indicate significant difference at $P < 0.01$ (t-test).

	Number of co-occurrences			H'	Isolated occurrences	
	Individuals	Species	Families		Individuals (%)	% coverage
Allagoptera arenaria	111	17	13	0.9469a	140 (61.7)	61.3
Andira legalis	25	8	8	0.5372b	29 (61.7)	50.5
Swartzia apetala	53	10	10	0.4152b	27 (37.5)	31.3

restinga nor in its main source of species, the Atlantic rain forest. This resprouting ability accounts for long-term persistence and may have evolved in response to more common local disturbances, such as drought, herbivory, wind, and flooding (see Araujo & Peixoto 1977, Bond & Midgley 2001). Resprouting is often related to long-term habitat occupancy by a successful invader and leads to retention of resources and restriction of nutrient losses (Hutchings & Bradbury 1986, Bellingham 1998).

The fact that all dominant and locally rare species found in this survey are resprouters, apparently well-suited to cope with fire, may represent a further constraint to recruitment from less competitive, seed-originated plants that often require a long lag phase following establishment before spread (Hobbs & Humphries 1995, Hastings 1996). Shoots and underground systems of clonal plants often fill large spaces (Herben & Hara 1997, Suzuki & Hutchings 1997) and are likely to promote dominance by showing superior competitive ability (de Kroon & Bobbink 1997).

Despite this common capacity to resprout and persist after fire, abundance and cover varied markedly between species. Only three species dominate the vegetation. This dominance has probably been achieved by the capacity to rapidly increase population size after a fire, rather than by persistence alone. *Allagoptera arenaria*, for example, is generally dominant in other *restingas* that do or do not have recurring fires (Lacerda *et al.* 1993). In the case of *Andira legalis*, five months after the fire of 1995 new ramet formation was already 27.7% of the former total before the fire (Cirne & Scarano 2001). This high rate of expansion in coverage immediately after disturbance is common for invasive plants as opposed to non-invaders (Hobbs & Humphries 1995, Hastings 1996, Maron & Jefferies 1999). *Andira legalis* is normally found in scattered populations along the sandy plains. It has not been reported as occurring as a dominant species in any of these areas, adding further evidence to our thesis that it is a native invader of our study site.

The predominantly negative interactions between dominants, and between the dominants and other species, suggest competition (Kent & Coker 1992, Bellingham 1998). Despite the higher species richness and diversity beneath the canopy of *Allagoptera arenaria* compared to the two legumes, many individuals of the palm were found alone. Thus, its occurrence does not necessarily precede the occurrence of other plants at this early-successional phase on the spit. This is in contrast with Zaluar & Scarano (2000), who found that in other *restingas Allagoptera arenaria* allows plant establishment underneath or around its canopy by providing a milder microclimate than the surrounding bare sand (see also Menezes & Araujo 2000). This function of the palm could not be observed at our site because fire has probably hindered establishment of plants via seed propagation.

Although *Andira legalis* reportedly fixates nitrogen in this system (Scarano *et al.* 2001) it showed no positive interactions with other species of the spit. *Swartzia apetala* has been reported to nodulate (Faria *et al.* 1984) but also showed no indication of positive interactions with other species. Although N_2-fixing plants potentially facilitate plant establishment, soil N may only become available to other taxa when these plants either die or shed large amounts of leaves and/or branches (Maron & Jefferies 1999).

Human-induced perturbations such as fire or deforestation, often linked to land speculation and predatory tourism, are ever more common in Brazilian *restingas*. We showed that some *restinga* species persist and even increase in population size after perturbations such as fire. However, local diversity may simultaneously decline and colonization by seeds may be hindered.

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