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Research article

Directional growth of a clonal bromeliad species in response to spatial habitat heterogeneity

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Abstract. Habitat selection by directional growth of plants has previously been investigated but field evidence for this phenomenon is extremely scarce. In this study we demonstrate directional clonal growth in *Aechmea nudicaulis*, a monocarpic, perennial bromeliad native to spatially heterogeneous sandy coastal plains (*restinga*) in Brazil. This habitat is characterized by a matrix of bare sand with interspersed vegetation islands. Due to very high soil surface temperatures and other stress factors such as drought, *A. nudicaulis* can only germinate inside vegetation islands. Nevertheless, this species is very common on bare sand. In this study we tested the hypothesis that clonal fragments occurring at the border and inside vegetation islands show habitat selection by growing preferentially towards the bare sand habitat (i.e. away from the center of vegetation islands).

We randomly chose 116 clonal fragments in two distinct micro-environments (inside vegetation islands, and in the border area between bare sand and vegetation islands) in the natural habitat of *A. nudicaulis* and measured their growth direction in relation to the island center. We measured the growth directions of entire clonal fragments (defined as the line that connects the oldest and the youngest ramets of a clonal fragment) as well as the growth direction of the youngest internode on each fragment (the growth direction of the youngest ramet in relation to its parent ramet). We used Monte Carlo simulations to test for deviations from randomness in the growth direction of clonal fragments and individual internodes. The clonal fragments of *A. nudicaulis* showed a significant tendency to grow away from the center of vegetation islands. In other words, the main growth direction of clonal fragments growing inside vegetation islands or at the border between bare sand and vegetation islands was preferentially directed towards bare sand environments. Individual internodes at the border of vegetation islands also exhibited this tendency to grow towards the outside of vegetation islands, but internodes growing inside vegetation islands did not show directional growth. These results provide the first field evidence for habitat selection through directional growth of a clonal plant species.

Key words: clonal growth, directional rhizome growth, habitat selection, restinga, tank bromeliad, *Aechmea nudicaulis*

Introduction

Natural habitats are not homogeneous but patchy. Spatial heterogeneity in environmental quality such as resource availability and other abiotic and biotic conditions is ubiquitous in natural environments, and it may occur at different spatial scales and in different intensities (Wiens, 1976; Caldwell and Pearcy, 1994; Stuefer, 1996). Spatial habitat heterogeneity poses a profound problem for sessile organisms like plants, which are usually limited to a single point in space where they have germinated. Unlike animals, plants cannot usually move to more favorable sites in their environment. They can, however, show directional growth which may allow for habitat selection through limited mobility within the local environment (Salzman, 1985; Bazzaz, 1991). Directional growth of clonal plants can be achieved by a selective activation or suppression of axillary meristems that produce horizontal stem structures (stolons, rhizomes), or by bending of growing stems.

Directional plant growth as basis for habitat selection has been investigated in the past (Strong and Ray, 1975; Salzman, 1985; Novoplansky *et al.*, 1990; Novoplansky, 1991; Kelly, 1992; Aphalo and Ballaré, 1995; Leeflang, 1999; Hay *et al.*, 2001). Directional growth of several plant species has been demonstrated under controlled conditions, and these results have usually been interpreted in terms of habitat selection (e.g., Salzman, 1985; Novoplansky *et al.*, 1990). However, convincing field evidence for habitat selection through directional plant growth is still very scarce. To our knowledge, one study has provided convincing field evidence for habitat selection in a tropical vine (Strong and Ray, 1975) and no published study has so far shown directional clonal growth in the field. In a recent study, Macek and Leps (2003) did both field and pot experiments to investigate the foraging behaviour of *Prunella vulgaris* L. and found that this species produces more stolons with shorter internodes under favorable conditions. However, they did not find any evidence for directional growth and habitat selection in *P. vulgaris*. The scarce evidence for directional growth in clonal plants seems to suggest that foraging tactics of many species are directed towards optimizing resource acquisition within rather than between neighbouring habitat patches (Hutchings and de Kroon, 1994).

The frequent occurrence and terrestrial growth habit of epiphytic bromeliad clonal species in the Brazilian *restingas* (sandy coastal plain vegetation) has raised speculations with respect to directional clonal growth and habitat selection by these species (Lacerda and Hay, 1982; Benzing, 2000; Zaluar and Scarano, 2000). The *restingas* are spatially very heterogeneous, temporally stable vegetation mosaics that cover the sandy plains of coastal Brazil (Lacerda *et al.*, 1993). The most common vegetation type in these systems is the so-called *open restinga*, which consists of scattered vegetation islands of varying sizes (an average of 5 – 100 m^2 of area), surrounded by bare white sand (Henriques *et al.*, 1986). The facultative epiphytic bromeliad *Aechmea nudicaulis* (L.) Griseb. grows as a terrestrial clonal plant in these open *restingas* and it occurs very frequently both inside vegetation islands and outside, on bare sand. Due to high soil temperatures (>60 °C at full sun light) *A. nudicaulis* seeds are unable to germinate in the bare sand (Pinheiro and Borghetti, 2003). In addition, successful seedling establishment is very unlikely outside vegetation islands, because the upper layers of the bare sand tend to be very hot and dry. It seems therefore that seed germination and seedling establishment can only take place inside vegetation islands and that this species spreads to the open areas through clonal growth (Benzing, 2000; Zaluar and Scarano, 2000). Although bare sandy areas could be colonized from vegetation islands by random non-directional growth, field patterns raised the suspicion that clonal fragments of *A. nudicaulis* growing inside vegetation islands may show non-random, directional growth toward bare sand habitats.

This study aims to test the hypothesis that clonal fragments of *A. nudicaulis* show habitat selection through directional rhizome growth. More specifically, we predicted that clonal fragments growing inside vegetation islands exhibit non-random directional growth toward the edge of vegetation islands, thereby contributing to the colonization of open areas through clonal growth. We tested this hypothesis in the field by sampling the growth direction of clonal fragments in the *restinga* and applying randomization tests to verify growth directionality (i.e. deviations from random growth in all directions).

Materials and methods

Study area

Most sandy coastal plains in the State of Rio de Janeiro consist of two beach ridges dating from the Holocene (5,000–3,000 yr BP). The oldest sandy plains date from the Pleistocene (120,000 yr BP; see Martin *et al.*, 1993). Araujo *et al.* (1998) classify the *restingas* of the State of Rio de Janeiro in ten zones according to their flora, which is related to local variation in climate and geological history. The data for this study were collected in the Restinga de Jurubatiba National Park (22°23′ S, 41°45′ W), approximately 200 km North of the city of Rio de Janeiro. The climate at the field site is markedly seasonal and dry due to the cold oceanic upwelling of the Cabo Frio region (Araujo, 1997). The annual rainfall of 1164 mm is concentrated in the summer months (November – February); mean annual temperatures are relatively high (mean = 23 °C, max = 30 °C, min = 20 °C). The abiotic conditions inside and outside vegetation islands are very dissimilar. The bare sand environment outside vegetation islands is characterized by potentially very high surface temperatures, high levels of radiation and low water and nutrient availability. The environment inside vegetation islands is more moderate as temperatures are lower, the air humidity and nutrient availability are higher and there is accumulation of litter in the soil.

Study species

Aechmea nudicaulis is a CAM (crassulacean acid metabolism) tank-bromeliad with widespread distribution throughout Central and South America (Smith and Downs, 1979). It occurs in distinct vegetation types from sea level to 1200 m a.s.l. (Wendt, 1997). *A. nudicaulis* is a clonal perennial species with monocarpic ramets. According to Pittendrigh (1948), this species belongs to the so-called 'ecological type III' species (i.e. bromeliads with water and nutrient absorbing trichomes in their leaves). These rosette plants form tanks that harvest water and litter, and they often house elements of the local fauna such as frogs and lizards (Oliveira *et al.*, 1994; Madeira *et al.*, 1995; Oliveira and Rocha, 1997). They may also host seedlings of shrubs and trees that cannot germinate and establish on the bare sand, thereby serving as nurse plants for these species (Fialho and Furtado, 1993; Zaluar and Scarano, 2000; Scarano, 2002). In addition, tank bromeliads harvest atmospheric nutrients and water, which may later become available to other plants (Hay and Lacerda, 1980; Hay *et al.*, 1981). Roots are predominantly or exclusively used to ensure mechanical stability of the ramets and to fix the plant to the substrate. *A. nudicaulis* grows as an epiphytic bromeliad in forests. However, in open *restingas* this species has a terrestrial growth habit (Sampaio *et al.*, 2002; Scarano, 2002).

Sampaio *et al.* (2002) described the clonal growth of this species in the *restinga*, which consists of the formation of sympodial rhizomes that form ramets. Most ramets produce one or two new ramets, before or after flowering. The internode length is around 10 cm. Rhizomes are initiated from axillary meristems present around the shoot base. New rhizomes can therefore grow in all directions. Clonal fragments do not usually grow in a straight line, but in a slight zigzag (see Fig. 1). The spatiotemporal variation in population growth (λ) rate of *A. nudicaulis* in the *restinga* is stable; the λ values did not significantly differ from unity in different habits, microhabitats and years (Sampaio *et al.,* in press).

Sampling

To assess the growth direction we randomly sampled 116 clonal fragments in the field by the point quadrat method. We defined a clonal fragment as a collection of ramets that were visibly connected to each other. Rhizome connections between ramets can easily be identified in *A. nudicaulis* as they

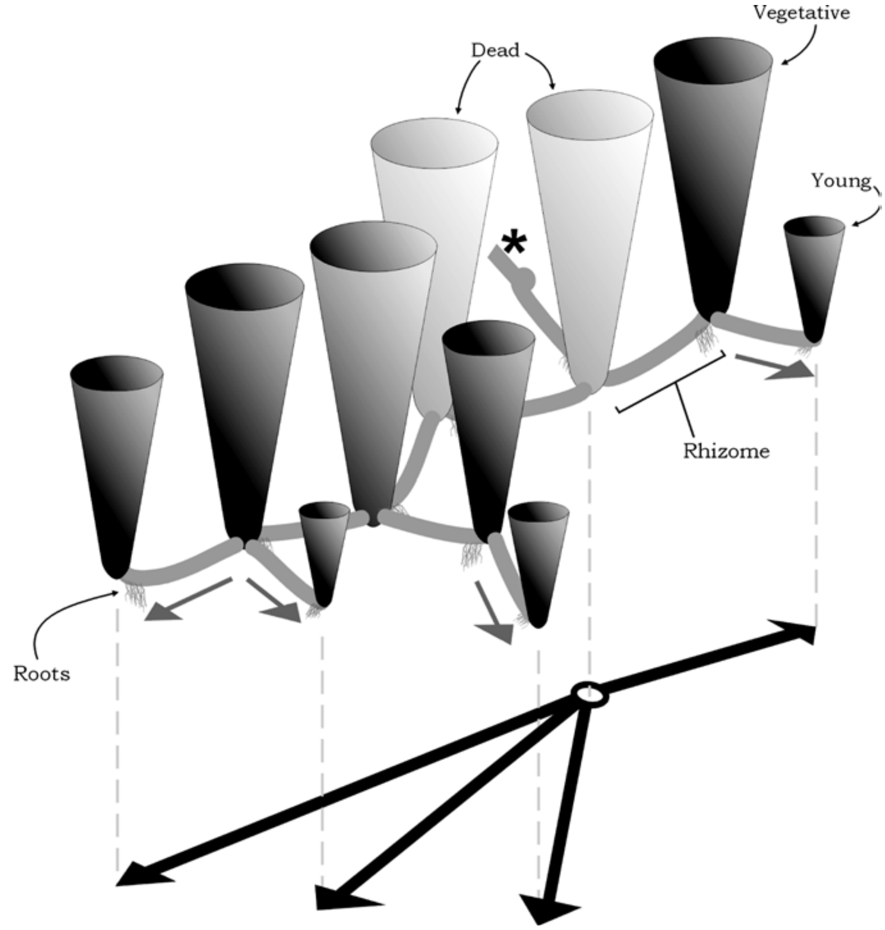

Figure 1. Scheme of a branched clonal fragment of *A. nudicaulis* showing different growth directions. The growth directions of clonal fragments were defined as the line between the oldest (ring) and the youngest ramet (arrow tip). The growth direction of the youngest internode is the line between the youngest ramet and its parent ramet. The black arrows indicate the growth directions of the clonal fragment and the grey arrows indicate the growth direction of the youngest internodes. The asterisk indicates the oldest rhizome of the fragment.

occur close to the soil surface (around 5 cm in depth). Ramet connections can be verified without disturbing the soil environment, either by probing with fingers or by carefully shaking a ramet and observing the movement of nearby ramets. We determined the growth direction of fragments (see below) and the growth direction of the youngest internode. We classified the clonal fragments into the following two groups according to the micro-environment of origin. They came either from (1) vegetation island borders, i.e. the area between the bare sand and vegetation islands, which represents an intermediate situation between these micro-environments, or from (2) shaded micro-environments inside vegetation islands. The size of the vegetation islands ranged from 5 to 100 m^2 and their form was approximately hemispherical. *Clusia hilariana* Schlecht. is the central tree in most vegetation islands and harbours a broad variety of species in its understorey (Liebig *et al.*, 2001; Scarano, 2002).

Measurement of growth direction

Growth directions were measured for entire clonal fragments as well as for the youngest internodes of each clonal fragment (see Fig. 1). The growth direction of a clonal fragment was defined as the line that connects the oldest and the youngest ramets of a clonal fragment. In the case of branched clonal fragments we determined each growth direction as well as the growth direction of each youngest internode (Fig. 1).

In order to measure the growth direction in relation to the island center, we first identified the center of the island and established a line between the

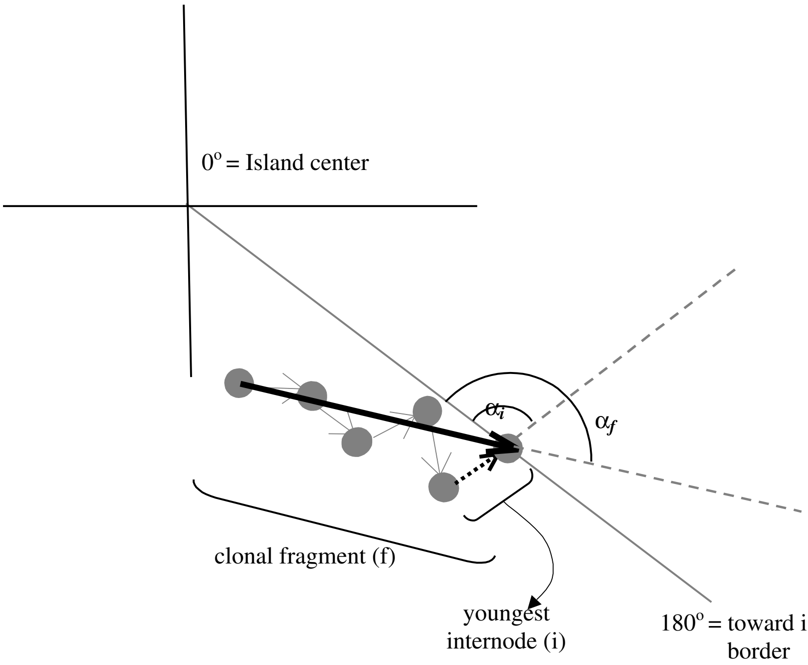

Figure 2. Measurement of the growth direction of *A. nudicaulis* in relation to the center of vegetation islands, for entire clonal fragments (α_f) and for individual internodes (α_i). The thick arrow indicates the direction of growth of the entire clonal fragment (f) and the dashed arrow indicates the growth direction of the youngest internode of the fragment. Ramets are represented by grey circles, the grey arrows show the growth direction of each ramet.

youngest ramet (growing tip) of the clonal fragment and the island center. The direction toward the island center was always considered 0°. The growth direction of fragments (α_f) and internodes (α_i) in relation to the island center was then measured as the angle between the 0°-line and the growth direction of the fragment or youngest internode, respectively (see Fig. 2). We measured the growth direction of the youngest internode separately because we expected individual internodes to respond to directional light signals during their development. Clonal fragments of *A. nudicaulis* do not usually grow along a straight line (divergence angles of 0° for successive internodes), but instead they tend to follow a zigzag path (Fig. 2). The overall growth direction of clonal fragments is therefore often different from the growth direction of individual internodes. For branched fragments, the growth direction of each rhizome tip was measured separately.

We calculated the degree of asymmetry of growth angles to test for a non-random distribution of growth directions in relation to the island center. The degree of asymmetry (DoA) was defined as follows:

$$\mathrm{DoA} = -\frac{\sum_{1}^{n} \cos(\mathrm{rad}(\alpha))}{n} \tag{1}$$

where α is the growth angle (in angular degrees) of a clonal fragment or individual internode in relation to the island center, and n is the number of growth angles in the data set. Fragments or internodes growing at an angle of 180° (i.e. growing straight away from the vegetation island center) get a score of 1 in the nominator of Equation (1), while structures growing directly toward the island center get a score of -1. Angles of 90° and 270° (growth in a neutral direction in relation to the vegetation island center) get scores of 0. All intermediate angles get intermediate scores according to the cosine-transformation. The degree of asymmetry approaches zero for data sets with a uniform or random distribution of growth angles. Note that data sets containing exclusively growth angles of 90° and 270° will also have a $\mathrm{DoA} = 0$. The degree of asymmetry has been devised to quantify the preferential occurrence of growth angles along the 0°–180° axis.

Data analysis

We used Monte Carlo simulations to test our hypotheses of non-random, directional growth of clonal fragments and individual internodes. We compared the observed distribution of growth directions (field data) with the distribution of randomly generated growth directions. We ran 25,000 simulations for each Monte Carlo test. Turbo Pascal 7.0 was used to run the simulations.

Separate Monte Carlo tests were performed for (i) the growth directions of entire clonal fragments and (ii) the growth direction of the youngest internode(s) on each fragment. In the first simulation, we tested the hypothesis that clonal fragments grow preferentially away from the vegetation island center. In this test we generated random growth directions (growth angles in relation to the island center) for each clonal fragment in relation to the vegetation island center and compared their distribution to the observed growth angles. We divided the circle of possible growth directions into four quadrants with respect to the center of vegetation islands (direction toward center = 0°). The quadrants were defined as follows: 315°–44° (i.e. towards the center of vegetation islands), 135°–224° (i.e. away from vegetation island center), 45°–134°, 225°–314° (i.e. growth in a neutral direction in relation to the vegetation island center). We determined the number of clonal fragments (or internodes) in each of the four quadrants for both the real data and for the simulated data. The hypothesis of preferential growth of clonal fragments away from the island center was considered confirmed ($p < 0.05$) if the observed number of clonal fragments (i.e. field data set) growing at angles between 135° and 224° was exceeded in less than 5% (i.e. 1250 out of 25,000 cases) of all cases in the corresponding randomization set. We also performed Monte Carlo simulations analogous to the ones described above to compare the degree of asymmetry (see definition above) of growth directions between observed and randomly generated growth angles. All randomization tests were performed with growth angles for entire clonal fragments as well as for growth angles of the youngest internode.

Results

Out of the total of 116 clonal fragments, 83 were found at the border of vegetation islands and 33 were situated inside vegetation islands. Most of the

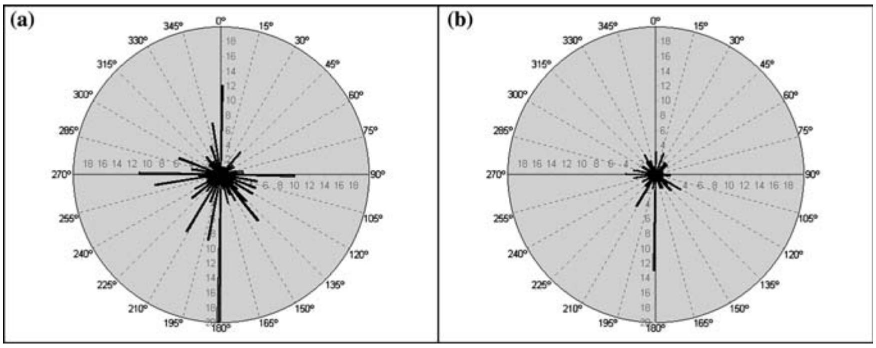

Figure 3. Frequency of growth angles of *A. nudicaulis* fragments (α_f) in relation to the vegetation island center: (a) island border; (b) island shade. Towards the center equals 0°; towards the border equals 180°.

clonal fragments were branched (55 at the border and 23 inside vegetation islands), with 2–14 actively growing tip per fragment. In total we measured 224 directions of growth at the border of vegetation islands and 89 inside vegetation islands.

Clonal fragments of *A. nudicaulis* growing inside vegetation islands and at the border between the bare sand and vegetation islands showed a clear and significant tendency for directional growth out of the vegetation islands (Fig. 3). The observed frequency of clonal fragments showing directional growth was significantly higher both at the border and inside vegetation islands than the expected frequencies generated by the randomization tests (Fig. 4 a, c). In addition, the observed number of clonal fragments growing from the border towards the center of vegetation islands was significantly lower than expected under random growth, implying that clonal fragments selectively avoided these growth directions (Fig. 4a). The youngest internodes of clonal fragments located at island borders showed a significant preference for growth

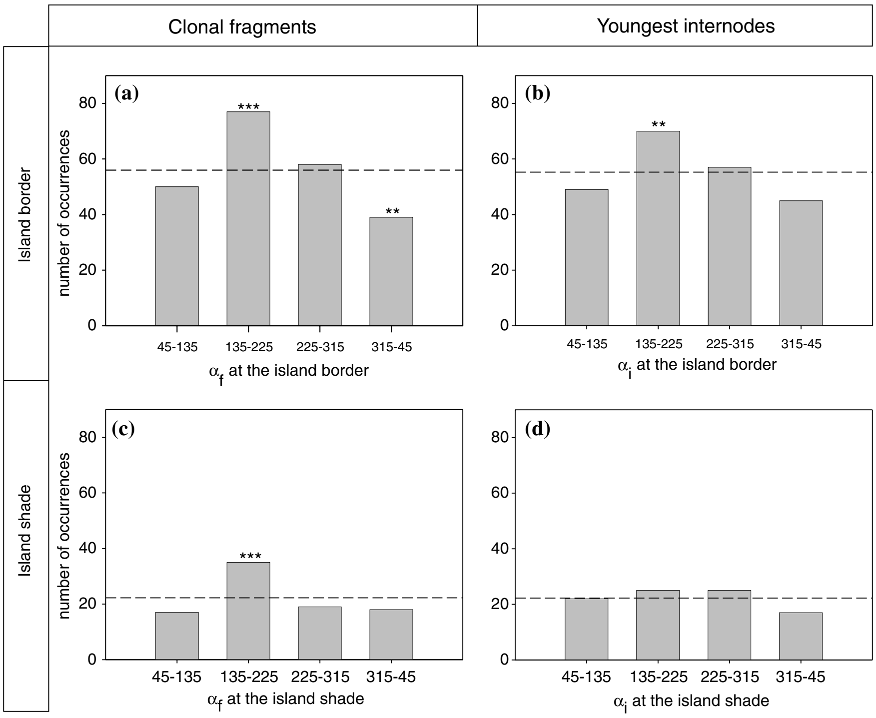

Figure 4. Results of Monte Carlo randomisation tests of the growth angles of *A. nudicaulis*. Graphs a and b represent vegetation island border, c and d vegetation island shade, for entire clonal fragments (a and c) and youngest internodes (b and d). The dashed line indicates no preference of growth direction. Significant deviations from randomness are indicated by $^{***}p < 0.0001$ and $^{**}p < 0.001$.

Table 1. DoA of growth angles of fragments and internodes of *A. nudicaulis* in the border and shade of vegetation islands

Micro-environment	Level	*n*	Degree of asymmetry of growth angles	*p*
Vegetation island border	Fragment	224	19.65	0.00004^{***}
	Internode		12.21	0.0056^{**}
Vegetation island shade	Fragment	89	20.54	0.0031^{**}
	Internode		8.93	0.1176

angles directed towards the outside of vegetation islands (Fig. 4b), while there was no evidence for directional growth of individual internodes growing inside vegetation islands (Fig. 4d).

Plants growing at the border of vegetation islands showed a degree of asymmetry that was significantly higher than expected under a random distribution of growth angles. This was true for entire clonal fragments as well as for the youngest internodes of fragments (Table 1). Inside vegetation islands, entire clonal fragments grew in an asymmetric fashion, while the growth of individual internodes did not deviate significantly from randomness in the shaded environment (Table 1).

Discussion

Our data provide clear evidence for directional growth and habitat selection of clonal fragments of *A. nudicaulis* in its natural habitat. To our knowledge this is the first field study reporting selective directional growth of a clonal plant in response to heterogeneous environmental conditions. The strong growth directionality of clonal fragments from vegetation islands towards open areas may help explain the large number of sun-exposed clonal fragments in the *restinga* even though it is clear that seeds of *A. nudicaulis* are unable to germinate and establish in the bare sand (Pinheiro and Borghetti, 2003). Hence, the results of our study confirm previous speculations that this bromeliad species might grow preferentially towards open areas by means of clonal expansion (Benzing, 2000; Zaluar and Scarano, 2000).

The youngest internodes of the clonal fragments located at the border of vegetation islands also showed a significant tendency to grow away from the island center towards the open sand environment. However, the internodes of clonal fragments growing inside vegetation islands did not show any growth directionality with respect to the island center. Even though our data provide clear evidence for strong directional growth of clonal fragments of *A. nudicaulis*, we can currently only speculate about the mechanisms by which selective clonal growth towards vegetation island borders might be achieved. Light signals (differential light intensity and/or light spectral quality such as red:far-red ratios between island center and island border) or light-related environmental signals (e.g. temperature, air humidity) are likely to be involved in generating non-random, directional growth patterns of clonal fragments (Aphalo and Ballaré, 1995; Leeflang, 1999; Novoplansky *et al.*, 1990).

The contrast in light intensity and light spectral quality between center-oriented and open-sand-oriented sites is probably bigger at the border than inside vegetation islands. Additional field measurements of light and light related environmental factors can help to elucidate the mechanisms of directional growth in *A. nudicaulis*. Clonal growth in specific directions may be achieved by differential suppression and outgrowth of meristems producing new internodes and offspring ramets. In our species numerous axillary meristems are situated in the leaf axils at the basis of ramets (see Fig. 1). This meristem bank potentially allows for changing or continuing the main growth direction of clonal fragments. It is currently not known, however, what environmental or developmental factors promote and inhibit the initiation of axillary meristems in *A. nudicaulis*. Field and laboratory experiments are needed to clarify this point.

Growth directionality is not commonly observed in clonal herbs from temperate systems (Aphalo and Ballaré, 1995; Leeflang, 1999; Hay *et al.*, 2001; Macek and Leps, 2003). This might be due to the fact that temperate herbaceous canopies tend to be dense and show a high variability in time. These features add to the unpredictability of the light climate in the horizontal direction, thereby selecting against the evolution of habitat choice by selective ramet placement in such environments (Hutchings and de Kroon, 1994; Huber, 1996; Stuefer, 1996; Huber *et al.*, 1999). Habitat selection through clonal growth can be expected to occur mainly in spatially heterogeneous environments with a high temporal predictability of spatial patterns at the time scale of average ramet or fragment life spans. These conditions are definitely met in the *restinga* system used in this study, and they may also apply to other systems, for which habitat selection through directional growth has been documented (tropical vines growing toward tree trunks, Strong and Ray, 1975; semi-desert plants avoiding neighbours, Novoplansky *et al.*, 1990).

The preferential growth of tank bromeliads from vegetation islands towards open sand areas may have strong effects on the dynamics of vegetation islands in the restinga system. Tank-bromeliads can function as nurse plants for major trees and bushes that form the overstorey of vegetation islands by providing ideal germination conditions inside their tanks (Fialho and Furtado, 1993; Zaluar and Scarano, 2000; Scarano, 2002). Therefore, directional growth and habitat selection of *A. nudicaulis* is likely to promote the formation of new vegetation islands and to facilitate the colonization of open sand habitats in the longer run (Hay *et al.*, 1981; Scarano, 2002).

Habitat selection through directional growth as shown in this study may (or may not, see next paragraph) represent a beneficial, adaptive trait of *A. nudicaulis*. The typical epiphytic growth habit of this and other members of bromeliad family has often been attributed to a reduced competitive ability for light (Pittendrigh, 1948; Medina, 1974). In our study site light is not usually a limiting factor for plant growth. Although it has been proposed that shrubs and trees such as *Clusia hilariana* have a nurse plant effect on the understorey vegetation (Liebig *et al.*, 2001), it is conceivable that competition for space, water, nutrients and even light might take place among understorey plants. Intense competition inside vegetation islands may favour plants with the ability to leave these crowded micro-sites and grow selectively into the far less competitive, bare sand environment. Even though the exposed micro-environments outside vegetation islands are more extreme in terms of abiotic factors such as soil surface temperatures, salinity, drought and temporarily high levels of solar radiation (Scarano, 2002), the bare sand habitat is definitely characterized by lower degrees of competition. From this point of view, habitat selection by directional clonal growth might be an essential and possibly adaptive element of a competition avoidance strategy in *A. nudicaulis*.

However, directional growth of *A. nudicaulis* towards high-light areas in their surrounding might not be the result of selection for habitat choice imposed by environmental heterogeneity in the restinga habitat, but it could represent a trait shaped by past selection for light-tracking abilities on the epiphytic form of this species. More studies are needed to answer the question of whether directional growth and habitat selection as shown in this study represents a constraint or an adaptation in *A. nudicaulis* growing in the restinga.

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References

Aphalo, P.J. and Ballaré, C.L. (1995) On the importance of information-acquiring systems in plant-plant interactions. *Funct. Ecol.* **9**, 5–14.

Araujo, D.S.D. (1997) Cabo Frio region. In S.D. Davis, V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos and A.C. Hamilton (eds.) *Centres of Plant Diversity: A Guide and Strategy for their Conservation*, WWF/IUCN, Oxford, pp. 373–375.

Araujo, D.S.D., Scarano, F.R., Sá, C.F.C., Kurtz, B.C., Zaluar, H.L.T., Montezuma R.C.M. and Oliveira, R.C. (1998) As comunidades vegetais do Parque Nacional da Restinga de Jurubatiba, Macaé, RJ. In F.A. Esteves (ed.) *Ecologia das lagoas costeiras do Parque Nacional da Restinga de Jurubatiba e do município de Macaé*, UFRJ, Rio de Janeiro, pp. 39–62.

Bazzaz, F.A. (1991) Habitat selection in plants. *Am. Nat.* **137**, S116-S130.

Benzing, D.H. (2000) *Bromeliaceae: Profile of an Adaptive Radiation*. Cambridge University Press, Cambridge.

Caldwell, M.M. and Pearcy, R.W. (1994) *Exploitation of Environmental Heterogeneity by Plants*. Academic Press, London.

Fialho, R.F. and Furtado, A.L.S. (1993) Germination of *Erythroxylum ovalifolium* (Erythroxylaceae) seeds within the terrestrial bromeliad *Neoregelia cruenta*. *Biotropica* **25**, 359–362.

Hay, J.D. and Lacerda, L.D. (1980) Alterações nas características do solo após a fixação de *Neoregelia cruenta* (R. Gran) L. Smith (Bromeliaceae), em um ecossistema de restinga. *Ciência e Cultura* **32**, 863–867.

Hay, J.D., Lacerda, L.D. and Tan, A.L. (1981) Soil cation increase in a tropical sand dune ecosystem due to a terrestrial bromeliad. *Ecology* **62**, 1392–1395.

Hay, M.J.M., Newton, P.C.D., Robin, C. and Cresswell, A. (2001) Branching responses of a plagiotropic clonal herb to localised incidence of light simulating that reflected from vegetation. *Oecologia* **127**, 185–190.

Henriques, R.P.B., Araujo, D.S.D. and Hay, J.D. (1986) Descrição e classificação dos tipos de vegetação da restinga de Carapebus, Rio de Janeiro. *Rev. Bras. Bot.* **9**, 173–189.

Huber, H. (1996) Plasticity of internodes and petioles in prostrate and erect *Potentilla* species. *Funct. Ecol.* **10**, 401–409.

Huber, H., Lukacs, S. and Watson, M.A. (1999) Spatial structure of stoloniferous herbs: an interplay between structural blue-print, ontogeny and phenotypic plasticity. *Plant Ecol.* **141**, 107–115.

Hutchings, M.J. and De Kroon, H. (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* **25**, 159–238.

Kelly, C.K. (1992) Resource choice in *Cuscuta europaea*. *Proc. Natl. Acad. Sci. USA* **89**, 12194–12197.

Lacerda, L.D., Araujo, D.S.D. and Maciel, N.C. (1993) Dry coastal ecosystems of the tropical Brazilian coast. In E. Van der Maarel (ed.), *Dry Coastal Ecosystems: Africa, America, Asia and Oceania* Elsevier, Amsterdam, pp.477–493.

Lacerda, L.D. and Hay, J.D. (1982) Habitat of *Neoregelia cruenta* (Bromeliaceae) in coastal sand dunes of Maricá, Brazil. *Rev. Biol. Trop.* **30**, 171–173.

Leeflang, L. (1999) Are stoloniferous plants able to avoid neighbours in response to low R:FR ratios in reflected light? *Plant Ecol.* **141**, 59–65.

Liebig, M., Scarano, F.R., de Mattos, E.A., Zaluar, H.L.T. and Luttge, U. (2001) Ecophysiological and floristic implications of sex expression in the dioecious neotropical CAM tree *Clusia hilariana* Schltdl. *Trees-Struct. Funct.* **15**, 278–288.

Macek, P. and Leps, J. (2003) The effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris* L. *Plant Ecol.* **168**, 31–43.

Madeira, J.A., Ribeiro, K.T., Lopez, L.C.S. and Rios, R.I. (1995) Colonization processes of associated tank communities in two bromeliads from the Maricá "restinga" (Rio de Janeiro, Brazil). *Bromélia* **2**, 18–31.

Martin, L., Suguio, K. and Flexor, J.M. (1993) As flutuações do nível do mar durante o quaternário superior e a evolução geológica de "deltas" brasileiros. *Boletim do Instituto de Geografia da Universidade de São Paulo, Publicação Especial* **15**, 1–186.

Medina, E. (1974) Dark CO_2 fixation and carbon isotope ratio in Bromeliaceae. *Evolution* **28**, 677–686.

Novoplansky, A. (1991) Developmental responses of *Portulaca* seedlings to conflicting spectral signals. *Oecologia* **88**, 138–140.

Novoplansky, A., Cohen, D. and Sachs, T. (1990) How *Portulaca* seedlings avoid their neighbours. *Oecologia* **82**, 490–493.

Oliveira, M.G.N. and Rocha, C.F.D. (1997) The effect of the complexity of the tank bromeliad *Neoregelia cruenta* (R. Graham) L. B. Smith on the associated animal community. *Bromélia* **4**, 12–22.

Oliveira, M.G.N., Rocha, C.F.D. and Bagnall, T. (1994) The animal community associated with the tank bromeliad *Neoregelia cruenta* (R. Graham) L. B. Smith. *Bromélia* **1**, 22–29.

Pinheiro, F. and Borghetti, F. (2003) Light and temperature requirements for germination of seeds of *Aechmea nudicaulis* (L.) Griesebach and *Streptocalyx floribundus* (Martius ex Schultes F.) Mez (Bromeliaceae). *Acta Bot. Brasi* **17**, 27–35.

Pittendrigh, C.S. (1948) The bromeliad-*Anopheles*-malaria complex in Trinidad. I. The bromeliad flora. *Evolution* **2**, 58–59.

Salzman, A.G. (1985) Habitat selection in a clonal plant. *Science* **228**, 603–604.

Sampaio, M.C., Perissé, L.E., Oliveira, G.A. and Rios, R.I. (2002) The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil. *Flora* **197**, 443–451.

Sampaio, M.C., Picó, F.X. and Scarano, F.R. (in press) Ramet demography of a nurse bromeliad in Brazilian restingas. *Am. J. Bot.*

Scarano, F.R. (2002) Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Ann. Bot.* **90**, 517–524.

Smith, L.B. and Downs, R.J. (1979) Bromelioideae (Bromeliaceae). *Flora Neotrop. Monogr.* **14**, 1493–2142.

Strong, D.R. and Ray, T.S. (1975) Host tree location behavior of a tropical vine (*Monstera gigantea*) by skototropism. *Science* **190**, 804–806.

Stuefer, J.F. (1996) Potential and limitations of current concepts regarding the response of clonal plants to environmental heterogeneity. *Vegetatio* **127**, 55–70.

Wendt, T. (1997) A review of the subgenus *Pothuava* (Baker) Baker of *Aechmea* Ruiz & Pav. (Bromeliaceae) in Brazil. *Bot. J. Linn. Soc.* **125**, 245–271.

Wiens, J.A. (1976) Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* **7**, 81–120.

Zaluar, H.L.T. and Scarano, F.R. (2000) Facilitação em restingas de moitas: um século de buscas por espécies focais. In F.A. Esteves and L.D. Lacerda (eds.), *Ecologia de Restingas e Lagoas Costeiras* NUPEM-UFRJ, Rio de Janeiro, pp.3–23.