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Spatial distribution and preferential substrate of *Neoregelia johannis* (Carriére) L.B. Smith (Bromeliaceae) in a disturbed area of Atlantic Rainforest at Ilha Grande, RJ, Brazil

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ABSTRACT - (Spatial distribution and preferential substrate of *Neoregelia johannis* (Carriére) L. B. Smith (Bromeliaceae) in a disturbed area of Atlantic Rainforest at Ilha Grande, RJ, Brazil). In bromeliad populations, amount of light and available substrates influence individuals spatial organization. In Atlantic Rainforest of Ilha Grande, the heliophylous bromeliad *Neoregelia johannis* is a large and abundant species. In this forest, it would be expected that *N. johannis* would occupy stable substrates, as large trunks, large branches, rock boulders or ground, with high sunlight, enough for the bromeliad survivor. In the present work, we analyzed the distribution and most used substrates of *N. johannis* in secondary forest. We analyzed the frequency of reproductive modes (sexual and vegetative) used by the bromeliad shoots, registering if the shoots were originated from seeds or by vegetative reproduction. The results indicated an aggregated distribution pattern (Ip = 0.052). The preferred substrate was boulders (91%), whereas tree trunks (6%) and the ground (3%) were rarely used. Small and fragile substrates are unstable to support large adults of this species, which may explain the predominant pattern of establishment over boulders within the secondary forest, as the presence of this substrate also results in more opened canopy cover. Approximately 50% of young individuals entered the population by vegetative reproduction. We conclude that the preferential habit and the aggregated distribution of *N. johannis* are due to the conjunction of preferred substrate with higher amount of light resulting from breaks in tree canopy over areas with rock blocks, and high frequency of recruitment by vegetative reproduction.

RESUMO - (Distribuição espacial e substrato preferencial de *Neoregelia johannis* (Carriére) L. B. Smith (Bromeliaceae) em uma área perturbada de Floresta Atlântica da Ilha Grande, RJ, Brasil). Em populações de bromélias, a quantidade de luz e os tipos de substratos disponíveis afetam a organização espacial dos indivíduos. Na Floresta Atlântica da Ilha Grande, *Neoregelia johannis* é uma espécie heliófila abundante e de grande porte. Nesta floresta, seria de se esperar que *N. johannis* ocupasse substratos estáveis, como troncos e galhos de grande porte, blocos de rocha ou o solo, com alta luminosidade solar, suficiente para a sobrevivência da bromélia. Neste trabalho, foram analisados a distribuição espacial e os substratos utilizados pela bromélia na floresta secundária. Para avaliar o modo de reprodução (sexuada ou vegetativa) mais utilizado pelas plântulas da espécie na área, foram analisadas as freqüências de brotos originados por sementes e por reprodução vegetativa. Os dados indicaram um padrão espacial agregado (Ip = 0,052). O substrato preferencial foi bloco de pedra (91%), enquanto tronco (6%) e solo (3%) foram raramente utilizados. Substratos de pequeno porte e frágeis são instáveis para suportar adultos desta espécie, o que justifica o estabelecimento predominante da bromélia sobre os blocos de pedra na floresta secundária, já que a presença dos blocos também resulta em aberturas na cobertura vegetal. Aproximadamente 50% dos indivíduos jovens são originados na população por reprodução vegetativa. Conclui-se que o hábito preferencial e a distribuição agregada de *N. johannis* devem-se à conjunção substrato preferencial com maior aporte de luz resultante da abertura da cobertura vegetal na área dos blocos de rocha e à elevada taxa de recrutamento por reprodução vegetativa.

Key words - Light in the microhabitat, preferential substrate, vegetative reproduction

Introduction

In tropical forests, epiphytes have a vertical distribution usually influenced by the amount of light, humidity and type of available substrates (Pittendrigh 1948, Johanson 1974, Sugden 1979, Reitz 1985, Ackerman 1986, Medina 1996, Rossi *et al.* 1997, Almeida *et al.* 1998). In bromeliad communities, the amount of light strongly affects the spatial organization (e.g. vertically and horizontally) in the habitat because each species survives only within a particular range of light (Pittendrigh 1948, Benzing 1980, Cogliatti-Carvalho *et al.* 1998). Moreover, the type and frequency of available substrates and the dispersion and reproductive patterns (Wilbur 1977, Henriques *et al.* 1984, Crawley & May 1987) affect bromeliad spatial distribution and also the individuals within the population (Ackerman 1986). Among bromeliads, usually four habits can be recognized: i) terrestrial, living on the ground on leaf-litter; ii) saxicolous, living on rocks; iii) epiphytes, when

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attached to trees, shrubs or lianas; and iv) facultatives, to those species occupying more than one habit category.

The heliophylous *Neoregelia johannis* (subfamily Bromelioideae) is a large bromeliad, whose leaves can reach more than 1 m in length when living in relatively shading microhabitats (Cogliatti-Carvalho *et al.* 1998). The sunlight reaching the microhabitat of this species strongly affects the ability of individuals to establish themselves on substrates and also the development, leaf color and morphology of adult plants (Cogliatti-Carvalho *et al.* 1998). Establishment of the plants on an appropriate (stable) substrate (Ackerman 1986) is crucial for the survival of large epiphytes. In the case of *N. johannis,* it would be expected that, as a result of its large body mass and its heliophylous habit, it would grow successfully only on stable substrates (Ackerman 1986), if subjected to an adequate sunlight range.

In the Atlantic rainforest of Ilha Grande, *N. johannis* occurs in primary and secondary forests (Almeida *et al.* 1998). Although this species is abundant in the Atlantic Rainforest of Ilha Grande (Almeida *et al.* 1998), its geographical distribution is precariously known. In primary forest of Ilha Grande, individuals of this species are strict epiphytes and occur in the canopy, attached to trunks or branches at the top of large trees (30 m high) (Almeida *et al.* 1998), where the amount of sunlight is higher compared to the lower strata. In the secondary forest of this island, some structural characteristics of the habitat, such as canopy cover, trunks diameter and amount of light in the lower strata, have been markedly modified after the removal of large trees due to human disturbances. Therefore, it would be expected that *N. johannis* in secondary areas would occupy other kinds of substrates able to support their large size and body mass when adults due to the absence of large trees and, consequently, to the higher amount of sunlight in the lower strata.

In the present study, we analyzed the substrates and spatial distribution of *N. johannis* in a secondary rainforest of Ilha Grande, analyzing how the occurrence and distribution of stable substrates in the forest affect the use of space by this bromeliad. Specifically, we addressed the following questions: i) what is the density of *N. johannis* in the studied area? - ii) What is the distribution pattern of this bromeliad in the area? - iii) Which substrate is most frequently used by *N. johannis* in the area? - iv) Which factors potentially influence the pattern of distribution and to which extent do they affect the occurrence of *N. johannis*? - v) Which is the main reproductive mode (sexual *vs* vegetative) of shoots in the area during the study?

Material and methods

The study was carried out in an area of secondary Atlantic rainforest of Ilha Grande, near the Vila Dois Rios village (23°11' S and 44°12' W), from September to December 1996. Ilha Grande is an island located in the south of Rio de Janeiro State, in southeastern Brazil, with an area of approximately 19,000 ha. The island is covered by Atlantic rainforest in different stages of regeneration due to human activities over the last centuries. Remnants of undisturbed primary forest persist only in the most inaccessible areas of the island, where only selective cuts seem to have occurred. The island is currently a State Park (Araújo & Oliveira 1988). The secondary forest area on which the present study was carried out has a 12 - 15 m high canopy and trees with trunks of 10 - 25 cm diameter at breast height (DBH), as well as numerous granite boulders (Almeida *et al.* 1998). The study area is located at 80 m above sea level, and has a warm and wet climate. Annual rainfall in the area is about 2,240 mm and annual mean temperature is about 23 °C (NUCLEN 1996).

One hundred plots of 3 x 3 m (9 m^2), totaling 900 m^2 of forest sampled, were randomly established. In each plot were recorded: i) the abundance of *Neoregelia johannis* (Carriére) L.B. (total number of rosettes with more than 20 cm of leaf length); ii) the substrate used by each rosette found; iii) the occurrence of potential available substrates (presence/absence of trunk, branch, liana, soil and rocks); iv) the surface area (in m^2) of rocks, measured as the multiplication of the larger and the smaller diameters, using a measuring tape (to the nearest cm); v) the DBH of tree trunks in cm, using a caliper.

To test if *N. johannis* develops on substrates in frequencies different from their frequency of availability, the frequency of substrates used by *N. johannis* were compared to the frequency of available substrates in the habitat using a Kolmogorov-Smirnov two group test (Siegel 1983).

In the 100 plots sampled the differences in the frequency of bromeliads among plots with and without rocks were tested using the Z test for proportions (Zar 1999). The differences between the total surface (in m^2) of boulders with and without *N. johannis* were tested using one-way ANOVA (Zar 1999). The relationship between the surface area of boulders (excluding boulders with no bromeliads) and the number of bromeliads present was tested by regression analysis (Zar 1999).

The distribution pattern of *N. johannis* in the habitat was analyzed using the standardized Morisita Index of dispersion (Ip), ranging from - 1.0 to + 1.0, with 95% confidence limits at + 0.5 and - 0.5 (Krebs 1989). If $Ip = 0$ the dispersion pattern is considered random, if $Ip > 0$, it is aggregated, and if $Ip < 0$, it is regular or uniform (Krebs 1989).

To estimate the effect of sunlight incidence on the abundance of bromeliads, the amount of sunlight was measured in 40 plots on a single day between 13:00 h and 15:00 h, in order to reduce the effects of time, weather and season in the light measurements. The amount of light (in lux) reaching the soil was measured in 20 plots where *N. johannis* occurred and 20 similar sized plots where the bromeliad was absent, measuring the light at the four corners and at the center of the plot, using a luxmeter Extech. The amount of sunlight reaching the plot was expressed as the mean of the five measurements for each plot. To evaluate whether the absence of *N. johannis* in some patches of the forest is associated with low light incidence in these areas, the mean amount of light in plots with and without bromeliads was compared using one-way ANOVA (Zar 1999). Regression analysis (Zar 1999) was used to evaluate if there is a relationship between the mean amount of light at the plot and the number of *N. johannis*.

To estimate the most frequent shoot reproductive mode (sexual or vegetative) of *N. johannis* in the study area, 20 additional plots of 9 m^2 (3 x 3 m) (a total sample area of 180 m^2 of forest) were established. For each shoot (until 20 cm of length from the base to the leaf apex) found in the plot, we recorded whether it was distant and isolated from another rosette of *N. johannis*, or if it constituted a ramet originating from lateral growth of an adjacent bromeliad. Shoots had originated from vegetative reproduction when were connected or had any evidence of previous connection with another rosette (including dead ones), whereas shoots that were isolated from any other rosette had originated by sexual reproduction. We then calculated the estimated proportion of shoots originating from vegetative and sexual reproduction.

The Systat program was used for statistic analysis.

Results

A total of 364 adult rosettes of *Neoregelia johannis* were found in the 100 plots sampled, or 3.64 ± 8.6 rosettes/plot of 9 m^2 of forest for the secondary Atlantic forest of Ilha Grande. Granite boulders were the preferred substrate of *N. johannis*: of 364 bromeliads sampled, 333 (91%) were on granite boulders. Twenty (6%) rosettes were attached to trunks, with a mean DBH of 22.5 ± 16.1 cm (N = 11), and 11 (3%) bromeliads were on the ground (figure 1A). The smallest trunk used as substrate by *N. johannis* had a DBH of 9 cm. The value of the standardized Morisita Index of dispersion (Ip) was 0.052 (Ip > 0). The frequency distributions of substrates used by the bromeliads differed statistically from those available in the habitat (Kolmogorov-Smirnov, D_{max} = 0.3778; F < 0.001; N = 100). The most frequently available substrates in the area were soil (94%), followed by branches (84%) and trunks (78%) (figure 1B).

The number of bromeliads in plots with boulders (x = 8.0 ± 11.4; N = 45) was statistically greater than the number of bromeliads in plots without boulders (x = 1.0 ± 0; N = 3) (Z Test, z = -5.836; P < 0.001). The mean total area of rocks in the plots where *N. johannis* occurred (x = 4.28 ± 3.49 m^2; N = 45) was statistically higher than the mean total area of rocks where the bromeliad was absent (x = 1.02 ± 1.25 m^2; N = 16) (ANOVA, $F_{1.59}$ = 13.17; P = 0.001; N = 61). The relationship between the area of granite boulders and the number of rosettes in the plots was positive and statistically significant (r^2 = 0.22; $F_{1.43}$ = 12.12; P = 0.001; N = 45).

The mean amount of light in plots where *N. johannis* was present (x = 1666 ± 1957 lux; N = 20) was significantly higher than that of the plots in which the bromeliad was absent (x = 120 ± 73 lux; N = 20) (ANOVA, $F_{1.38}$ = 12.02; P = 0.001; N = 40). There was a

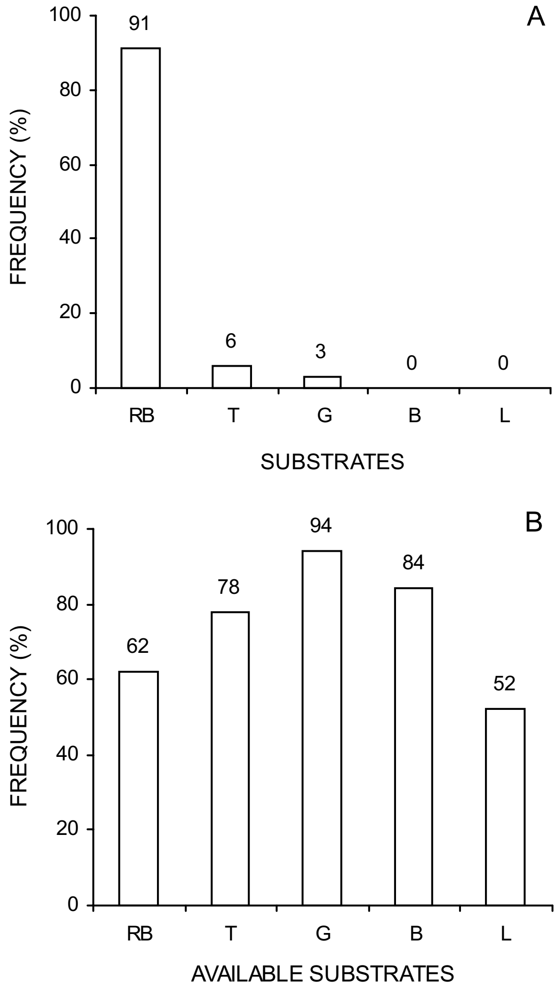

Figure 1. Frequency of substrates used (A) by *Neoregelia johannis* in a secondary forest of Ilha Grande, and the frequency of available substrates (B) in this area. RB = rock block; T = trunk; G = on ground; B = branch and L = liana.

positive and significant relationship between mean amount of light in the plots and number of bromeliad rosettes ($r^2 = 0.52$; $F_{1.18} = 6.559$; $P < 0.05$; $N = 20$).

A total of 148 shoots were found in the 20 plots sampled, and 73 (49%) of them had originated from vegetative reproduction, and 75 (51%) had presumably originated by sexual reproduction, since they did not present any link with any other rosette nor proximity with another individual. From the total of shoots, 105 (71%) were on granite boulders, 41 (28%) were attached to trunks and only 2 (1%) were on the ground. From the total of shoots originated by vegetative reproduction, 58 (79%) were on rock blocks, 13 (18%) were attached to trees and only 2 (3%) were on the ground, whereas from the total of shoots originated by seeds, 47 (63%) were on rock blocks and 28 (37%) were attached to trees.

Discussion

Neoregelia johannis occurs in high density in the area studied, mainly on granite boulders, indicating that in the secondary forest the saxicolous habit predominates. In this forest, few individuals occurred attached to trunks or on the ground. Although the latter was widely available and stable to support adults of this large bromeliad, it is always covered by trees with until 15 m of high in the area studied, which propitiate relatively shading microhabitats and probably difficult the establishment of the heliophylous *N. johannis* on the ground. Otherwise, there are no or few trees over the granite boulders in the secondary forest studied, what contributes to higher incidence of sunlight in this microhabitat resulting in higher abundance of this bromeliad species. Habitat choice (habitat selection) by a plant species should result in higher biological efficiency, higher dispersion ability, recruitment and growth on that substrate (Bazzaz 1991, Schupp 1995). The fact that adult individuals of *N. johannis* were not found attached to tree trunks with less than 9 cm diameter reinforces this idea, since these substrates would be too unstable and fragile (Pittendrigh 1948) to support large adults of this species.

The vertical variation in the spatial distribution pattern of epiphytes may be affected by several factors such as substrate characteristics, light incidence at each forest stratum, water and nutrients availability (Medina 1996) and available space (Bennett 1986). In addition, the frequent disturbances in tropical forests can also strongly influence the horizontal dispersion pattern of epiphytic communities (Ackerman 1986), leading to a loss of available substrates and consequently to a decline in plant species. In the secondary Atlantic forest of Ilha Grande, *N. johannis* can occur in the lower stratum, scattered on boulders, probably due to any of the following reasons: i) loss of large branches and trunks as a result of forest disturbance; and ii) opening of the canopy cover with consequent higher sunlight amount reaching the lower stratum.

Large trees with thick trunks constitute stable habitats to support large bromeliads (Ackerman 1986). This, together with the higher amount of sunlight close to the canopy in the primary forest, can explain why at the primary forest of Ilha Grande large heliophylous epiphytes (such as *N. johannis*) occur on branches many meters above ground on the canopy on large and tall trees, up to 30 m high (Almeida *et al.* 1998). At this forest, in microhabitats near the soil, the plants are exposed to relatively lower daily variations in temperature, light and humidity (Aragão 1967), with lower light intensity, defaulting the establishment of heliophylous species (Almeida *et al.* 1998). On the other hand, at disturbed forests, the higher rate of light incidence allows the occurrence of heliophylous species at lower strata (Almeida *et al.* 1998). This is indicative that *N. johannis* has a facultative habit, being saxicolous in the secondary forest and epiphyte in the primary forest at Ilha Grande.

The standardized Morisita Index of dispersion (Ip = 0.052) indicates that *N. johannis* has an aggregated dispersion pattern in the secondary forest studied. This probably results from the interaction of some intrinsic and extrinsic factors, such as availability of stable substrates, appropriate light conditions and the bromeliad's reproductive mode (vegetative). Because in the secondary forest our data showed that *N. johannis* occurs predominantly on rock blocks, the aggregated dispersion pattern of this bromeliad may be partially explained by the presence of granite boulders. The rock blocks are substrates stable enough to support the mass of adult *N. johannis*. Our data showed that 22% of the bromeliad abundance in the area was explained by the size of the rock blocks in the forest which means that the larger the surface area of the rock blocks, the more bromeliads can attach to them. However, individuals of this bromeliad will survive on these substrates only if a minimum mean amount of sunlight appropriate for its maintenance reaches the rock blocks (Cogliatti-Carvalho *et al.* 1998).

The mean amount of light reaching the rock blocks (which, in general, are clearings, not covered by canopy) was significantly higher (approximately nine times higher) than the light amount reaching other portions of the forest studied. The amount of light reaching the microhabitat is essential for the survival of the heliophylous *N. johannis*, being approximately 940 lux the minimum mean amount of light for the bromeliad survival (Cogliatti-Carvalho *et al.* 1998). This indicates that the portions of the forest with light incidence below this value does not allow the establishment of *N. johannis*. Our data also showed that approximately 52% of *N. johannis* abundance in the secondary forest can be explained by incident light, indicating that the higher the mean amount of light in the microhabitat the more individuals of *N. johannis* will occur, given that boulders are present (these data exclude the effects of variations of physical factors). The absence of available stable substrates in some portions of the area studied, such as boulders or trunks of large trees, may explain the absence of *N. johannis* in microhabitats where light incidence is enough for its survival. However, it is important to consider that other factors such as seed dispersal and reproductive patterns (Henriques *et al.* 1984, Ackerman 1986, Freitas *et al.* 1998) also affect plant spatial distribution in tropical forests.

In the secondary forest studied, the shoots of *N. johannis* may reproduce sexual and vegetatively, being approximately 50% of young individuals (until 20 cm of leaf length) originated by vegetative reproduction. This fact can also explain the spatial distribution of this bromeliad species in the area. The vegetative reproduction can result in an aggregated dispersion pattern because the individuals tend to scatter on the substrate (Henriques *et al.* 1984, Crawley 1990). However, the vegetative reproduction depends on the disturbance level of the site and on the area available (Crawley 1990). In habitats that have suffered some disturbance, such as by fires or deforestation, plants reproducing vegetatively have better chances to survive (Janzen 1980, Cook 1983) because they can readily recover from the disturbance. On the other hand, sexual reproduction needs some adaptations to occur successfully, because the seeds can be preyed upon, or do not germinate due to lack of nutrients, or can fall on unfavorable microhabitats for germination and seedling growth, or may compete for space (Wilbur 1977). It is known that, in bromeliad populations, shoots that reproduce by seeds grow slowly and have higher mortality range compared to shoots that reproduce vegetatively. The same was observed for *N. johannis* (Cogliatti-Carvalho *et al.*, unpublished data).

In disturbed forest areas, where there are many rock blocks, *N. johannis* will be abundant, if there is appropriated light incidence. However, the predominant saxicolous habit of this species in the secondary forest will be gradually substituted by the epiphytic habit, as the vegetation grows and the forest regenerates. So, the aggregated spatial distribution and the preferred saxicolous habit of *N. johannis* in the secondary Atlantic Rainforest of Ilha Grande result from different factors: i) the occurrence of stable substrates (represented by block rocks); ii) the high amount of sunlight reaching the boulders through clearings in the forest cover, due to the absence of trees growing on these boulders; and iii) the high amount of new individuals recruited by vegetative reproduction.

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