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HABITAT CHOICE IN TWO FACULTATIVE EPIPHYTES OF THE GENUS *NIDULARIUM* (BROMELIACEAE)

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ABSTRACT. *Nidularium procerum* and *N. innocentii* (Bromeliaceae) are facultative epiphytes which grow in a swamp forest, within the Brazilian Atlantic rain forest domain, both as terrestrials and as epiphytes. In order to test the hypothesis that habitat choice takes place for these species, we estimated the number of terrestrials versus epiphytic ramets in a 0.25 hectare plot and performed transplant experiments to assess the viability of epiphytic growth in terrestrial ramets. Space for fixation, rosette stability and lack of competitors seemed to account for both species preference for the flooded ground, which is possible through their shoot autonomy for feeding and, possibly, rhizome flood-tolerance. It remains to be seen what are the constraints to seed production, since seedlings are not found on either ground or tree trunks.

INTRODUCTION

Habitat selection, a concept more often applied to animals, has been recently explicitly used for plants as well. Bazzaz (1991) extensively reviewed the subject and claimed that habitat selection in plants is the outcome of evolutionary adjustments to environmental factors resulting in better functioning in a given habitat than in others. Habitat choice is a component of this concept and refers to the ability to be dispersed, to recruit and grow into preferred patches (Schupp 1995). The ecological features presented by a given plant will invariably lead to fixation in a given patch and, as such, can be seen as a choice mechanism regarding habitat. Facultative epiphytes can anchor on land, on tree trunks, or in both media in the same community (Benzing 1990) and, thus, provide interesting material for studies on plant habitat choice. The epiphytic substrates are smaller and patchier than the terrestrial ones, with a greater microclimatic variation (Benzing 1986). This may imply distinct selective pressures upon reproductive traits and on fitness.

Two species of tank bromeliads, *Nidularium procerum* Lindman and *Nidularium innocentii* Lemaire, are facultative epiphytes which occur as terrestrials and/or as epiphytes from the base up to 2 m high on trees of the Atlantic forest (Veloso & Klein 1957, Waechter 1986), from sea level to 1300 m of altitude (Smith & Downs 1979). These two species were recently found in large terrestrial populations on the muddy soil of a swamp forest (40 m of altitude) in the Atlantic forest lowlands (Scarano *et al.* 1997), where their occurrence as epiphytes was apparently less conspicuous. This has prompted us to ask which factors were involved in habitat choice (epiphytic vs. terrestrial) by the populations of these two species in this swamp forest. In order to answer this question we quantified the incidence of epiphytism vs. terrestrial habit for both species and performed transplant experiments to assess the viability of epiphytic growth in terrestrial ramets. Although the study site is within both species geographic distribution range (along the Brazilian coastal forests, from the southern-most State of Rio Grande do Sul to the northeastern State of Bahia), there has been no previous report of either species occurrence in swamp forests.

MATERIALS AND METHODS

The study was conducted in a 0.25 ha (50 × 50 m) plot of swamp forest located in the Reserva Biológica de Poço das Antas (22°30′S, 42°15′W), municipality of Silva Jardim, State of Rio de Janeiro, southeastern Brazil. This region is within the domain of the broadly termed Atlantic rain forest. Three distinct soil water regimes were found in the plot, and characterized three distinct patches: a permanently flooded patch (c. 0.125 ha), a periodically flooded patch (c. 0.065 ha), and a flood-free patch (c. 0.065 ha). The permanently flooded patch was densely occupied by *N. procerum* and sparse trees, most-

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ly *Tabebuia cassinoides,* which form an open canopy. The periodically flooded patch (100–200 d per yr) had a denser canopy and a soil densely covered by *N. innocentii.* The understory of the flood-free patch is more deeply shaded and showed neither of the *Nidularium* species. Scarano *et al.* (1997) provide a detailed description of this site.

The terrestrial ramets of *N. innocentii* found inside the plot occurred in well-delimited groups and no isolated ramet was found. Since the ramets were distributed in clumps and visually occurred in much smaller frequency than those of *N. procerum,* they were all counted. Due to the high density of *N. procerum* over a large area, we estimated the number of terrestrial ramets by counting those within each of twenty-five 2 × 2 m random quadrats (a total of 100 m^2). In order to assess occurrence in the epiphytic habitat, ramets were counted on all trees with diameter at breast height ≥ 5 cm. Additionally, the height where the ramets occurred and whether they were originated by seed or by vegetative propagation were also noted. We considered as vegetatively propagated epiphytic ramets those connected to terrestrial ramets or with any evidence of previous connection (broken or dead rhizome), and counted the number of ramets in each of these two cases.

Ten terrestrial ramets of each species were collected within the plot, and individually transplanted, by tying up with strings the intersection rhizome/external leaf base onto tree trunks at 1 and 2 m of height. Care was taken to select trees which were already *Nidularium* phorophytes and had similar diameters and bark (see Kernan & Fowler 1995). Each ramet was tied up at the same side of the trunk where an epiphyte conspecific rosette was already established. Thus, the tree surface and light regime to which each transplanted plant was subjected were similar to naturally occurring epiphytes of each species. Formation of fixation roots, flowering, formation of new ramets and mortality were observed during 3 yrs (August 1994–July 1997).

Results

TABLE 1 clearly shows that the species studied more commonly occurred as terrestrials, rather than epiphytes, despite permanent or periodic flooding. In the terrestrial habitat, 436 ramets of *N. procerum* occurred within the sampled quadrats (0.01 ha) exclusively within the permanently flooded patch (0.125 ha). If we assume this density throughout, potentially c. 5,000 *N. procerum* ramets occupied the study area and c. 43,600 occupied 1 ha. A total 1,364 ramets of *N. innocentii* occurred in 4 groups covering 0.03 ha of the periodically flooded habitat, completely segregated from the *N. procerum* population.

TABLE 1. Number of ramets occurring on epiphytic versus terrestrial habit in two *Nidularium* species of a swamp forest in Brazil.

N. procerum permanently flooded patch (0.125 ha)		*N. innocentii* periodically flooded patch (0.065 ha)	
Terrestrial	Epiphyte	Terrestrial	Epiphyte
5,000	54 (N = 226 trees)	1,364	21 (N = 66 trees)

Of the 406 trees sampled in the plot, 226 occurred in the permanently flooded patch, 66 in the periodically flooded patch and 114 in the flood-free patch. *N. procerum* occurred as an epiphyte on 34 (15%) trees of the permanently flooded patch and did not occur on trees in the other patches. *N. innocentii* occurred on 14 (21%) trees of the periodically flooded patch and did not occur on trees in the other patches. Both colonized as epiphytes only the base of the trunks. The maximum height of fixation found for *N. procerum* was 1.15 m and for *N. innocentii* was 0.52 m. Mean height (±standard deviation) was 0.40 ± 0.29 m and 0.27 ± 0.14 m respectively. In the epiphytic habitat, no rosette originated from seed was found. All were vegetatively originated and 62% of the *N. procerum* and 64% of the *N. innocentii* were disconnected from the parent shoot.

All terrestrial ramets tied onto trunks developed roots for fixation. After 2 yrs, all ramets survived and 4 (40%) of the *N. innocentii* and 3 (30%) of the *N. procerum* flowered and then developed new ramets. However, the new ramets could not fix themselves in an upright position to the bark surface and died in the third year, since they could not trap water in their tanks.

Discussion

Terrestrial *N. procerum* occurred exclusively in a permanently flooded patch and *N. innocentii* was exclusive to a periodically flooded patch in the swamp studied. Scarano *et al.* (1999) have explained this habitat segregation on the basis of the differences in light regime between the two patches and of the differences in the photosynthetic pathway for carbon fixation between the two species. In addition to confirming this habitat segregation, the present results also indicate that a choice for the terrestrial, inundated habitat, rather than the epiphytic one, has taken place for both species.

The reduced proportion of ramets occurring

in the epiphytic habitat was surprising since these two tank bromeliads are facultative epiphytes which did not lose their epiphytic properties: terrestrial ramets transplanted onto tree trunks, performed fixation, growth, flowering and production of new ramets. The epiphytic habitat was only reached by a few plants vegetatively since no seedlings were found on the sampled trees. The absence of epiphytic *N. procerum* and *N. innocentii* on patches other than the ones where they grow terrestrially reinforces the hypothesis that seed propagation into the epiphytic habitat is unsuccessful.

Despite the commoness of a trade-off between sexual reproduction and vegetative propagation (Abrahamson 1975, Bennett 1991), it remains to be seen as to whether failure in the accomplishment of sexual reproduction takes place in the earlier steps of the regenerative process (from pollination to seed maturation) or later (from dispersal to establishment phases), and as to whether favorable years for sexual reproduction occur over a longer time scale. This question is relevant for both epiphytic and terrestrial habitats since no seedlings were found on the ground either, although flowering has occurred yearly for both species between June and September for the past 4 yrs. A parent-offspring conflict (see Uma Shaanker *et al.* 1988), i.e., the habitat is beneficial to the parent and not to the seeds produced by them, could possibly occur here, if viable seeds are at all produced.

Thus, since seedling establishment did not take place during the study period on either flooded ground or tree trunks, the preferential occurrence of both facultative epiphyte species of *Nidularium* on flooded ground rather than on tree trunks is due to limits imposed by the latter habitat which are absent in the former. Fixation of new ramets formed by plants attached to trees did not occur since they could not reach an upright position (possibly due to an increase in weight and/or to a loss of balance of the plant as the new ramet is formed) and thus, could not trap water. Space is one of the main limits to epiphyte distribution (Bennett 1986), since a lot more space is available on the ground rather than on tree trunks, whereas interspecific competition is likely to constrain facultative epiphyte distribution on the forest floor. However, shade and permanent flooding should also limit the occurrence of herbaceous plants on the forest floor. The lack of competitors favored the high density of bromeliads on this site. Curiously, one should expect that flooding would limit the distribution of typical xerophytes, such as bromeliads, which did not evolve under this selective pressure. This may not be so since these plants are largely independent of their underground organs for nutrition. A combination of shoot autonomy for feeding and some degree of rhizome flood-tolerance (see Brändle 1991 for review) may confer to these species the capacity to grow as "epiphytes on mud." The lack of competitors, the higher availability of space for vegetative propagation and the higher shoot stability provided by the flooded ground are more favorable to establishment and fitness than tree trunks.

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