LIVING ON THE EDGE: ADAPTATIONS BY EPIPHYTIC BROMELIADS TO LIGHT INTENSITY AND DESICCATION IN EXPOSED CANOPY HABITATS

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Abstract: Bromeliads in the tree canopy of high elevation forest in Costa Rica are subject to high variance in sun and wind exposure. However, adaptations such as red pigmentation to block UV-B and cupped leaves to hold more water may allow some species of bromeliad to occupy high exposure habitats. I compared two distinct but unidentifiable species of bromeliads in Cuericí, Costa Rica, with respect to exposure to sunlight, red pigmentation, and water holding capacity. Species 1 had more red pigmentation and held more mL water/ g plant than species 2. Also species 1 tended to be larger and more abundant in exposed habitats than species 2. These results are consistent with the hypothesis that increased red pigmentation and water storage help species 1 to better resist damage caused by light and water stress, allowing it to grow larger than species 2 in high exposure habitats.

Key Words: bromeliad, sun intensity, tree canopy

INTRODUCTION

Bromeliads living in the Costa Rican tree canopy in high elevation forest are exposed to large fluctuations in light intensity, wind, and water availability. Perhaps moderating the effects of light and water stress, some species of bromeliad have red pigmentation (which may protect against UV-B radiation) and a whorled leaf structure which forms tanks that store water. Two species of epiphytic bromeliads dominate the upper canopy of oak forests in Cuericí, Costa Rica: species 1 has distinctive, variable red pigmentation and large, concave leaves; species 2 is usually green colored and has narrower leaves. I tested three predictions derived from the hypothesis that red coloration and water holding capacity are adaptations for high light and low water conditions: (1) redness of species 1 increases with exposure and increases more dramatically than species 2; (2) leaf structure of species 1 allows greater water storage in mL water/g plant than that of species 2; and (3) species 1 is more abundant and grows larger than species 2 in more highly exposed areas.

METHODS

I studied bromeliads on 27 Jan 2006 at the Cerro de la Cuericí research center, sampling on the trail with northwestern aspect. Few bromeliads occurred under the darker, wetter southeastern aspect (≈ 3% the density under a trail with a NE aspect). For each randomly selected tree, I randomly sampled one bromeliad each of species 1 and 2 (yielding n = 30 and 32 bromeliads, respectively). For each bromeliad, I estimated the size, redness, and exposure on ordinal scales of 1 to 8, with 1 being the lowest size, redness, or exposure and 8 being the highest. I defined redness as the visually apparent intensity of the red pigmentation in bromeliad leaves, and I defined exposure as the level of

canopy openness around the bromeliad, taking into account shading around and above the bromeliad, as well as proximity to tree canopy edges. I also tested the water-holding capacity of both species, sampling eight bromeliads of each species (from recently fallen intact plants) with a similar range of sizes, first recording their dry weight and then measuring the volume of water each bromeliad retained after I had submerged it in water.

Taking the liberty of analyzing ordinal data as interval data, I tested for patterns in redness and size with a general linear model that included species, exposure, and the interaction between species and exposure using JMP 5.0.1. I also analyzed the difference in leaf water holding capacity between the two species.

RESULTS

I found both species across all levels of exposure, but I found species 1 more often than species 2 in high exposure habitats (t_{60} = 2.01, P = 0.050). The relationship between size and exposure differed between species (Table 1); while the size of species 1 did not vary with exposure, the size of species 2 decreased with exposure (Figure 1). Redness was positively related to exposure in both species (Table 1), but more so for species 1 than species 2 (Figure 2). Finally, species 1 tended to hold more mL water/g plant compared to species 2 (Fig. 3).

DISCUSSION

Results indicate that bromeliad species diver with respect to redness and water storage and that these trends are related to their distribution across habitats. Results also support the tentative conclusion that redness and water storage ability are adaptation of species 1 for high exposure environments.

The small size of species 2 at high exposures could potentially be explained by age structure if individuals of species 2 in high exposures tended to be younger. This seems unlikely to explain the patterns I recorded because (1) species 2 individuals in high exposures are probably not new colonizers because these exposed habitats must be about as old as less exposed habitats; and (2) if these individuals are young, this would imply that older plants in the same exposure all died at about the same time.

A better explanation for the difference in size between species 1 and species 2 in high exposure habitats is species differences in resistance to the damaging effects of canopy exposure.

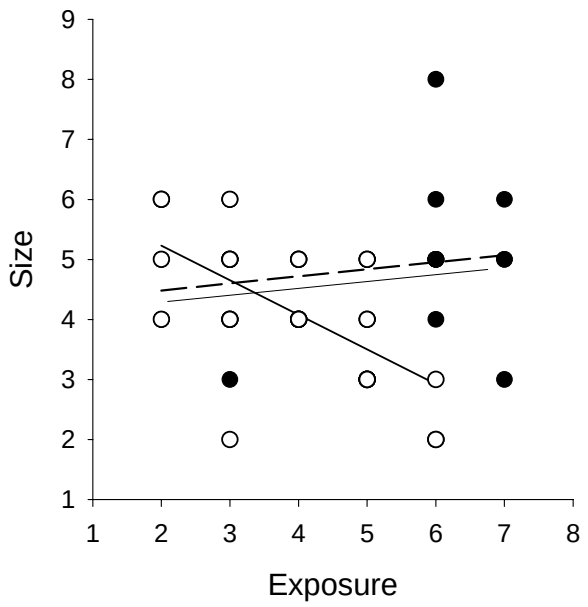

Figure 1. The effect of exposure on the size of bromeliad species 1 (closed dot) and species 2 (open dot) in Cuerici, Costa Rica. Species 1 plant size did not change with exposure (dotted line: P =0.32), but the species 2 plant size decreased with increasing exposure (solid line: r^2 =0.39, df =31, P>0.001). Exposure and size were visually estimated for each bromeliad on a scale of 1-8.

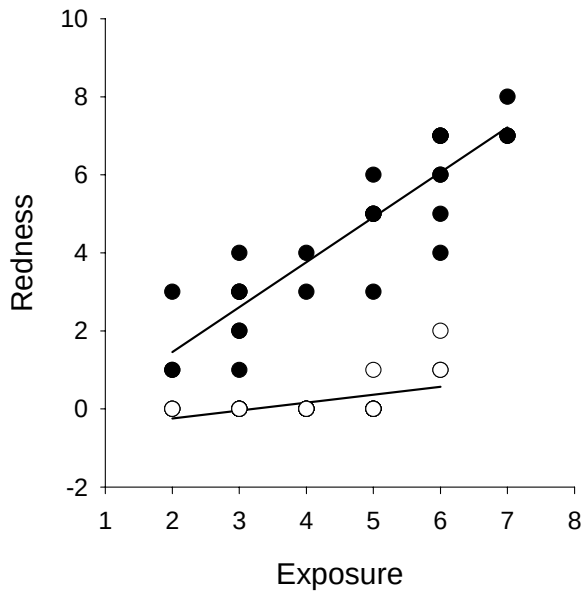

Figure 2. The effect of exposure on the intensity of red pigmentation of bromeliad species 1 (closed dot) and bromeliad species 2 (open dot) in Cuerici, Costa Rica. The redness of species 1 plants increased more with exposure (r^2 =0.84, df =29, P>0.001) than the redness of species 2 plants (solid line: r^2 =0.30, df =31, P=0.001). Exposure and redness were visually estimated for each bromeliad on a scale of 1-8.

Table 1. Tests of the relationships between exposure and red coloration, and exposure and size for two epiphytic bromeliad species at Cuerici, Costa Rica.

	Redness			Size		
	t	df	P	t	df	P
Exposure	21.35	1	<0.001	3.43	1	0.001
Species	10.41	1	<0.001	-2.55	1	0.013
Exposure*Species	7.28	1	<0.001	3.86	1	<0.001

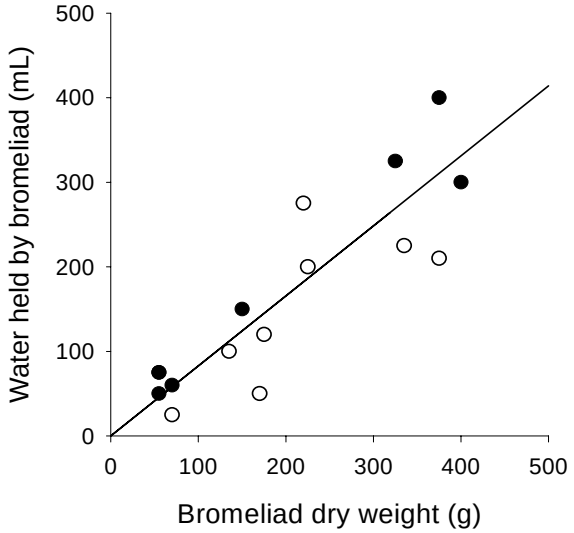

Fig. 3. The difference in water holding capacity of two species of bromeliad in Cuerici, Costa Rica. Closed circles are species 1, open circles are species 2, and the line shows the expected mL/g for all species. Species 2 holds more water in mL/g plant than species 1 (Matched Pairs, t = -2.24, df = 15, P = 0.04)

Species 2 displays extreme plasticity in red pigmentation, which may allow it to tolerate more extreme light intensities by dispersing or absorbing potentially damaging UV light. Species 2 can also store a larger reserve of water, which may allow it to cope with variable water availability and resist desiccation from wind and sun, all of which increase in exposed habitats. Red pigmentation and greater water storage may confer higher growth rate or greater survival (or both), that would explain the greater size of species 2 in open habitats. Larger size, in turn probably confers greater reproductive success.