

EFFECTS OF SOIL ORGANIC LAYER DEPTH AND LIGHT AVAILABILITY
ON INDIVIDUAL SIZE OF THE BAMBOO *CHUSQUEA* SP.
IN A NEOTROPICAL CLOUD FOREST

SAMANTHA R. KAPLAN, THOMAS J. LOBBEN, AND TIFFANY D. CHANG

Faculty editor: David R. Peart

Abstract: *Chusquea* sp. is an abundant bamboo near Monteverde Biological Station, Costa Rica. We hypothesized that increased soil organic layer depth and light availability would increase *Chusquea* sp. size, as measured by average shoot height, number of shoots, average basal shoot diameter and clump density, but our hypothesis was not supported. The clone morphology of *Chusquea* sp. is apparently insensitive to these variables within the range of variation we encountered.

Key words: Monteverde, water retention, canopy cover

INTRODUCTION

Chusquea is a native bamboo genus at Monteverde, Costa Rica. Bamboo shoots sprout at varying diameters and reach different heights. A previous study of a particular species (referred to as *Chusquea* sp.), showed that the bamboo was more abundant where light and soil moisture levels were highest (Erickson et al 2001). We hypothesized that shoot thickness and height, rather than abundance, might be better indicators of available resources.

We predicted that high light availability and soil organic layer depth would both increase bamboo size. Organic layer depth tends to be correlated with the ability of soil to retain water (e.g. Brady et al. 1996).

METHODS

We conducted our study on 24 and 25 January 2008 on either side of the Principal, División, and Mirador trails near Monteverde Biological Station, Costa Rica. We randomly sampled 20 clumps of *Chusquea* sp. within 3m of the trail. We used several measures of bamboo clump size: number of shoots, average shoot height, average shoot diameter and the density of stems per unit area in the clump.

To calculate clump density (number of shoots per unit area), we divided number of shoots by clump area (calculated as length x width). If either length or width was > 2m, we established a plot centered on the center of the clump, with dimensions calculated as follows. The length of

the plot was the length of the clump or 2m, whichever was greater. The width of the plot was the width of the clump or 2m, whichever was greater.

We counted the number of stems in each clump, measured basal diameter of 5 randomly selected stems per clump, and estimated the average height of all stems in a clump by measuring the height of a representative shoot. We used a GPS device to measure the elevation at each clump and took four canopy cover measurements (using a spherical densiometer) at nearby locations estimated to be representative of the clump's available light. Finally, we took a soil core sample next to each clump to measure organic layer depth.

We log transformed clump density and number of shoots, and square root transformed average basal shoot diameter, to satisfy assumptions of normality.

RESULTS

Organic layer depth and canopy cover did not affect average shoot height, number of shoots, average basal shoot diameter or clump density (MANOVA Wilks' $\lambda = 0.577$, $df = 8, 28$, $P = 0.388$). We also ran 8 individual regressions using all independent and dependent variables to explore relationships. We found one significant result; shoot height to basal diameter ratio

increased with organic layer depth ($r^2 = 0.22$, $df = 19$, $P = 0.04$). However, there is a 37% probability of finding one significant relationship by chance after running 9 tests, so this relationship may be spurious.

DISCUSSION

Changes in organic layer depth and canopy cover did not affect *Chusquea* sp. size. We confirmed Erickson et al.'s (2001) observations that *Chusquea* sp. does not grow below 1700m. Apparently, *Chusquea* sp. size is insensitive to depth of soil organic matter and light availability, within the range of variation in our samples (organic matter depth: 0 – 23cm; average canopy cover: 0 - 89%).

If the positive relationship between shoot height to basal diameter ratio and organic layer depth is real, it may indicate that *Chusquea* sp. grows taller and thinner with greater soil water retention. We suggest that *Chusquea* sp. responds to greater intra- and interspecific competition in sites with high water availability, by producing taller shoots that may overtop neighboring plants.

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MORPHOLOGICAL VARIATION OF EPIPHYTIC BROMELIADS WITH HEIGHT ABOVE GROUND

ROBERT H. YANKER III, ALANNA H. PURDY, BRIAN M. LAPPAS, AND ALEX C. SPINOSO

Faculty editor: David R. Peart

Abstract: Epiphytic tank bromeliads in secondary forest are morphologically plastic in response to abiotic factors in the tree canopy (Bader 1999). We hypothesized that a bromeliad assemblage in a high elevation primary cloud forest at Monteverde, Costa Rica would show the same morphological trends. Specifically, we predicted that canopy bromeliads would have a narrower shape, smaller size, and a greater capacity (per unit size) to store water than understory bromeliads, to deal with light, wind, and nutrient stress. As predicted, bromeliad volume (calculated from bromeliad height and diameter) significantly decreased with height above ground. Two non-significant trends were consistent with our predictions: bromeliads tended to be narrower (greater height:width ratio) and to have larger tanks in proportion to plant size, with height above ground.

Keywords: vertical stratification, nutrient gradient, moisture stress

INTRODUCTION

Light, water, and nutrient availability influence vascular epiphyte morphology (Bader 1999). In the more exposed and xeric canopy habitat, bromeliads with tanks tend to have a narrow tubular shape; this minimizes water loss by evaporation, damage by direct radiation (Benzing 1990), and the chance of being dislodged by wind. Individuals growing in the shady and humid conditions of the understory tend to have a greater diameter, which allows them to gather more light (Bader 1999).

Based on this evidence, we hypothesized that abiotic factors in the high elevation cloud forest of Monteverde would affect

Bromeliaceae morphology. We predicted that bromeliads higher on the tree would be narrower and smaller, reducing their exposure to wind and sun, while those towards the base would be broader and thus absorb more light. We predicted that canopy bromeliads would also have greater tank capacities due to greater potential for water stress higher on the tree.

METHODS

We sampled on January 24, 2008 in a primary tropical cloud forest along The Great Divide, ca. 1 km E of the Estación Biológica Monteverde, Costa Rica. We studied type III Bromeliaceae (epiphytic species with tanks that absorb water

and nutrients through foliar scales at the leaf base; Pittendrigh 1948), from the Bromelioideae and Tillandiodeae subfamilies. We opportunistically sampled 6 recent tree falls along the ridge of the Great Divide.

We measured the trunk length of each tree and divided it into four equal sections. We randomly chose one bromeliad from each section for further testing. On one of the 24 study sections, no bromeliads were present. We recorded the distance of the bromeliad from the base of the tree (height above ground), bromeliad height (from the base of the bromeliad roots to the tallest leaf) and width (leaf span at the bromeliad's widest point). We measured tank volume by filling it with water and emptying it into a graduated cylinder.

We estimated bromeliad volume by calculating the volume of a cone using measures of height and width. We quantified a shape index for each bromeliad using a height:width ratio. To quantify proportional tank volume we calculated tank volume:bromeliad volume.

RESULTS

Bromeliad volume decreased with height above ground; ($r^2 = 0.22$, $df = 21$, $P = 0.03$; Fig. 1). We found a non-significant positive trend for height:width ratio to increase with

increasing height above ground ($r^2 = 0.11$, $df = 21$, $P = 0.13$). There was a weak suggestive trend for relative tank size to increase with height above the ground ($r^2 = 0.10$, $df = 21$, $P = 0.13$).

Bromeliad height did not change with height above the ground ($r^2 = 0.05$, $df = 21$, $P = 0.32$), though bromeliad width decreased as height above the ground increased ($r^2 = 0.22$, $df = 21$, $P = 0.02$). There was no relationship between tank volume and height above the ground ($r^2 = 0.03$, $df = 21$, $P = 0.46$).

With six separate statistical tests, there was a 26.5% chance of finding one significant relationship by chance alone.

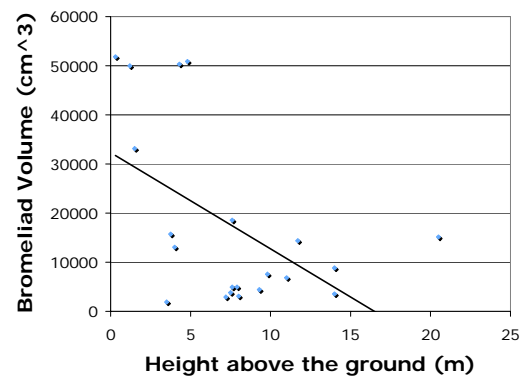


Fig. 1 Bromeliad volume vs. height above ground for fallen trees along the Mirador trail on the Great Divide at Monteverde, Costa Rica.

DISCUSSION

We suggest that bromeliad morphology was driven by light and mechanical stress, although we were unable to measure those abiotic factors. Canopy bromeliads tended

to be smaller than understory bromeliads (Fig. 1), suggesting that larger bromeliads are limited to lower sections on the tree or that smaller plant size is selected for in the canopy habitat.

Although statistically insignificant, greater tank volume relative to bromeliad volume in individuals high above ground suggests that moisture stress, perhaps due to greater evaporation and reduced rainfall during the dry season, may be important in the canopy.

Although the pattern of greater height:width ratios in canopy bromeliads was not significant, we believe that wind and light stress influenced the directionality of the data. The streamlined shape found in the canopy could reduce the chance of being blown down and exposure to direct radiation. Bromeliads closer to the ground tended to have a lower height:width ratios which may maximize light absorption in dim light.

Overall, we believe our data indicate that bromeliad volume and

width in this high elevation primary cloud forest are influenced by gradients in light, wind stress, and moisture. The results also suggest that canopy bromeliads have a greater capacity to store water and tend to have a narrower, taller shape than understory bromeliads. To make stronger inferences about these patterns, it would be necessary to quantify abiotic gradients and obtain larger samples.

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EFFECTS OF ALTERNATIVE COFFEE GROWTH METHODS ON ARTHROPOD DIVERSITY AND THE INCIDENCE OF LEAF FUNGAL INFECTIONS

JENNA M. SULLIVAN AND LIA M. CHEEK

Faculty editor: David R. Peart

Abstract: We hypothesized that arthropod diversity and abundance would increase from sun to shade to traditionally grown plants of coffee (*Coffea arabica*), and that *Mycena citricolor* fungal infections would be more prevalent in the shade. Our results did not support either hypothesis; however, *M. citricolor* may be more prevalent (marginally significant) on shade-grown coffee plants.

Keywords: Monteverde, Costa Rica, coffee plantation, *Coffea arabica*, *Mycena citricolor*

INTRODUCTION

Alternative coffee plantation methods may influence the diversity and abundance of arthropods. Arthropods, in turn, affect the diversity and abundance of higher trophic levels (Brown 1997). The fungus *Mycena citricolor* infects coffee plants and prefers cool, moist conditions (Heyner Vaula, pers. comm.). We hypothesized that 1) arthropod abundance and diversity would increase from sun to shade to traditionally grown coffee plants, and 2) there would be less fungal infection in sun grown coffee than in shade grown coffee plants.

METHODS

We conducted our study on 24-25 Jan. 8 in Monteverde, Costa Rica at the Don Juan coffee plantation, which produces sun

grown coffee with minimal pesticide use (Heyner Vaula, pers. comm.). Some plants were shaded by windbreak trees, and others grown without pesticides or pruning ("traditional method"), were no longer harvested. In each treatment (sun, shade, and traditional), we collected leaf litter in a circle of radius 40 cm, centered on the bases of six randomly chosen coffee plants. Under each plant, we installed one pitfall trap flush with the ground, using a plastic cup of diameter 7 cm. We assessed *M. citricolor* infection by randomly selecting two branches from sampled plants, counting the percentage of leaves affected by the fungus, and averaging the two estimates.

RESULTS

There was no difference in arthropod abundance or diversity

between sun, shade, and traditionally grown sample areas. (ANOVA, $F = 0.63$, $df = 2, 15$, $P = 0.54$; ANOVA for Shannon Diversity Index $F = 0.48$, $df = 2, 14$, $P = 0.63$). The percent of fungus-infected leaves grown in the shade was higher than those grown in the sun (marginally significant; Table 1; one-tailed t-test, $t=1.62$, $df=8$, $P=0.07$).

Table 1. Percent *Coffea-arabica* leaves affected by *Mycena citricolor* fungus on sun and shade grown coffee at Don Juan plantation, Monteverde, Costa Rica.

Plantation Method	Mean % Leaves Affected	Standard Error
Sun	41.8	0.074
Shade	16.5	0.137

DISCUSSION

Coffee plantation method (sun, shade, or traditional) did not affect arthropod diversity or abundance. We found low arthropod abundance in all plantation methods, possibly due to natural chemical defenses such as caffeine and tannins, present in coffee leaves. Because the sun and shade plantations were so close together, the arthropods we sampled may have been affected by both growing methods.

Our marginally significant results for fungus infected leaves suggest a higher prevalence of *M. citricolor* on shade-grown coffee plants (Table 1). Farmers in the Monteverde area may prefer to grow

coffee in the sun to better control fungal growth.

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DELAYED GREENING AND THE EFFECT OF LIGHT AVAILABILITY ON CHLOROPHYLL DENSITY IN *DIPLAZIUM URTICIFOLIUM*

IAN G. WHEAT AND DYLAN D. THOMAS

Faculty editor: David R. Peart

Abstract: Many young leaves are a lighter shade of green than mature leaves, but it is not clear whether this reflects changing chlorophyll densities with age. Based on delayed greening theory, we predicted that younger fronds of the fern *Diplazium urticifolium* would have lower chlorophyll densities than mature fronds. We also hypothesized that younger fronds would have greater chlorophyll densities in high light than in low light, because in high light the greater potential carbon gain would outweigh the risk of loss to herbivory. We found lower chlorophyll density in younger fronds, consistent with delayed greening, but no significant difference in chlorophyll densities between high light and low light environments, possibly due to more herbivory in high light.

Key Words: physiological constraint, growth rate, trade-offs, inducible

INTRODUCTION

Delayed greening, whereby plants withhold chlorophyll from young leaves until they are adequately defended, is a common adaptation to reduce losses to herbivory. Plants depend on chlorophyll to convert light into chemical energy, but chlorophyll is costly, and the youngest leaves are most susceptible to herbivory (Coley and Kursar, 1996).

We investigated how chlorophyll density (g/m^2) in the fern *Diplazium urticifolium* is affected by light availability and age. The youngest frond of *D. urticifolium* has the lightest shade of green, and becomes darker with age. This color change could be explained by increasing density of chlorophyll

(Erickson et al. 2001) or changes in frond thickness and physical structure with age.

We hypothesized that younger fronds delay greening because they are less well defended, and losing chlorophyll to herbivory is costly. Thus, we predicted that young fronds would have lower chlorophyll densities than mature fronds.

Delayed greening may be an inducible trait, optimized to an individual plant's environment (Vu et al., 2007). Plants in higher light receive more energy return per unit chlorophyll than plants in low light (Chazdon et al., 1996). We hypothesized that for young fronds in high light, the greater potential energy gain per unit chlorophyll would outweigh the risk of loss to

herbivory, and predicted that chlorophyll densities should be greater in high light than in low light. Finally, we hypothesized that if delayed greening is inducible with respect to light, then between high light and low light chlorophyll densities should differ in young fronds but converge to a similar value as the frond matures.

METHODS

On 23 and 24 Jan 2008 we sampled 24 *D. urticifolium* sporophytes in the forest above the Monteverde Biological Station in Costa Rica. We selected plants by walking a random number of steps (between 1 and 60) along the Sendero Principal Trail, then turning in a random compass direction and picking the first *D. urticifolium* encountered. We collected the youngest frond and a random mature frond of the fern sampled, and recorded whether it was in high light (gap) or low light (under canopy). We photographed the two fronds of each fern on a neutral gray surface in a dark room with an Olympus 770 SW set at ISO 100, using its flash.

To test if fern size had a confounding effect on chlorophyll density, we counted the number of blades (leaflets) on each frond and the length and width of the middle blade. We estimated blade area by multiplying blade length by width,

frond area by multiplying blade area by number of blades, and total fern foliage area by multiplying frond area by number of fronds.

We extracted the average RGB values of four randomly selected blades of every frond with the imaging software Gimp 2. Using the formula: $\text{chlorophyll density} = 0.952 - 1.76 \cdot (R-B)/(R+B)$ (Kawashima and Nakatani, 1998) we estimated the chlorophyll density (g/m^2) of the four blades of each frond. Of the 188 blades, six had negative chlorophyll values; this was not critical as we required only relative densities to test our predictions. There was little variation in chlorophyll density estimates between the four blades of a frond, and we averaged them to obtain a composite value.

RESULTS

Fern size did not significantly affect chlorophyll density in terms of blade area ($F = 1.14$, $df=1$, 45, $P = 0.29$), frond area ($F = 1.13$, $df=1$, 45, $P = 0.29$), or total frond foliage area ($F = 1.63$, $df = 1$, 45, $P = 0.21$).

As predicted, chlorophyll densities were significantly lower in younger than older fronds (two-way ANOVA, $F = 14.6$, $df = 1$, 44, $P < 0.0001$). Contrary to our predictions, there was no significant difference in chlorophyll densities between high light and low light environments ($F = 2.81$, $df = 1$, 43, $P = 0.10$). There was no interaction between light and age

($F = 0.11$, $df = 1$, 43 , $P = 0.74$, Figure 1), further evidence that delayed greening was not inducible in response to light.

Chlorophyll levels were lower in the light green leaves than in the darker leaves, shown by a negative

linear relationship between green brightness (from RGB values) and chlorophyll density, which was calculated independently of green brightness ($F = 7.10$, $df = 1$, 45 , $P = 0.01$).

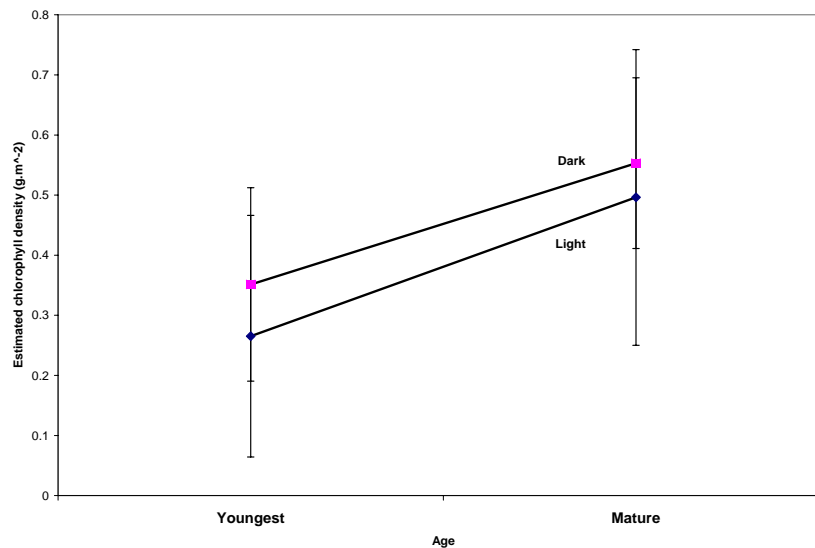


FIGURE 1. Estimates of chlorophyll densities in young and mature fronds of *D. urticifolium* in high light and low light environments at Monteverde, Costa Rica, using RGB color values and a formula from Kawashima and Nakatani (1998).

DISCUSSION

Regardless of fern size and light availability, young fronds had a lighter coloration and lower chlorophyll densities than mature fronds. This is consistent with delayed greening theory, with ferns investing less chlorophyll in their vulnerable young fronds, mitigating losses to herbivory. However, rapid expansion of young fronds could also reduce chlorophyll density (Coley and Kursar, 1996).

While it is generally assumed that leaves have higher chlorophyll

density in high light than in low light, both shade tolerant and intolerant plants appear to have converged on a similar chlorophyll density in mature leaves, regardless of light availability (Chazdon et al. 1996). Our results are consistent with chlorophyll densities in mature leaves being relatively fixed, since we did not detect a difference between high light and low light environments.

It has been asserted that delayed greening is an inducible trait in young leaves with respect to herbivory (Vu et al., 2007). Our

result suggests that it is not inducible with respect to light availability in young fern fronds, but data on chlorophyll densities over a range of frond ages would be necessary to confirm this. Also, if there is greater herbivory in high light, that would increase the value of delayed greening in high light, and confound assessment of light as a factor affecting delayed greening.

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FLOURISHING FLOWERS AND PICKY POLLINATORS IN THE GAPS OF A CLOUD FOREST AT MONTEVERDE, COSTA RICA

YIRAN GU AND ELEANOR B.R. PASCALL

Faculty editor: David R. Peart

Abstract: Resources for plant reproduction may be severely limiting in the forest understory. We hypothesized that there would be more flowers in gaps than under the canopy. We counted the number of flowers in paired gap and non-gap areas and divided morphospecies into 3 morphological syndromes (cupped, spike, and tubular). We found more flowers in gaps than in non-gaps, possibly due to increased light and nutrient availability in gaps. Cupped flowers had greater, and tubular flowers lower, relative abundance in gaps compared to non-gaps.

Keywords: forest gap, morphological syndrome, flower abundance, pollinator, Monteverde

INTRODUCTION

Limited resource availability in the understory may restrict forest plants' capacity to reproduce. Large tree falls create gaps, increasing temperature, light and possibly nutrient availability at the forest floor. Unlike canopy species, understory plants generally do not need to reach the canopy to mature, so they can use the energy and nutrient resources available in gaps to reproduce.

We compared flower counts in gap and non-gap areas, to assess the importance of gaps for reproduction in non-canopy woody species. We hypothesized that there would be more flowers in gaps than in nearby non-gap areas.

Morphology of flowers can often be used to predict pollinator type (Nadkarni and Wheelwright 2000). Tubular flowers are usually

pollinated by hummingbirds, which can trapline for long distances through the understory, and thus provide effective pollen dispersal even when flowers are sparse. Cupped flowers and spike inflorescences are usually pollinated by insects, which typically do not travel large distances. Therefore, it may be advantageous for plants with cupped flowers and spike inflorescences to forgo reproduction when resource availability is low, and wait to flower until a gap opens. Thus, we hypothesized that the relative abundance of cupped flowers and spike inflorescences would be greater in gaps, while that of tubular flowers would be greater in non-gaps.

METHODS

On 24 and 25 Jan 2008, we sampled 7 paired gap and non-gap

areas in the high elevation cloud forest at Monteverde, Costa Rica. We found gaps of similar ages (old enough to have enhanced understory growth and young enough to still be open) along the established trails, Sendero Principal and Sendero Mirador. We ran 2 m-wide belt transects through the longest axes of the gaps. Transects ranged from 10 to 20 m in length. For each gap transect, we ran a paired transect of the same length in closed-canopy forest (“non-gap”) ca. 10m away. We paired the transects to reduce the effects of potentially confounding variables, such as slope, aspect, local site characteristics, and elevation.

In each belt, we counted flowering plants, the number of flowers on each plant, and the number of flowers in each morphological syndrome: cupped, tubular, and spikes. Spike inflorescences were counted as single flowers, and we did not count flower buds or fruits.

We square-root transformed the flower counts to meet the normal distribution assumption of paired-t tests. We excluded data from one high-elevation pair because reduced forest stature at high elevation strongly affected canopy cover, which increased similarity between the gap and non-gap areas.

RESULTS

Flowers were significantly more numerous in gaps than in non-gaps (paired-t = -3.28, df = 5, P = 0.022). Relative abundance of morphological syndromes differed between gaps and non-gaps: while spike inflorescences dominated both habitats, proportionally more cupped than tubular flowers were in gaps, and proportionally more tubular flowers were in non-gaps (Figure 1. Pearson $\chi^2 = 52.31$, df = 2, P < 0.001).

Flower assemblages differed between gaps and non-gaps. Within each morphological syndrome, there was minimal overlap between the morphospecies flowering in the two habitats (Figure 2).

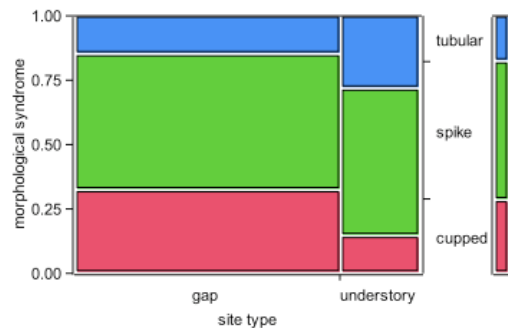


FIGURE 1. Relative abundances of morphological syndromes in gap and non-gap areas in a montane cloud forest at Monteverde, Costa Rica. Pearson $\chi^2 = 52.31$, df = 2, P < 0.001.

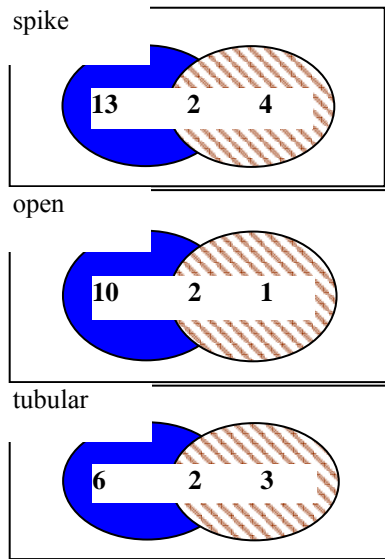


FIGURE 2. Number of flower species in gaps (solid) and non-gaps (striped), showing overlap of morphotypes between site types for open, spike and tubular syndromes.

DISCUSSION

The greater abundance of flowers in gaps supported our hypothesis that resource availability in gaps aids understory plant reproduction.

The limited overlap of morphotypes between gaps and non-gaps (Figure 2) suggests that the greater abundance of flowers in gaps is not simply due to plants' opportunistic utilization of resources. Rather, species may be specialized for the two different habitat types. If so, certain understory species might require gap conditions to flower, while others can reproduce in shade.

Increased abundance of cupped flowers in gaps would probably attract more insect pollinators.

Higher temperatures in gaps also increase insect activity levels, which may translate into more flower visits per insect. In addition, there were more white and yellow flowers in gaps than in non-gaps (personal observation). These flowers should support more insects in gaps.

Hummingbirds are also likely to be attracted to gaps, where tubular flowers are more numerous than in non-gaps. However, we predict that more birds than insects would forage in non-gaps, given the higher ratio of tubular to open flowers in non-gaps.

Gaps benefit more than just canopy species, which invest available resources in growth toward the canopy. Gap conditions may also be essential for the flowering of many species that can persist, but not flower, in the shade. Thus, gaps also affect assemblages of pollinators that thrive on the resources offered by flowering plants.

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