Spatial patterns in herbivory within understory bamboo stands

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Abstract: Spatial patterns of herbivory may be affected by nutritional quality of plants, heterogeneity in predation risk and/or herbivore movement patterns. These patterns may vary with plant density. We studied the distribution of herbivory damage in a monospecific stand of bamboo at La Estación Biológica Cuericí, Costa Rica. If high density patches of bamboo offer herbivores a higher quality food resource, then we would expect to see increased herbivory damage in these areas, which could tend to homogenize bamboo densities across the stand. Alternatively, if herbivores prefer low density patches, they could amplify spatial variance in bamboo density. We found no relationship between shoot density and herbivore damage. However, herbivore damage was correlated with light availability, perhaps because fast-growing plants in high light areas have more nutritious young leaves than plants in low light areas. Monospecific, even-aged stands of bamboo may be surprisingly heterogeneous in ways that influence consumers and even predators of consumers.

Key Words: Chusquea tonduzii, *conspecific density, PAR*

Introduction

Plant populations can experience patterns of herbivory ranging from highly aggregated to uniformly distributed. These patterns may be affected by the nutritional quality of the plant, heterogeneity in predation risk and/or herbivore movement patterns. Spatial patterns of herbivory may be related to plant density. Plants that are in aggregations may be easily located, offer refuge from predators or potentially be more nutritious if resource competition limits energy available for anti-herbivore defense. In this scenario, herbivores tend to increase plant mortality the most in high-density patches, which would tend to homogenize plant density patterns. Alternatively, herbivores may be concentrated in patches of low host density, which would tend to increase spatial heterogeneity of plant density.

We tested for spatial patterns in herbivory by sampling bamboo shoots of a high altitude forest in Costa Rica. These high altitude forests are characterized by an oak canopy and a dense bamboo understory. The bamboo is semelparous with synchronous reproduction of stands every 25 to 30 years, creating large even-aged stands (Carlos Solano, pers. comm.). As a natural system with low plant diversity and high vegetative cover, these bamboo stands lend themselves particularly well to studies of herbivory patterns because both variation in species distribution and confounding biotic interactions are minimized. Herbivores have the potential to influence plant development within these stands without interference from interspecific plant competition. Because these bamboo stands are nearly monospecific, they could be especially susceptible to herbivory (Maynard Smith 1974), in part because herbivores would have little need for far-ranging movements.

Methods

On 26 - 27 January 2002, we surveyed a bamboo stand underneath a canopy dominated by two oak species, *Quercus costaricesis* and *Quercus copeyensis*. The site was located near La Estación Biológica Cuericí, San Jose Province, Costa Rica at an elevation of 2894 m. We identified the bamboo as *Chusquea tonduzii* based on descriptions by D. H. Janzen (1983). All shoots in the area were the same age, as they were part of a mass germination in 1991 (following synchronous reproduction and death of the previous cohort, Carlos Solano, pers. comm.).

Twenty bamboo shoots were surveyed during the study. Shoots were chosen haphazardly so that none was closer than 10 m to any other. For each shoot, we recorded the height (from the ground to the highest point of the stem) and the length of the stem. Note that height above ground was frequently much less than length because most stems had not grown vertically. We also used a quantum sensor to measure photosynthetically active radiation (PAR) at 5 points around the top of each stem (~0.5 m from the stem). All PAR measurements were recorded within a 15 min period of relatively even cloud cover that produced a diffuse light regime in the understory. We measured PAR at 3 of the 20 plants twice, once during our initial measurements around the 20 plants, and then a second time immediately following completion of initial measurements. Replicate measurements of these 3 plants were nearly identical to initial measurements (± <5%). We also recorded the number of conspecifics within a 2 m radius of each focal shoot as a measure of plant density.

Herbivore damage was classified as scrapes, cuts or punctures. Scrapes were 1 - 2 cm long strips where mesophyll had been removed (apparently by an herbivore feeding from the upper leaf surface) but the lower epidermis was still largely intact. Cuts were round or angled interruptions in leaf edges (usually interruptions of 1 - 2 cm on leaf margins). Punctures were small (<1 mm) holes poked into the mesophyll. Herbivore damage of each shoot was estimated by examining 1 - 2 of the compound blades originating from each node. For each blade, we recorded the presence or absence of each type of herbivore damage. For each shoot, we then calculated the proportion of blades that suffered each type of herbivore damage.

In our analyses, we grouped herbivore damage into two classes representing large herbivorous invertebrates (cuts and punctures) and small herbivorous invertebrates (scraping). The rationale was that cuts and punctures are likely caused by larger animals that are presumably more mobile and might therefore exhibit different spatial patterns in their abundance and feeding damage. We then tested for correlations among plants between herbivory damage and environmental variables (PAR and plant density).

Results

All bamboo plants had at least some herbivore damage on the leaves. However, we did not observe any herbivores actively feeding on bamboo during the course of our study. The most common damage was scraping (Table 1). Ten to hundreds of small mites were present on the underside of many bamboo leaves and we suspect that they caused this scraping damage. Cuts and punctures were rare in comparison to scraping damage. Both cuts and punctures were consistent with damage caused by large mobile herbivorous insects such as grasshoppers and katydids, which are often nocturnal. Overall, levels of herbivore damage to bamboo appeared quite low. We estimate that <10% of the photosynthetic tissue was damaged on the most damaged plant in our sample.

TABLE 1. Summary of feeding damage on 20 bamboo plants in montane forest near Cerro de la Muerte, Costa Rica.

	Number of Plants	Proportion of leaves per plant in affected plants			
		Mean	SD	Min	Max
Scrapes	20	0.65	0.26	0.18	0.97
Cuts	11	0.10	0.07	0.03	0.24
Punctures	7	0.07	0.05	0.03	0.14

TABLE 2. Correlations across 20 bamboo plants (1 plant = 1 shoot) between measures of plant size, local density of conspecifics, herbivory and photosynthetically active radiation (PAR).

Variable	Shoot Height	Shoot Length	Shoot Density[a]	Scrapes[b]	Cuts and punctures[b]	PAR[c]
Shoot Height	1.000	-	-	-	-	-
Shoot Length	0.700***	1.000	-	-	-	-
Shoot Density	0.045	-0.149	1.000	-	-	-
Scrapes	-0.101	-0.320	-0.002	1.000	-	-
Cuts & Punctures	0.523*	0.282	0.083	0.317	1.000	-
PAR	0.638**	0.173	0.286	0.170	0.625**	1.000

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$
[a]shoots/12.6 m^2
[b]proportion of leaves per plant with damage
[c]mMoles• m^{-2}• s^{-1}

Bamboo stems were 1.2 – 4.1 m long and 1.2 - 3.4 m tall, while stem density ranged from 8.8 – 125.7 shoots/12.6 m^2. Average length, height and density of our study shoots were (mean ± SD): length = 2.51 ± 0.92 m, height = 2.00 ± 0.54 m, and density = 52.1 ± 30.1 stems/12.6 m^2. PAR was generally low around the top of bamboo shoots, but was variable among plants: 23.42 ± 24.79 μmoles•m^2•s^{-1}.

Not surprisingly, there were positive correlations between shoot height, shoot length and photosynthetically active radiation. However, there were also correlations with cut and puncture damage from herbivores. The proportion of leaves with cuts and punctures was greater in tall plants that were experiencing relatively high light. Scraping damage was not correlated with any other measured variable (Table 2).

Discussion

Our hypothesis that herbivore damage is proportional to bamboo stem density was not supported. Neither scraping damage (from small herbivores) nor cuts and punctures were correlated with conspecific density. Apparently there is no tendency for herbivores to homogenize the local density of bamboo plants by feeding preferentially in areas of high plant density or to increase the variance in local density of bamboo by feeding preferentially in areas of low density.

The frequency of cuts and punctures was correlated with photosynthetically active radiation, suggesting that bamboo that receives more light is preferred by herbivores. Tropical herbivores often feed preferentially on younger leaves because of their relatively high nitrogen content and low toughness (Coley and Kursar 1988). If height from the ground is an accurate measure of growth, the positive correlation between PAR and stem height indicates that bamboo has higher growth rates in patches with more sunlight. Presumably, stems growing at higher rates tend to bear more young, nutritious leaf tissue. Future research might employ leaf tissue feeding trials to test whether herbivores exhibit preferences for young leaves and/or fast growing bamboo plants. One problem with this hypothesis is that shoot length, which is a better measure of plant growth, was not correlated with herbivory.

An alternative hypothesis is that herbivores prefer to feed in the sun (perhaps because basking increases development rate). A problem with this hypothesis is that some herbivores causing cut and puncture damage are probably nocturnal. Future research might examine herbivore feeding activity times on

bamboo or the rate of larval development in high light areas.

It makes sense that cut and puncture damage was more obviously correlated with environmental parameters if these herbivores are relatively large and mobile. If stems exposed to more sunlight are a better resource patch for herbivores, one would expect mobile herbivores to concentrate their foraging there. Conversely, the mites thought to be causing the scraping herbivory probably lack the ability for directed movements through the stand. The random distribution of the mites across the bamboo stands may be a consequence of their dispersal mechanism, perhaps by the wind.

Regardless of its cause, nonrandom patterns of invertebrate distributions have consequences for their predators. For example, these bamboo stands are important habitat for the large-footed finch, *Pezopetes capitalis*, which forages for invertebrates by kicking up leaves on the forest floor. It could be hypothesized that large-footed finches forage preferentially in the vicinity of high light patches because there is a high abundance of orthopteran insects hiding in the litter there. Light gaps in high altitude oak forests could potentially influence spatial patterns in the abundance of species at several different trophic levels (e.g., bamboo, orthopterans and large-footed finches).

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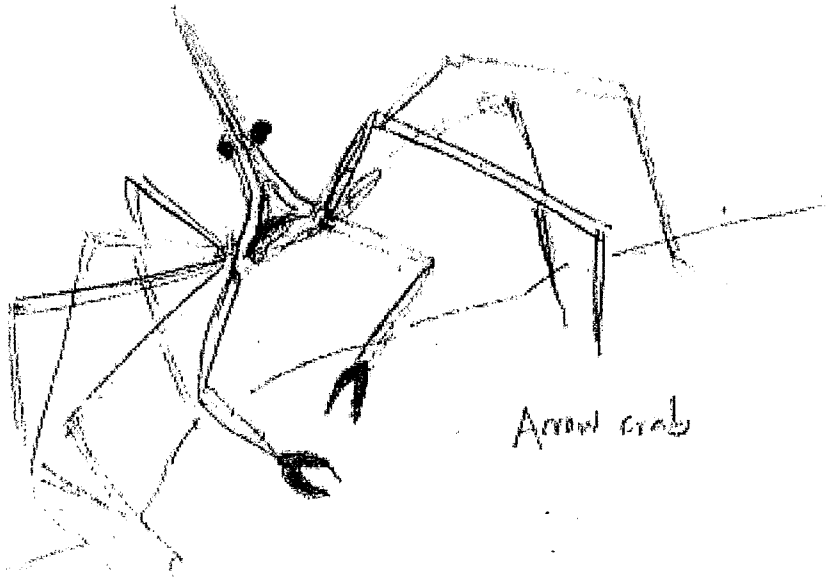
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