Regeneration in highland tropical oak forest gaps

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Abstract: Oak forests in the Talamanca Range of Costa Rica have been under heavy anthropogenic pressure for the past century. They have been converted to pasture and felled for charcoal. The successional dynamics of these forests are poorly understood, and little is known about the relationship between the bamboo understory and oak canopy regeneration. We hypothesized that the presence of bamboo, which colonizes both understory and gaps, and grows especially fast in gaps, would inhibit the establishment and survival of slow-growing oak seedlings. We found that areas of low canopy cover were densely covered with bamboo, and therefore had few oak seedlings. A better understanding of the interactions between these species might lead to more effective forestry practices for the preservation and management of the remaining fragments of this endangered community type.

Key Words: bamboo, masting, Quercus copeyensis, Quercus costarincensis, *succession,* Swallenchola subtessella

Introduction

The clearing of forests for agriculture, farming and lumber harvest has affected many tropical ecosystems worldwide. Once-expansive forests have been fragmented and surrounded by pasture and cropland. As land is preserved and efforts are made to restore these forests, it is imperative that we understand the processes involved in tree regeneration in the understory and in forest gaps and edges.

Forests dominated by *Quercus costarincensis* and *Quercus copeyensis* were once prevalent in the Costa Rican highlands. Over the last century, these forests have been rapidly harvested as a source of charcoal (Burger 1983). Little is known about their regenerative dynamics. Oaks grow slowly and produce massive crops of acorns at 2 – 7 year intervals. Masting may be an effort to overwhelm seed predators (Burger 1983). In addition to oak, bamboo (*Swallenchola subtessella*) is prevalent in many of these forests (Hartshorn 1983). Bamboo thrives on the edges of forests and in newly formed gaps, but is also found under the canopy. While bamboo propagates vegetatively, it also reproduces sexually at 15-year intervals, when populations flower, seed, and then die synchronously. It has exponentially fast vegetative growth and quickly colonizes disturbed areas (Janzen 1983).

It has been suggested that dominance by bamboo in gaps and in the shrub layer of oak stands may inhibit oak regeneration (Hartshorn 1983). Forest fragmentation, which increases gap and edge habitats, may favor bamboo over oak. We hypothesized that gaps, defined as areas with recently fallen canopy trees, increase bamboo density and bamboo cover, which in turn reduces oak seedling recruitment. We predicted was that oak seedlings would be less abundant in areas with higher bamboo density, and that areas of lower canopy cover would have higher bamboo density and lower oak seedling density.

Methods

We conducted our study between 2600 and 3000 m elevation at Cuerici Biological Station, Cerro de la Muerte, San Jose Province, Costa Rica. We chose five transects that appeared typical of oak forest in the preserve. At 20 m intervals along each transect, for a total of 25 sample points, we counted the number of bamboo shoots in one 4 m^2 quadrat and measured the diameter at ground level of 10 random shoots. Basal area of bamboo shoots, used as a measurement of bamboo density in the plot, was determined by calculating the average basal area of the ten sampled shoots, and

multiplying that by the number of total shoots counted in the quadrat. Canopy cover was estimated after the bamboo had been gently brushed aside. In one 25 m^2 quadrat centered at the same point, we counted the number of oak saplings and estimated canopy cover with a spherical densiometer.

We used nonparametric Spearman's rank correlation to assess the relation between bamboo basal area and oak sapling density, percent canopy cover and bamboo basal area, and number of oak saplings and percent canopy cover.

Results

Fewer oak seedlings were present in areas with higher bamboo density (Fig. 1; Spearman Rho = - 0.72, $P < 0.001$). Higher bamboo density was positively correlated with lower percent canopy cover (Spearman Rho = - 0.70, $P < 0.001$). The data further suggest that oak seedling recruitment occurs only when canopy cover is relatively high (Fig. 2). Oak seedling density increased with canopy cover (Spearman Rho = 0.74, $P < 0.001$).

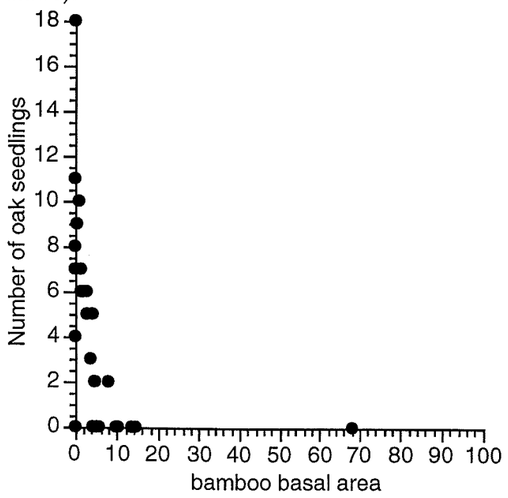

FIG. 1. Relationship between bamboo basal area and number of oak seedlings at Cerro de la Muerte, Costa Rica. Basal areas represent means of 10 randomly chosen stems (n = 25).

Discussion

We found that oak seedling recruitment was influenced by gaps in a process mediated by bamboo. In accordance with our first prediction, higher bamboo density led to lower oak seedling recruitment (Fig. 1). Density of bamboo stands was highest in gaps, where oak seedling recruitment was decreased (Fig. 2). These results support our prediction that gaps tend to decrease oak seedling recruitment by increasing bamboo cover.

Bamboo is an effective gap colonizer because it can expand its cover in newly opened gaps with rapid vegetative growth as well as with seeds (in reproductive years) and advance regeneration (from past reproductive events). Oak cannot expand laterally with vegetative growth or exploit high- light environments to the same degree. It is a slow growing, late-successional species capable of reproducing in low-light, canopy-covered habitats.

Edge and gap habitats favor early successional species. Fragmentation of forests increases the proportion of high light

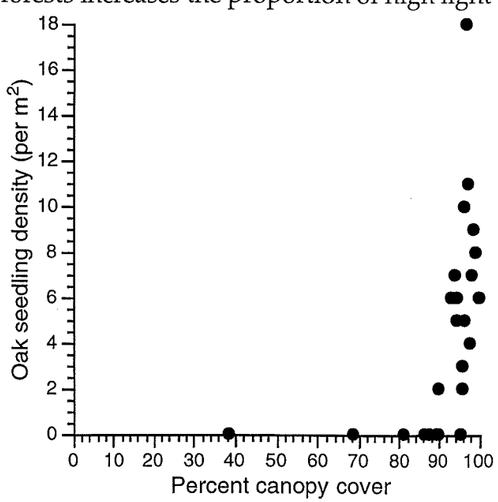

FIG. 2. Relationship between percent canopy cover and number of oak seedlings at Cerro de la Muerte, Costa Rica (n = 25).

habitats beneficial to gap colonizers. Even selective logging creates large gaps, which favor bamboo over oak.

Oak and bamboo rely on different successional niches. They interact in their use (and effects on) light resources in a cascading fashion from the oak canopy to the bamboo understory and finally to the ground level where oak seedlings are recruited. Their periodic, synchronized reproductive strategies further complicate how these species affect each other's survival and reproduction. Further study is warranted to better understand the effect of these periodic reproductive events on oak and bamboo seedling recruitment.

The survival of these forests depends on the maintenance of the natural, wind-generated disturbance regime, without additional canopy disturbance by human activities. By favoring early successional bamboo, additional disturbance and habitat fragmentation puts these vanishing oak forests at risk of total extirpation.

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