abundance and sugar concentration, and pollinator visits. It would be interesting to examine mite dispersal patterns under realistic conditions to see if this pattern persists.

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DISTRIBUTION AND ABUNDANCE OF LIANAS IN PRIMARY AND SECONDARY FORESTS AT CERRO DE LA MUERTE

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Abstract: To evaluate the effect of forest structure on liana distribution and abundance, we compared the abundance and cross-sectional area at breast height of lianas between primary forest and secondary montane forests. Primary forest had a higher density of lianas and trees than secondary forest. The mean cross-sectional area of each liana and the number of lianas per tree were not significantly different for the two forest types. The number of lianas per tree was positively related to tree cross-sectional area, possibly because larger trees provide more surface area upon which lianas can climb. Lianas likely colonize and attain greater canopy cover in primary forests than secondary forests, though the species of lianas in each forest type may differ.

Key Words: cross-sectional area, montane forest, structural parasite

INTRODUCTION

Lianas are an important component of tropical forest structure, contributing significantly to total leaf production, woody biomass, and species diversity (Bullock 1990). As photosynthetic structural parasites on trees, liana success is affected by forest structure. Previous work by Laurance (2001) showed that liana abundance was greater near forest edges and in disturbed areas and decreased with tree biomass (Laurance 2001).

Over time, forest structure develops and changes through successional processes. To test changes in liana community with changing forest structure, we examined the difference in liana abundance and size between primary and secondary montane forests in the Talamanca Range, Costa Rica. Similar to disturbed areas, secondary forests have higher light availability and a greater height-stratified network of small branches and stems than primary forests

(Begon et al. 1990). The lack of structural variability and light, characteristic of primary forests, may limit lianas in these environments. For these reasons, we predicted that secondary forests would have greater numbers of lianas and larger lianas, as measured by total liana cross-sectional area at breast height, than would primary forests.

METHODS

We selected six 10 m x 10 m plots, three in primary forest and three in the adjacent secondary forest along the western part of the lookout loop trail north of the Estacion Biologica Cuerici at Cerro de la Muerte, Costa Rica. Primary forest plots were located approximately half way between the Estacion Biologica Cuerici and the Mirador in old growth forest. Secondary forest plots were located adjacent to the Estacion Biologica Cuerici in an area disturbed by farming approximately 50 years ago (Bellow and Piluk 1998). We quantified abundance and diameter at breast height (DBH) of all trees and lianas in each plot. Diameter at breast height was used to calculate cross-sectional area of trees and lianas. We also noted whether each liana was associated (in contact) with a tree at breast height.

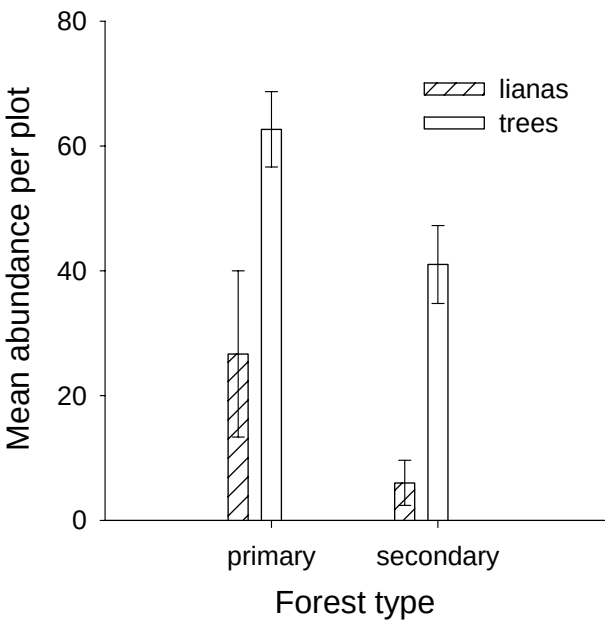

Figure 1. Mean abundance (± 1 SE) of lianas and trees in 10 m x 10 m plot in primary and secondary forests. Primary forest had a greater abundance of lianas and trees (analysis performed on ln transformed data; see text).

Abundance and cross-sectional area at breast height of trees and lianas were compared between forest types using one-way ANOVAs. Because our sample size was small, we were unable to evaluate the assumptions of normality and homogeneity of variances. As a conservative approach, we transformed the data using natural log. Because we had a balanced experimental design we felt justified in using parametric tests (Box 1954). A linear regression was used to examine the relationship between the number of lianas per tree and tree DBH. All analyses were performed using JMP 5.0.1.

RESULTS

More lianas and trees occurred in primary forest than secondary forest ($F = 9.23$, $df = 1, 4$, $P = 0.04$; $F = 17.99$, $df = 1, 4$, $P = 0.01$, respectively; Fig. 1). Total cross-sectional area of lianas at breast height was greater in primary forest (mean ± SE, 92.2 ± 17.7 cm^2) than in secondary forest plots (18.9 ± 17.7 cm^2; $F = 11.10$, $df = 1, 4$, $P = 0.03$). The same result was found for total tree cross-sectional area at breast height

(3.35 ± 1.16 m^2 and 0.24 ± 1.16 m^2, respectively; F = 8.68, df = 1, 4, P = 0.04). Mean tree cross-sectional area was marginally greater in primary forest plots than secondary forest plots, 563.5 ± 207.4 cm^2 and 60.1 ± 207.4 cm^2 respectively (F = 4.98, df = 1, 4, P = 0.09). The number of lianas per tree increased with tree diameter in primary forests plots (r^2 = 0.41, df = 22, P = 0.0008), but the relationship did not exist in the secondary forest plots because no tree was host to more than one liana (Fig. 2).

There was no difference between mean cross-sectional area of each liana in primary forest (4.0 ± 0.86 cm^2) and secondary forest plots (2.9 ± 0.86 cm^2; F = 0.50, df = 1, 4; P = 0.52). Likewise, the ratio of total liana cross-sectional area to total tree cross-sectional area was not different between forest types (0.0060 ± 0.0029 and 0.0069 ± 0.0029, respectively; F = 2.98, df = 1, 4, P = 0.16).

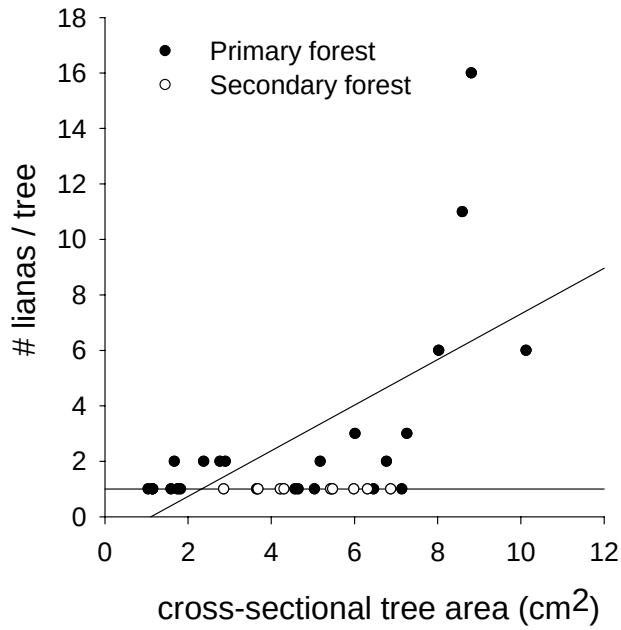

Figure 2. Number of lianas per tree by tree cross-sectional area at breast height in primary and secondary forest. Primary forest had a greater range of tree cross-sectional areas at breast height. The number of lianas per tree was positively related to the tree cross-sectional at breast height in primary forest (y = 0.82x - 0.91). No relationship existed for the secondary forest data. No trees in the secondary forest had more than one liana (tree cross-sectional area ranged from 17.3 to 962.1 cm^2). Line through secondary forest data (open dots) shows mean number of lianas per tree. The slope of the relationship was not significantly different from zero.more than one liana (tree cross-sectional area ranged from 17.3 to 962.1 cm^2). Line through secondary forest data (open dots) shows mean number of lianas per tree. The slope of the relationship was not significantly different from zero.

Discussion

We found that the primary forest had more trees and supported more lianas than the secondary forest. Our prediction that a secondary forest would have more lianas than a primary forest was based on the probably false assumption that a secondary forest would have a greater density of small branches and trees than a primary forest that would provide physical support for young lianas.

We did not measure the canopy cover of lianas or trees. This information is necessary to definitively compare the structural advantage (ratio of leaf biomass to woody biomass) of lianas over trees between primary and secondary forests. However, liana leaf biomass can be inferred based on the cross-sectional area of each liana, with lianas of greater cross-sectional area having more leaves. The mean total cross-sectional area of lianas was higher in primary forest, implying that the primary forest probably had more liana canopy cover than the secondary forest. Further, because lianas are structural para-

sites, their investment in woody biomass per unit area leaf is relatively smaller than for trees. It follows that as a tree grows larger, the ratio of liana cross-sectional area to that of the tree would decrease even if the ratio of canopy cover between the liana and tree remained constant. The ratio of total liana cross-sectional area to that of trees did not differ between the primary and secondary forests we studied. Thus, canopy cover due to lianas is probably proportionally greater in primary forests than secondary forests than implied by liana cross-sectional area alone.

There were no trees in the secondary forest supporting more than one liana at breast height. In the primary forest, the number of lianas per tree, ranging from 1 to 16, was positively related to tree cross-sectional area, possibly because larger trees have more surface area for the lianas to colonize.

Mean area per liana did not change between primary and secondary forests, likely due to the prevalence of small lianas in both forest types. Their presence implies that lianas are able to colonize in primary forests as readily as secondary forests, which we predicted would be difficult in the poorly lit understory. Primary forests may not have low light levels, as we assumed, or lianas may not be strongly affected by the variation in light conditions between primary and secondary forests.

Though we collected no quantitative data on the species of lianas in our primary and secondary forest plots, there appeared to be no overlap between forest types. It is possible that different liana species that require different environmental conditions are colonizing the different forests. Studying the distribution of liana species will be a key to understanding how forest succession changes liana communities.

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