DISTRIBUTION OF *BURSERA SIMARUBA* OVER THREE HABITATS OF VARYING MOISTURE AVAILABILITY

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Abstract. *Bursera simaruba* is one of the trees with photosynthetic bark common in the Palo Verde dry forest. Trees with photosynthetic bark have the advantage of being able to photosynthesize even after shedding their leaves in effort to conserve moisture. As this adaptation would be most beneficial in areas of high moisture stress, we tested whether the relative density of *B. simaruba* is greater in a dryer habitat than in a wet one. We found that both the number and the relative densities of *B. simaruba* were significantly higher in the drier habitat.

INTRODUCTION

Many species of trees in the Palo Verde dry forest area have photosynthetic bark, including many of those in the families *Burseraceae, Bombacaceae,* and *Fabaceae.* Most of these tree species are deciduous, shedding their leaves during the dry season between November and May. Because this trait has evolved separately in at least three different families of tropical trees, there must be an adaptive advantage to photosynthetic bark in this dry forest habitat. During the dry season, many trees conserve water by shedding their leaves to reduce the surface area for evaporation. As a consequence, most of these trees are unable to photosynthesize during the dry season. However, trees with photosynthetic bark, may continue to photosynthesize on a smaller scale.

In Costa Rica, *Bursera simaruba* is mostly found in dry forests. It has photosynthetic bark and is one of the most common trees in Palo Verde National Wildlife Refuge. We hypothesized that if photosynthetic bark is an adaptation to dry habitats, *B. simaruba* would be found in proportionately higher densities in relatively more dry compared to wetter habitats within tropical decidous forests.

METHODS

We sampled *Bursera simaruba* in three different habitats of varying soil moisture in Palo Verde National Wildlife Refuge, Costa Rica: i) along the slope of a hill, ii) on two rocky peaks, and iii) in the saddle between the two peaks. The rocky peaks, defined as the habitat, were composed of steep, exposed limestone, and retain very little water from rainfall. The saddle was relatively flat, and receives much of the runoff rainwater accumulated in the base between the two peak areas which makes it a more moist habitat. The slope between the rocky peaks and saddle is able to retain some rainwater in the soils, but loses some as it washes down the hill. Therefore, we considered the slope is to have an intermediate level of moisture.

On 13 January 1995, we surveyed the Sendero Cerro Calizos trail from the biological station up to the Mirador Guayacan, down through the saddle and up the Mirador del Cactus. All *B. simaruba* within a 10 m transect on both sides of the trail were counted. Total tree density in each of the three habitats was estimated by a series of three 10 m^2 density sub-plots per habitat. The sub-plots were chosen at random within the transect of each habitat. The mean of the three sub-plot densities in each habitat was used as the total tree density for each habitat.

RESULTS

We found the density of *Bursera simaruba* was highest on the peak, intermediate in the slope, and lowest in the saddle (Table 1) with no significant difference in total tree density among the three habitats (F=0.821, df=2,24, P=0.5). The proportion of *B. simaruba* density to the overall tree density in our sample plots differed significantly among the three habitats (G=57.56, df=2, P<0.001; Fig. 1). The proportion of *B. simaruba* was largest on the rocky peak (0.066), intermediate in the saddle (0.017), and lowest in the saddle (0.005).

TABLE 1. Density of *Bursera simaruba* and of total trees in each habitat

Habitat	Density of *B. simaruba* per $100m^2$	Mean density of total trees per $100m^2$ (±SE)
Saddle	0.06	11.33 (±5.03)
Slope	0.27	15.67 (±9.16)
Peak	1.16	17.67 (±1.53)

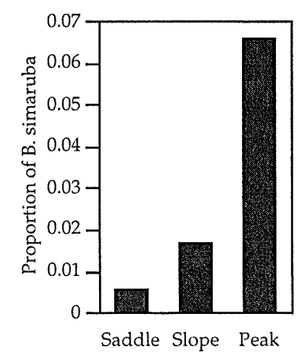

FIG. 1. Proportion of *Bursera simaruba* in three different habitats: saddle, slope, and peak.

DISCUSSION

The proportion of *Bursera simaruba* in the forest decreased along a moisture gradient within the tropical dry forest. One possible explanation for this is its photosynthetic bark. By allowing photosynthesis to continue even during leaf loss periods, photosynthetic bark may provide a competitive advantage to *B. simaruba* in the driest habitats. In addition, because many other species are also deciduous in the dry season, the canopy is much more open than during the wet season when trees leaf out. *B. simaruba's* bark will be exposed to high light in the dry season, enabling it to photosynthesize more efficiently than other trees without photosynthetic bark.

In contrast, *B. simaruba* was less abundant in the saddle, suggesting that it is less competitive in moist habitats. Water stress is less likely in the moister saddle, therefore, deciduous species may lose fewer leaves resulting in a dense canopy. Hence, the bark of *B. simaruba* receives less light than in the peak habitat. The abundance of lianas, understory vegetation, and leaves retained by other species in the saddle during the dry season may also compound the low light situation. *B. simaruba* loses its leaves very early in the dry season, so for a relatively long period of time it is unable to photosynthesize using its leaves, and its bark may be shaded. Other trees that shed their leaves later in the season are able to produce energy over a longer period of time throughout the year, and may surpass *B. simaruba's* levels of growth and reproduction.

It is possible that the success of *B. simaruba* in the dryer habitats is due to some factors besides photosynthetic bark. For example, *B. simaruba* may produce seeds that germinate more successfully in dryer environments. Although we did not study any other species with photosynthetic bark, we noticed that *Ceiba pentandra* was absent from both the peak and the slope. The only place we did notice any *C. pentandra* was in the saddle, the moister habitat. Further research should study whether *C. pentandra* and other photosynthetic trees are also found in proportionally different densities over a moisture gradient. In addition, the specific adaptations of the *B. simaruba* to dry habitats need to be more clearly defined. It appears that *B. simaruba* is present in higher densities in the dryer habitat; more research needs to be done to find out why.