jacanas in site 3 also foraged at lower rates, suggesting lower food abundance than in other habitats. Thus an open water site with only scattered water-lilies appears to be poor Jacana habitat. Reduced rates of aggression in this site may be a consequence of increased territory size (and therefore reduced interactions) in resource poor habitats.

Sites 1 and 2 differed in the composition but not extent of vegetative cover. Sites 1 and 2 had higher densities of jacanas, and higher foraging rates, than the open water site and appear to represent better jacana habitat. Among these, the mimosa habitat (site 2)Interestingly site 2 had more aggressive interactions among jacanas than the grass-sedge site (site 1), perhaps because of higher "effective densities" (Jackson and Kopplin, 1996) in the mimosa site. Both vegetation and jacanas appeared to be relatively clumped within the mimosa site compared to the grass-sedge site.

Across sites, aggression rates were higher in the early morning than late morning, perhaps because jacanas reassert territories or compete for more valued sites or resources earlier in the morning. While rates of foraging did not differ significantly with time of day, we only measured foraging in morning sessions so we cannot predict how foraging rates might vary across the whole day. Jackson and Kopplin (1996) found that foraging rates varied significantly over the course of the day, and were highest in mid afternoon. It is also questionable to what extent foraging rate is a good measure of prey availability, as a jacana in a resource-poor environment may forage at a greater rate to compensate for the scarcity of prey. Another weakness of our study was the lack of replication of habitat patches within habitat types. Our understanding of jacanas would benefit from studies that include direct measures of prey availability, replication of sites, and the use of marked birds of known sex.

## LITERATURE CITED

Cook, S. P., H. A. Dunn, K. K. Ingram, and M. B. Royer. 1993. The effect of macrophyte vegetation and water depth on the distribution of pond snails. Pp. 32-34 *in* T. S. Bansak and M. Seandel, eds. Dartmouth Studies in Tropical Ecology.

Jackson, C. D. R., and S. E. Kopplin. 1996. Behavior of *Jacana spinosa* as a function of neighboring density. Pp. 25-27 *in* A. L. Mannan and D. S. Canny, eds. Dartmouth Studies in Tropical Ecology.

Jenni, D. A. 1983. *Jacana spinosa* (Jacana Centroamericana, Mulita, Cirujano, Gallito de Agua, Northern Jacana). Pp. 584-586 *in* D. H. Janzen, ed. Costa Rican Natural History. University of Chicago Press, Chicago.





# EFFECTS OF SOIL MOISTURE AND IRRADIANCE ON DISTRIBUTION OF *BURSERA SIMARUBA*

MATTHEW J. UNGERER AND ANA I. BAPTISTA

*Abstract.* Trees with photosynthetic bark can conserve water in the dry season by shedding their leaves while continuing to photosynthesize. This adaptation may be more beneficial in areas of high irradiance. We hypothesized that the density of *Bursera simaruba*, a tree with photosynthetic bark, would be highest in water-stressed areas with high solar irradiance. We measured soil moisture, irradiance, and number of *B simaruba* across three subplots on a south slope, a north slope and a flat area. South-sloped sites had higher irradiance, lower soil moisture and higher *B. simaruba* density. *B simaruba* may have a competitive advantage in areas of high irradiance and low moisture.

*Key words: aspect, gumbo limbo, photosynthetic bark, slope*

## INTRODUCTION

The gumbo limbo (*Bursera simaruba*) is a deciduous tree with distinctive orange, flaky bark (Stephens 1983). *B. simaruba*, like many trees of the tropical dry forest, shed their leaves during the dry season to conserve water. Unlike most deciduous trees *B. simaruba* continues to photosynthesize via its bark. The bark of *B. simaruba* may be an adaptation to dry, sunny habitats (Osterling and Barnhorst 1995). If so, *B. simaruba* may be relatively more abundant on south-facing aspects. We tested this by comparing the local density of *B. simaruba* to irradiance and soil moisture across sites ranging from a southern aspect to a northern aspect.

## METHODS

We subsampled three different sites near the OTS field station in Palo Verde National Park, Guanacaste, Costa Rica. Three 400 $m^2$ subplots were established along east-west transects on: 1) a north facing slope, 2) a south facing slope (both at an altitude of 60 m on the Sendero Cerros Calizos trail) and 3) a flat area along the Sendero Natural de Venada. The south-slope and north-slope sites were sampled on consecutive days between 08:30 and 10:30. The flat site was sampled at 13:00 on the first sampling day. Irradiance was measured every 2 m along the edge of each subplot using a digital light meter. Water availability at each site was estimated with two soil samples per subplot. Fresh weights of these samples were recorded before air-drying to constant weight and reweighing. Measurements of irradiance and soil moisture were averaged to yield one vale for each subplot. The number of *B. simaruba* > 3 m tall were counted within each subplot.

Measurements of irradiance, soil moisture and *B. simaruba* density were log-transformed to equalize variance across treatments. We tested for differences among sites in irradiance, soil moisture and *B. simaruba* density with a one-way ANOVA and used correlations analysis to test for relationships between irradiance, soil moisture and *B. simaruba* density.

## RESULTS

Irradiance differed significantly among sites ($F_{2, 6} = 166.61$, $P < 0.0001$) decreasing from the south-slope to the flat site to the north-slope (Fig. 1a). Soil moisture was marginally lower on the south-slope than on the other sites ($F_{2, 6} = 4.59$, $P = 0.062$; Fig. 1b). *B. simaruba* density was ≈ 10-fold higher on the south-slope than on the other two sites ($F_{2, 6} = 10.05$, $P = 0.012$ (Fig. 1c).

TABLE 1: Correlations among % soil moisture, mean irradiance and *B. simaruba* density (n = 9 subplots).

| | *B. simaruba* density | % soil moisture |
|---|---|---|
| % Soil moisture | r = -0.497<br>P = 0.17 | • |
| mean irradiance (μA) | r = 0.72<br>P = 0.027 | r = -0.605 P = 0.084 |

*B. simaruba* density was positively correlated with irradiance, but negatively correlated with soil moisture (Table 1). Soil moisture and irradiance among the three sites were also negatively correlated (Table 1).

## DISCUSSION

Our results support the hypothesis that *B. simaruba* is more abundant in areas of high irradiance. In nature, irradience and soil moisture tend to covary. Thus, the south facing slopes on which *B. simaruba* was most abundant tended to be both sunny and dry. The increased abundance of *B. simaruba* on southerly aspects could be directly attributable to the positive effects of high sunlight, but it could also be that the competitive ability of *B. simaruba* is enhanced in areas of water stress. Most tree species in sunlit areas were deciduous and had lost their leaves. Without the benefit of photosynthetic bark these trees may incur a greater carbon debt during the dry season and accomplish less annual growth than *B. simaruba* . Conversely, the competitive ability of *B. simaruba* may be reduced in less water-stressed areas. Comparing tree growth rates across sites with different slope and aspect (e.g., between the limestone hills at Palo Verde) is one way to test this hypothesis.

Because all sites were not tested at the same time of day it is possible that some of the inter-site variation in irradiance was due to the sampling time. We suggest that similar studies in the future measure irradiance at the same time in each site.

## LITERATURE CITED

Osterling, W.L., and A. V. Barnhorst, 1995. Distribution of *Bursera simaruba* over three habitats of varying moisture availability. Pages 25-26 *in* C. D. Wray and N. D. Pouliot, editors. Dartmouth Studies in Tropical Ecology.

Stevens, G. 1983. *Bursera simaruba* (Indio Desnudo, Jiñocuave, Gumbo Limbo). Pages 201-202 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago, Illinois, USA.

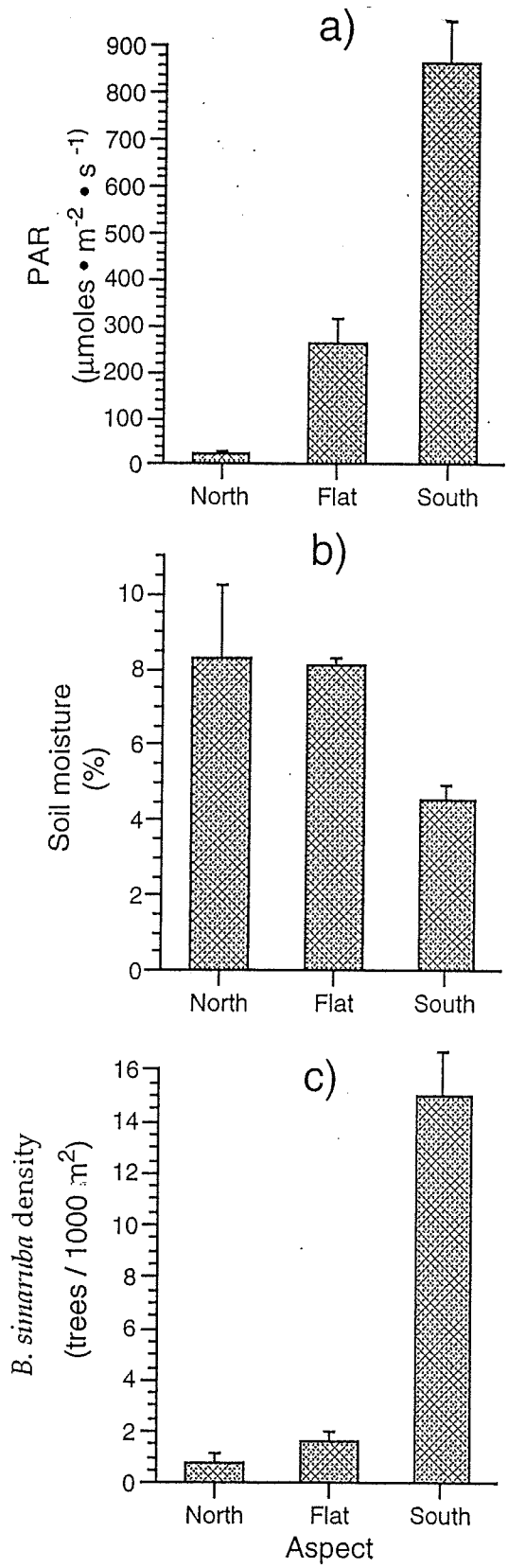


FIG. 1. Mean (±1SE) of a) photosynthetically active radiation b) soil moisture c) *B. simaruba* density.