fitness than trees with litter, then, by creating a more favorable environment for the tree, the ants create a more hostile environment for themselves by maintaining habitat for the ant lions, one of their predators.

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EPIPHYTE ABUNDANCE AND DISTRIBUTION IN CANOPY TREES OF VARYING BARK MORPHOLOGY

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Abstract. We studied the distribution and abundance of epiphytes in relation to bark characteristics of trees in a tropical dry forest in Costa Rica. We found significantly more epiphytes on rough barked trees than on smooth barked trees. Of these epiphytes, bromeliads dominated the crotches of rough barked trees while orchids were more abundant on the straight sections of the central branches where there were few leaves and deep crotches. Because not all trees with rough bark had epiphytes, we assume that other mechanisms must also be involved in epiphyte-tree interactions. If epiphytes lead to a reduction of tree fitness, trees should exhibit various strategies to prevent colonization by epiphytes. (CNO)

INTRODUCTION (SAW)

Epiphytes are commonly found on trees of many species in the tropics. Bromeliads and orchids, two commonly epiphytic plant types, utilize trees with varying bark textures. A tree with rough bark offers many exploitable surfaces, including deep grooves and crevices or large crotches where debris tends to collect. Colonizing a smooth bark tree is probably more difficult, perhaps due to a lack of such grooves and crevices; furthermore, wind may displace most small epiphytes attempting colonization. With the effect of bark type on epiphyte colonization in mind, we hypothesized that more epiphytes would occur on rough-barked trees than on those with smooth bark.

METHODS (SAW)

Trees along the main road and the Sendero la Verda at the OTS Palo Verde field site were censused on 10 January 1992. The bark of all trees was categorized as smooth (uniform bark, no striations, absence of crevices), medium (some striations, few cracks and crevices, slight peeling but not uniformly), or rough (deep crevices, long grooves, heavy peeling). All canopy trees greater than 15m in height were scanned for epiphyte density and location. One of four tree locations was assigned to each visible epiphyte. The main stem area was termed "middle tree", subdivided into middle crotch (m+) and middle periphery (m-), which is a non-crotched area. Similarly, the outer brances of the tree were designated as either periphery/crotched areas (p+) or periphery/non-crotched areas (p-).

RESULTS (TCB)

Of 190 canopy trees studied, 52 had been colonized by epiphytic species of bromeliad and/or orchid (Table 1). The total number of bromeliads and orchids found on these trees was 644. These were distributed among 47 smooth-, 58 medium-, and 75 rough-barked trees.

There was a significant difference (χ^2 test, $p<0.005$; Table 2) between the abundance of the three epiphytes on the different bark types. Trees with rough bark had more epiphytes than those with smooth or medium bark; there was no difference between the number of epiphytes on smooth- and medium-barked trees ($p>0.995$).

Table 1. Epiphyte abundance on trees with varying bark morphologies.

	Rough Bark	Medium Bark	Smooth Bark
# trees sampled	75	47	58
# trees with epiphytes	41	5	6
Total # epiphytes	537	100	17
Total # bromeliads	377	94	5
Total # orchids	160	6	12

The distribution of epiphytes on branches as opposed to crotches was not significant for bromeliads or orchids. Orchids were found more in the middle of the tree, on branches, while bromeliads appeared to grow most often in the periphery of the tree (Figures 1 and 2).

Discussion (TCB)

Epiphytes intercept resources that a host tree might otherwise receive, and this can be a setback for a tree in resource limited areas such as tropical forests (Benzing 1983). Trees should therefore adopt strategies whereby they minimize the potentiality for epiphyte recruitment. We examined the role of bark morphology in discouraging epiphytic growth.

Rough bark channels rainfall differently than smooth, possibly resulting in retardation of nutrient motion along the branches and stem (Gersper and Holowaychuk 1970). Additionally, litter falling on branches with rough bark may tend to lodge in crevices, creating nutrient-rich microenvironments. Epiphyte seeds that fall on these sites may germinate more successfully than those that fall on sites lacking a nutrient rich base. Our results tended to support this idea: we found more epiphytes on rough-barked trees than on those with smooth or medium bark. However, any epiphyte load at all does not seem to be to the tree's advantage, and thus we believe that rough bark must somehow benefit the tree enough to offset the costs of epiphytosis. Rough bark, in its interception of rainfall nutrients and collection of litter, may benefit the tree in the same way it benefits the epiphytes: a tree may grow adventitious roots to tap the nutrient pools, or in some cases nutrients may be absorbed directly by the bark (Benzing 1983; Waring and Schlesinger 1985).

Table 2. Breakdown of chi-squared analysis on epiphyte abundance and distribution in trees with varied bark morphology.

Number of epiphytes in trees with differing bark morphology	
smooth vs. medium	p>0.995
medium vs. rough	p<0.005
smooth vs. rough	p<0.005
Number of bromeliads or orchids in crotches versus on branches	
BROMELIADS	
smooth vs. medium	0.1<p<0.5
medium vs. rough	p<0.005
smooth vs. rough	0.5<p<0.9
ORCHIDS	
smooth vs. medium	0.05 < p < 0.1
medium vs. rough	0.05 < p < 0.1
smooth vs. rough	p < 0.01

Not every rough-barked tree species in our study had epiphytes growing on it. This implies that there are other factors involved in tree-epiphyte interactions. One of these may be a chemical defense. We noticed that trees in the family Fabaceae had almost zero incidence of epiphytosis, no matter what their bark morphology (which was often rough). One possible explanation is that the species of that family exude chemicals through the bark, thus discouraging epiphytic recruitment and survival.

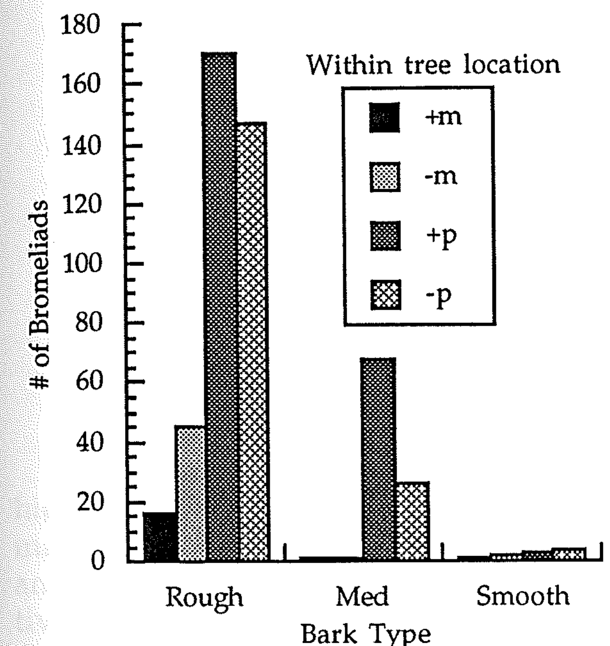

Figure 1. Bromeliad distribution in trees with varying bark morphology.

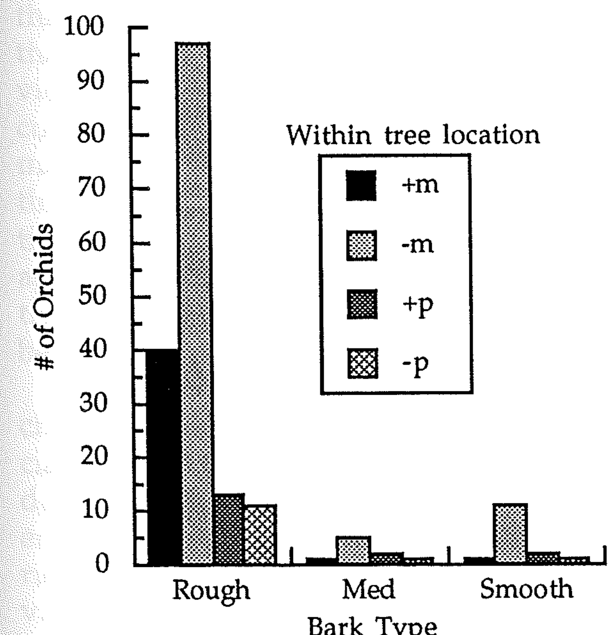

Figure 2. Orchid distribution in trees with varying bark morphology.

Another factor that may be important is general tree morphology. We chose to look at all canopy species no matter what their morphology. Thus some were tall with straight stems and small crowns, while others forked many times and had large, well-developed crowns. Certain morphologies may discourage epiphytes, but further study would be necessary to quantify this.

A final factor of note was the effect of local evironmental parameters that may facilitate epiphyte growth. We surveyed two areas: one along the Sendero la Venada and one along the main road. Trees along the road had much higher epiphyte abundances than those along the trail. Nutrients in road dust have been shown to influence roadside vegetation chemistry, and this might account for the differences in epiphyte loads in the two areas (Friedland, pers. comm.). Rough bark in this instance provides more places for dust to settle and collect.

We also looked at the within-tree distribution of epiphytes and found that while orchids are mostly on branches in the interior of the tree, bromeliads are found all over the periphery, in branches and crotches. We argue that this is due to differences in the life history patterns of the two epiphyte types (i.e., differences in seed dispersal, attachment mechanisms, germination, or growth requirements). Orchids, for example, may require the shade in the middle of the canopy, while bromeliads may require higher light conditions. These ideas remain to be tested.

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