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SHORT COMMUNICATION

The importance of treefall gaps as foraging sites for leaf-cutting ants depends on forest age

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Variation in local abundance of herbivores is influenced by several abiotic and biotic factors, but it may often be determined by the local availability of plant resources (Quinn *et al.* 1997). Leaf-cutting ants, common defoliators of plants in the Neotropics, are more abundant in early successional forests than in old-growth forest (Jaffe & Vilela 1989, Vasconcelos & Cherrett 1995). A recent study showed that the high density of mature leaf-cutting ant nests in early successional forests was mainly determined by the availability of pioneer plant species, largely preferred by the leafcutters (Farji-Brener 2001). The dominance of pioneer species in early successional forests decreases foraging costs for leaf-cutting ant colonies, and thus these habitats can support a high density of mature colonies. On the other hand, the effective defence mechanisms of shade-tolerant species, which dominate primary habitats, could explain the low density of mature leaf-cutting ant colonies in old-growth forests (palatable forage hypothesis, see Farji-Brener 2001). According to this hypothesis, it is proposed that leaf-cutting ant colonies in old-growth forests should concentrate their foraging effort in treefall gaps, in which sun and pioneer plant species (preferred by leafcutters), are readily available (Farji-Brener 2001, Nichols-Orians 1991*a*, *b*; Wetterer 1994). However, this prediction of the palatable forage hypothesis has not yet been explicitly documented.

In this study we determined the relationship between treefall gaps, the successional stage of a tropical wet forest, and the amount of leaf-cutting ant herbivory. We documented the level of ant herbivory in treefall gaps and the surrounding forest understorey in old-growth and secondary forests. If the presence of mature leaf-cutting ant nests in old-growth forest strongly depends on the existence of treefall gaps for forage, we expect a higher level of ant herbivory in old-growth forest treefall gaps than in those located in secondary forests.

We conducted this study at La Selva Biological Station of the Organization for Tropical Studies (10° 26′N, 83° 59′W) in the Atlantic lowlands of Costa Rica, in February 2002. The area is a wet premontane forest and receives a mean annual rainfall of 4000 mm. La Selva Biological Station includes old-growth forests and patches of forest in different successional stages (McDade *et al.* 1994). Colonies of leaf-cutting ants, mainly *Atta cephalotes*, are common within La Selva (Nichols-Orians 1991*a*, *b*). To determine the level of herbivory by leaf-cutting ants in treefall gaps in forests of different successional stages, we located 10 treefall gaps in the old-growth forest along CCL and CCC trails, and six in the secondary forest (~30 y old) along STR trail (McDade *et al.* 1994). All treefall gaps were around 6 mo old (O. Vargas, *pers. comm.*). Although gap area was more variable in the secondary forests, the mean (± 1 SE) area estimated for the treefall gaps sampled in primary and secondary forests was not statistically different, 20 ± 3 m^2 and 53 ± 24 m^2 respectively ($n_1 = 10$, $n_2 = 6$, $U = 45$, $P = 0.13$). In an area of 10 × 10 m located at the centre of each treefall gap, we randomly selected 10 plants (1–2.5 m height) to determine ant herbivory. These plants include several unidentified woody species with comparable number of leaves. The percentage of herbivory by leaf-cutting ants was estimated for each plant as the number of leaves with damage due to leaf-cutting ants/total number of leaves. The pattern of foliar damage caused by leafcutters is unique and easily recognized (Barrer & Cherrett 1972, A.G. Farji-Brener, *pers. obs.*). Since local density of leaf-

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cutting ant colonies can affect the amount of ant foliar damage at a site, we randomly selected 10 plants (1–2.5 m height) in 10 × 10 m as a site-control effect in the forest understorey next to each treefall gap. Each 10 × 10-m plot was considered as an experimental unit with two paired treatments (treefall gap and understorey forest), and characterized by a mean percentage of leaf-cutting ant herbivory. We thus used the non-parametric Wilcoxon paired-sample test to compare (for primary and secondary forests separately), the percentage of leaves attacked by ants between treefall gaps and the adjacent understorey. We also used a regression analysis to determine whether variation in gap area explained the amount of leaf-cutting ant herbivory. In this analysis, data were arcsine transformed to meet the assumptions of normality.

The amount of leaf-cutting ant herbivory in treefall gaps was not related to their area ($F_{1,14} = 0.59$, $P = 0.45$), but was influenced by the successional stage of the forest. While the foliar damage caused by leafcutters was an order of magnitude higher in treefall gaps than adjacent understorey in old-growth forest ($T_{+(2),10} = 55$, $P = 0.006$), leaf-cutting ant herbivory was similar between treefall gaps and the adjacent understorey in secondary forest ($T_{+(2),6} = 12$, $P = 0.28$, Figure 1). This suggests that, in old-growth forests, treefall gaps are a very important source of palatable plants and supports the palatable forage hypothesis (Farji-Brener 2001).

Plants in treefall gaps were probably younger and have a faster rate of leaf turnover than those in the forest understorey (Coley 1983). Consequently, plants in treefall gaps have less time exposed to leaf-cutting ant damage and their leaves can accumulate damage over a shorter period. Nevertheless, they suffered greater ant herbivory than understorey plants ($T_{+(1),16} = 115$, $P = 0.0003$). Additionally, while leaf-cutting ant densities in La Selva Biological Station are lower in old-growth forest than in secondary forest (Farji-Brener & Illes 2000, Perfecto & Vandermeer 1993), the percentage of leafcutter herbivory in treefall gaps was similar among old-growth and secondary forests ($U = 38$, $n_1 = 10$, $n_2 = 6$, $P = 0.41$). Thus, time exposed to herbivores and nest density cannot explain the differences in leafcutter herbivory found in this study. However, the reduction in damage in the old-growth understorey might reflect a greater diversion of ants to the canopy than occurs in secondary forest. This aspect deserves further study.

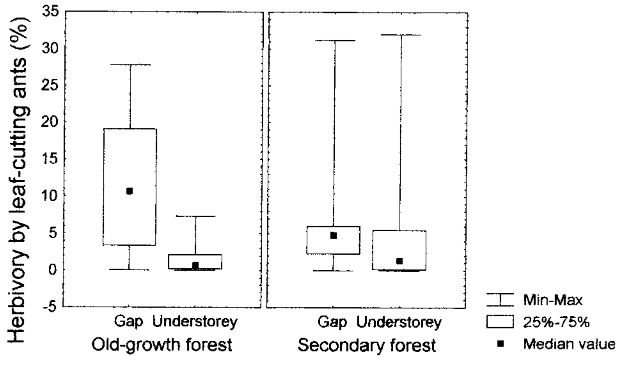

Figure 1. Herbivory by leaf-cutting ants (%) in treefall gaps and paired understorey sites in forests that differ in successional stage. See text for methodological details.

The concentration of foraging effort by the ants mainly in treefall gaps in old-growth forests appears to be a consequence of both the effective defence mechanism of shade-tolerant species that dominate the forest understorey in these habitats, and the high aggregation of palatable plants in treefall gaps. Variation in forest canopy structure between old-growth and second-growth stands influences understorey light availability and its spatial distribution (Nicotra *et al.* 1999), and thus the amount and distribution of palatable plants for leafcutters (Shepherd 1985). The even-aged, homogeneous canopies of second-growth forests have small gap sizes and high frequency of microsites at intermediate light levels. In contrast, old-growth stands have greater representation of both low- and high-light microsites, and a greater overall variance in light representation (Nicotra *et al.* 1999). Palatable plants for leafcutters are generally associated with high-light environments (Nichols-Orians 1991*a*, *b*) for at least two reasons. Pioneer species, which dominate treefall gaps, allocate fewer resources to chemical defences and have higher nutritive status than shade-tolerant species, which dominate the undisturbed understorey (Coley 1983). In addition, leaves of the same species that expanded to maturity under different light conditions also show large differences in chemistry, and in their acceptability to leaf-cutting ants. For example, leaf-cutting ants preferred the leaves of seedlings that were grown at 20% light to leaves of seedlings grown at 2% light (Nichols-Orians 1991*a*, *b*). This association of palatable plants with high-light environments, and the spatial distribution of light availability within forests determines that food resources for leafcutters in secondary forest are dispersed, whereas in old-growth forest they are mostly concentrated in treefall gaps. Therefore, treefall gaps are more important to maintain mature leaf-cutting ant colonies in old-growth forest than in secondary forests (Farji-Brener 2001, Nichols-Orians 1991*a*, *b*; Shepherd 1985, Wetterer 1994). In other words, treefall gaps in old-growth forest are like islands of palatable resources immersed in an unpalatable forest ocean for leaf-cutting ants.

The relative importance of top-down and bottom-up forces in explaining the distribution and abundance of herbivores has received considerable attention in the literature (Price *et al.* 1980, Stiling & Rossi 1997, Williams *et al.* 2001). Bottom-up forces are theorized to affect herbivore populations through food limitation. In contrast, top-down forces propose that predators and parasites regulate herbivore populations. Although predators can eventually limit the abundance of leaf-cutting ants (Rao 2000), our results support the hypothesis that availability of palatable resources is the most important factor in determining mature leaf-cutting ant abundance (Farji-Brener 2001). Hence, leaf-cutting ants are a good example of how bottom-up forces can explain the distribution and abundance of herbivores.

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