LEVELS OF LEAF HERBIVORY IN AMAZONIAN TREES FROM DIFFERENT STAGES IN FOREST REGENERATION

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ABSTRACT — Leaves from 120 canopy trees and 60 understory tree saplings growing in primary and secondary forests near Manaus, Brazil, were collected for determination of standing levels of herbivory (percent leaf area lost). Overall, levels of herbivory on leaves of central Amazonian trees were low. About one quarter of the leaves examined (n = 855) had no damage at all. In most other Neotropical sites studied the mean percentage of herbivory was found to vary between 5.7 and 13.1%, whereas in Manaus it was only 3.1%. The data presented here support the contention that levels of herbivore damage are positively related to soil fertility. No significant difference was found in herbivory levels between canopy trees and understory saplings. Also, there was no difference in damage between leaves from pioneer and late successional trees. Field assays of preference, however, revealed that leaves from pioneer trees are more palatable to leaf-cutting ants (*Atta laevigata*). This effect was dependent upon leaf age, being observed in mature leaves, but not in young leaves. The greater rate of leaf production in secondary forests may be a factor accounting for the greater abundance of leaf-cutting ants in secondary compared to primary forests.

Key-words: ants, *Atta laevigata*, herbivory, insect-plant interactions, Amazon forest

Níveis de Dano Foliar por Herbívoros em Árvores Amazônicas de Diferentes Estágios na Regeneração Florestal.

RESUMO — Folhas de 120 árvores do dossel e de 60 arvoretas do sub-bosque foram coletadas em florestas primárias e secundárias de terra-firme próximas a Manaus, para medição dos níveis de herbivoria (porcentagem da área foliar danificada por herbívoros). Os níveis de herbivoria foram baixos. Cerca de 25% das folhas examindas (n = 855) não tinham dano algum. Na maioria das outras florestas Neotropicais estudadas a porcentagem média de herbivoria ficou entre 5,7 e 13,1%, enquanto em Manaus este valor foi de apenas 3,1%. Os dados apresentados aqui dão apoio a hipótese de que os níveis de herbivoria são positivamente relacionados a fertilidade do solo. Não houve diferença no nível de herbivoria entre árvores do dossel e arvoretas do sub-bosque. Também, não encontrou-se diferença entre folhas de plantas pioneiras da mata secundária e aquelas de final de sucessão encontradas na mata primária. Testes de preferência, entretanto, mostraram que folhas das plantas pioneiras são mais palatáveis as saúvas (*Atta laevigata*). Este efeito foi dependente da idade foliar, tendo sido observado em folhas maduras mas não em folhas jovens. A maior taxa de produção de folhas na floresta secundária pode ser um dos fatores responsáveis pela maior abundância de saúvas na mata secundária do que na mata primária.

Palavras-chave: formigas, *Atta laevigata*, herbivoria, floresta Amazônica, interações inseto-planta

INTRODUCTION

The relative contribution of herbivores to nutrient cycling and energy flow in the ecosystem depends primarily on the amount of plant production consumed by these animals. Many studies on forest ecosystems have used standing levels of herbivory (percent leaf area lost at a given point in time) as an estimate of plant consumption (e.g., Jordan & Uhl, 1978; Adis *et al.*,

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1979). This measure tends to underestimate actual herbivory rates (Lowman, 1984; Filip *et al.* 1995), but in many cases it is the only measure possible, given the logistic limitations of continued access to the forest canopy. Regardless of methodological problems, herbivory levels in *terra-firme* (upland) forests of central Amazonia appear lower than in other tropical forests (Fittkau & Klinge, 1973), but comparative data is lacking. In a study on biomass and trophic structure of a *terra-firme* forest near Manaus, Fittkau & Klinge (1973) noticed that leaves do not show any signs of heavy attack by animals, and argued that this might be correlated with the low nutrient content of leaves from the forest of that region. Leaf nutrient content is usually low in tropical trees growing in nutrient-poor soils (Vitousek & Sanford, 1986), such as near Manaus. Furthermore, when nutrients are limiting, plants tend to allocate more resources to the production of secondary compounds (Coley *et al.*, 1985). Thus, the combination of a low leaf nutritional value and high content of secondary chemicals may keep herbivore populations at low levels in forests growing on poor soils.

Leaf-cutting ants (*Atta* spp.) are perhaps the most conspicuous and important herbivores in many tropical forest sites. Wint (1983), for instance, reported that *Atta* was responsible for as much as 80% of the leaf damage in the canopy of the Panamanian forest he studied. In contrast, leaf-cutting ants are extremely rare in some parts of Amazonia and Venezuela, particularly in the primary forest (Vasconcelos, 1988; Jaffe & Villela, 1989), although when forest is cleared and the area left to regrowth, ant nest densities increase substantially (Vasconcelos & Cherrett, 1995). Such an increase may result from changes in abiotic conditions, particularly increased light, since *Atta* nests appear to develop poorly in shady conditions (Jaffe & Vilella, 1989; pers. obs.). Alternatively, leaf-cutting ant populations may increase after primary forest is cleared because of changes in plant resources. Leaves from pioneer tree species which colonize cleared areas, may be more palatable to leaf-cutting ants because of lower investment in the production of certain defensive compounds than late successional species from mature forest (Coley, 1983; Coley *et al.*, 1985). In this paper, I test the hypothesis that trees from different stages in forest regeneration differ in their palatability to leaf-cutting ants, by conducting assays of leaf preference with field colonies of *Atta laevigata* (Fr. Smith). Standing levels of herbivory were also measured on leaves of trees from different stages in forest regeneration, as a way of comparing overall levels of herbivory among different forest types. Finally, standing levels of herbivory were used to obtain a preliminary comparison of herbivory levels in forests near Manaus versus those in other Neotropical sites.

METHODS

Study sites

The study was conducted in, or in areas immediately adjacent to, the Reserva Florestal Adolfo Ducke and the Estação Experimental de Silvicultura Tropical of INPA, located respectively, 28 and 45 km north of Manaus (3°05'S, 60°00'W), Brazil. Precipitation in Manaus averages 2100 mm annually and varies seasonally, with a rainy period between November and May and a dry period between June and October (Ribeiro, 1976). Most of the vegetation in the study areas consists of undisturbed, primary forest, characterized by a high diversity of tree species (most of which represented by less than one adult individual per ha), a canopy height of about 35 m, with some emergent trees reaching up to 50 m, and a relatively open understory with many stemless palms (Guillaumet, 1987). In a few areas, however, secondary forests were present due to primary forest clearing and burning 7-10 years ago. The secondary forests studied were dominated by trees, 6-10 m in height, of the genus *Vismia* (Guttiferae). Forests dominated by *Vismia* are common in areas of central Amazonia that have been subjected to moderate use as pasture or agriculture (Lucas *et al.*, 1998).

Measurements of foliar herbivory

Leaves from 60 primary-forest understory-saplings, from 60 primary-forest canopy-trees, and from 60 secondary-forest canopy-trees were collected. For this, I established six line transects in primary forest and six in secondary forest. The transects were 45 m long and at least 200 m apart. Ten trees and 10 saplings (primary forest only) were then chosen at random, maintaing a minimum distance of 5 m between trees. Climbing and the use of a pruner was necessary to collect leaves from canopy trees in primary forest.

The number of species sampled in each forest habitat or forest strata was variable. Fifty-two species of canopy trees and 49 species of saplings were found in primary forest. The secondary forest was less diverse and, among the 60 selected trees, 31 species were found, of which three species of *Vismia*, together, comprised 38% of the sampled trees. Other common species in secondary forest were *Goupia glabra* (Celastraceae) and *Bellucia* sp. (Melastomataceae). All of these are typically pioneer species, none of which were found in the transects established in primary forest, where only late successional species were recorded.

To minimize variation in leaf age, only mature, fully expanded leaves were collected for determination of the amount of herbivory. Herbivory (percent total leaf area lost to herbivores) was determined using a transparent plastic grid with precision of 0.25 cm^2. From each selected plant, 3 to 6 leaves were measured.

Assays of preference with leaf-cutting ants

In this experiment leaves from the same canopy trees described above were used. I used leaves from canopy trees only because leaves growing in shady conditions, such as those in the forest understory, differ from those in the canopy in terms of their nutritional and defensive characteristics against leaf-cutting ants (Hubbell & Wiemer, 1983; Nichols-Orians, 1991). I determined plant palatability to leaf-cutting ants (or their fungus) by placing leaves alongside an active foraging trail. Comparisons were made between leaves from trees in primary forest versus those in secondary forest (i.e., between late successional versus pioneer trees).

Six tests (assays) with two *A. laevigata* colonies were done. In each assay, leaves from 10 pioneer and 10 late successional trees were presented simultaneously. When young and mature leaves from a given tree were available, both were presented (one of each type), otherwise only the mature leaf was given. The position of the leaves from different trees along the trail was determined at random. The contour of each test leaf was drawn on a piece of paper before and 1 hour after the assays, and the area removed by the ants measured using a transparent plastic grid. Leaves used in the assays were collected a few hours prior to their use, and were kept fresh in sealed polythene bags on crushed ice.

RESULTS

Levels of leaf herbivory

Overall levels of leaf herbivory were low. About one quarter of the leaves examined had no damage at all, and more than two-thirds of the leaves had less than 3% damage (Fig. 1). No significant difference in leaf herbivory was found between pioneer and late successional trees (Mann-Whitney U-test, $n_1 = 285$, $n_2 = 296$, $p = 0.41$) nor between understory saplings and canopy trees (Mann-Whitney U-test, $n_1 = 285$, $n_2 = 274$, $p = 0.72$; Fig. 1). The mean (± 1 S.E.) percent of damage in leaves of pioneer trees from the secondary forest canopy was 2.6 ± 0.3 % (n = 296), whereas in late successional trees from the primary forest canopy it was 2.9 ± 0.3 % (n = 285). The percent of leaf damage in saplings of late successional trees growing in the primary forest understory was 3.8 ± 0.5 % (n = 274).

Damage by leaf miners and by galling insects was rare. Less than 4% of the leaves presented damage by these types of herbivores (Tab. 1). The incidence of necrosis or of skelotinized leaves was greater; these types of damage were recorded in 10 to 15% of the leaves. The most common type of damage, observed in over 60% of leaves, was caused by chewing insects (Tab. 1).

Assays of preference

Although there was no difference in standing levels of leaf herbivory between pioneer and late successional trees, field assays of preference with the leaf-cutting ant *A. laevigata* revealed that the former tend to be more palatable. The mean area cut by ants from mature leaves of pioneer trees was 2.7 times greater than that removed from late successional trees

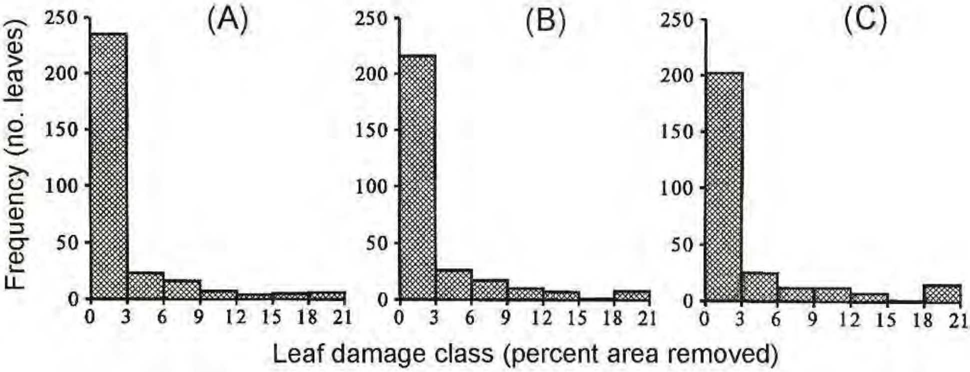

Figure 1. Frequency distribution of leaf herbivore damage in (A) pioneer trees from secondary forest canopy, (B) late successional trees from primary forest canopy, and (C) saplings of late successional trees growing in primary forest understory.

Table 1. Types of leaf damage in canopy trees and understory tree saplings from forests near Manaus, Brazil. Values represent the percentage of examined leaves showing that type of damage. Note that the same leaf could have been assigned to more than one damage category.

HABITAT	Type of Leaf Damage				
	Caused by Miners	Caused by Galls	Skelotinized or with Necrosis	Caused by Chewing Insects*	Not Damaged
Secondary forest canopy	1.0	3.1	11.2	66.3	28.0
Primary forest canopy	3.3	2.4	15.3	70.3	25.9
Primary forest understory	1.5	0.6	15.6	72.7	24.2

* including physical damage which could not be distinguished from damage by chewing insects.

(Tab. 2). However, given the wide variation in area cut from different leaves, the difference was only close to significance (Mann-Whitney U-test, $n_1 = 56$, $n_2 = 58$, $p = 0.066$). In contrast, the mean area cut from young leaves of pioneer trees did not differ from that of late successional trees (Mann-Whitney U-test, $n_1 = 27$, $n_2 = 14$, $p = 0.52$). Consumption of young leaves by leaf-cutting ants was much greater than of mature leaves (Mann-Whitney U-test, $p < 0.001$; Tab. 2)

DISCUSSION

Overall, standing levels of leaf herbivory in trees and saplings from forest near Manaus were lower than those found in most other Neotropical forest sites from which data with comparable methodology are available. In these sites, the mean percentage of damage was found to vary between 5.7 and 13.1%, whereas in Manaus it was only 3.1% (Fig. 2). Only San Carlos de Rio Negro, in Venezuela (Jordan & Uhl, 1978; Uhl 1987), shows herbivory lev-

Table 2. Area removed (cm²) by leaf cutting ants (*Atta leavigata*) from leaves of pioneer and late successional trees during leaf preference assays. Values are the mean (S.D.) area removed 1 hour after detached leaves were presented alongside an active ant foraging trail. In each assay (n = 6), leaves from 10 pioneer and 10 late successional trees were presented to the ants.

Leaf Age	Pioneer trees from secondary forest canopy		Late successional trees from primary forest cannopy	
	Means (SD)	No. leaves tested	Mean (SD)	No. leaves tested
Young	1.0	3.1	11.2	66.3
Mature	3.3	2.4	15.3	70.3

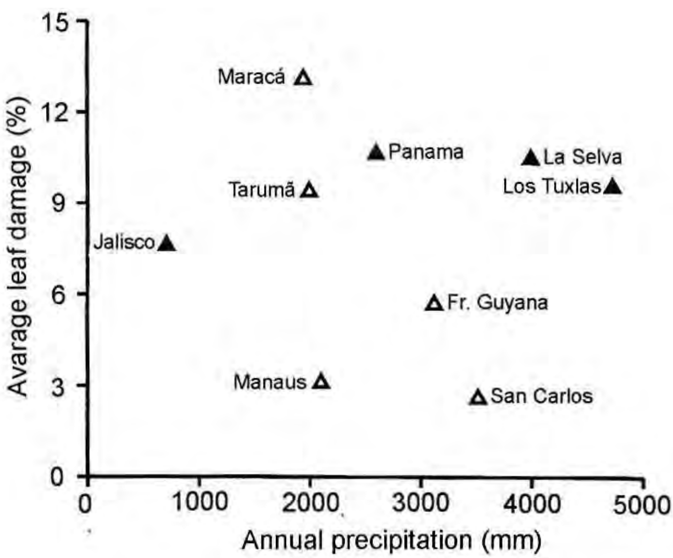

Figure 2. Average levels of herbivore damage (percent leaf area lost) in nine Neotropical forest sites with varying soil conditions and rainfall regimes. Open symbols represent sites with unfertile soils, and filled symbols those with moderately fertile soils. Data from: Manaus (this study), San Carlos (Jordan & Uhl, 1978; Uhl 1987), French Guyana (Newbery & de Foresta, 1985; Sterck *et al.*, 1992), Jalisco (Filip *et al.*, 1995), Tarumã (Adis *et al.*, 1979), Los Tuxlas (Dirzo, 1984; de la Cruz & Dirzo, 1987), La Selva (Marquis & Braker, 1994), Panama (Wint 1983, Leigh & Smythe, 1978), Maracá (Nascimento & Proctor, 1996).

els as low as those presented here. Variation in standing levels of leaf herbivory across different Neotropical sites was not correlated to annual precipitation (r_s = -0.08, n.s.). There were also no clear-cut differences in herbivory levels between forests growing on unfertile soils, namely those from the Amazon basin, versus those growing on moderately fertile (volcanic) soils in Central America (Fig. 2). However, with the exception of the studies in Maracá Island (Nascimento & Proctor, 1994) and in the *igapó* forest at Tarumã-Mirim River (Adis *et al.*, 1979), levels of herbivory in forests growing on nutrient-poor soils are lower than those reported for sites on more fertile soils. The study by Adis *et al.* (1979) at the Tarumã-Mirim was in seasonally-flooded forest and, therefore, may not be comparable with the other studies, all conducted in upland forests. On Maracá Island, the concentration of some nutrients (P e K) are similar to those reported for other forests on moderately fertile soils (Villela, 1998), indicating that soils on that island are not as poor as those in Manaus or San Carlos. Therefore, the possibility that soil fertility may in part explain differences in herbivory levels between different Neotropical sites cannot be ruled out.

Studies with five Australian tree species indicate that herbivory is greater on understory than on canopy leaves (Lowman, 1985), a pattern that did not hold for the community-wide analysis presented in here. Measurements of herbivory rates (area consumed per unit of time) are necessary to determine if herbivory really does not decrease with forest height, since differences in microclimate, leaf chemistry, and predation between the canopy and the understory are suggested to cause differences in herbivore pressure between these two forest strata (Coley & Barone, 1996).

Also, no difference was found in standing levels of herbivory between pioneer and late successional trees. However, some other studies have shown that leaves from early successional species suffer greater damage (Coley, 1983; Dirzo, 1984; but see Newbery & de Foresta, 1985; de la Cruz & Dirzo, 1987). These contrasting results may be due to differences in methodology, reinforcing the need for measures of herbivory rates on central Amazonian plants before any generalizations can be made. It is also possible that pioneer trees from central Amazonian forests are better protected against herbivores than those growing in sites with better soils (e.g., Coley, 1983). In fact, leaves from many of the common pioneer species in secondary forests of Manaus (e.g., *Vismia*, *Cecropia*, *Bellucia* and *Goupia*) do show very high lignin, phenolic acid, and tannin contents (Mesquita *et al.*, 1998).

Results from leaf palatability trials with *A. laevigata*, however, suggest that leaves from pioneer trees are more palatable to at least some herbivores. It must be noted that differences in palatability were restricted to mature leaves. No difference was observed in the palatability of young leaves from trees of different successional stages, and young leaves were highly preferred over mature leaves by leaf-cutting ants (Tab. 2). A greater proportion of trees in secondary forests were harbouring young leaves compared to mature forest (45 versus 23.3%). This suggests that differences in leaf production between these two types of forest, perhaps more than differences in the mean palatability of mature leaves, may account for the higher abundance of leaf-cutting ants in secondary compared to primary forests.

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