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

Heraldo L. VASCONCELOS

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

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.,

1Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), Cx. Postal 478, 69011-970 Manaus, AM, Brazil

1979). This measure tends to underes-
timate 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 ter-
rafme (upland) forests of central
Amazonia appear lower than in other
tropical forests (Fittkau & Klinge,
1973), but comparative data is lack-
ing. In a study on biomass and trophic
structure of a terra-firme forest near
Manaus, Fittkau & Klinge (1973) no-
ticed 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 com-
bination of a low leaf nutritional value
and high content of secondary chemi-
cals 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, particu-
larly 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 in-
creased light, since Atta nests appear
to develop poorly in shady conditions
(Jaffe & Villella, 1989; pers. obs.). Al-
ternatively, leaf-cutting ant popula-
tions may increase after primary for-
est 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 invest-
ment in the production of certain de-
fensive compounds than late succes-
sional 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 palatabil-
ity to leaf-cutting ants, by conduct-
ing 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, stand-
ing levels of herbivory were used to
obtain a preliminary comparison of
herbivory levels in forests near
Manaus versus those in other Neo-
tropical 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, maintaining 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 cm². 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.

<table>
<thead>
<tr>
<th>HABITAT</th>
<th>Type of Leaf Damage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Caused by Miners</td>
</tr>
<tr>
<td>Secondary forest canopy</td>
<td>1.0</td>
</tr>
<tr>
<td>Primary forest canopy</td>
<td>3.3</td>
</tr>
<tr>
<td>Primary forest understory</td>
<td>1.5</td>
</tr>
</tbody>
</table>

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

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.

<table>
<thead>
<tr>
<th>Leaf Age</th>
<th>Pioneer trees from secondary forest canopy</th>
<th>Late successional trees from primary forest canopy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Means (SD) No. leaves tested</td>
<td>Mean (SD) No. leaves tested</td>
</tr>
<tr>
<td>Young</td>
<td>1.0 3.1</td>
<td>11.2 66.3</td>
</tr>
<tr>
<td>Mature</td>
<td>3.3 2.4</td>
<td>15.3 70.3</td>
</tr>
</tbody>
</table>

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).
levels as low as those presented here. Variation in standing levels of leaf herbivory across different Neotropical sites was not correlated to annual precipitation ($r_c = -0.08$, 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 and 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.

**ACKNOWLEDGMENTS**

I thank Josimar F. Menezes for the collection of leaf samples from large canopy trees, and José Maria Vilhena for helping with the measurements of leaf damage. I am also grateful to Claude Gascon, Ilse Walker, and two anonymous referees for reading and commenting on previous versions of this paper. This study was supported by funding from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and from the Biological Dynamics of Forest Fragments Project (INPA/Smithsonian Institution). This represents publication number 248 in the BDFFP Technical Series.

**Literature cited**


Lowman, M.D. 1984. An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than
we thought? Biotropica, 16: 264-268


