

Comparison of Herbivores and Herbivory in the Canopy and Understory for Two Tropical Tree Species¹

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ABSTRACT

The Janzen–Connell model of tropical forest tree diversity predicts that seedlings and young trees growing close to conspecific adults should experience higher levels of damage and mortality from herbivorous insects, with the adult trees acting as either an attractant or source of the herbivores. Previous research in a seasonal forest showed that this pattern of distance-dependent herbivory occurred in the early wet season during the peak of new leaf production. I hypothesized that distance-dependent herbivory may occur at this time because the new foliage in the canopy attracts high numbers of herbivores that are limited to feeding on young leaves. As a consequence, seedlings and saplings growing close to these adults are more likely to be discovered and damaged by these herbivores. In the late wet season, when there is little leaf production in the canopy, leaf damage is spread more evenly throughout the forest and distance dependence disappears. I tested three predictions based on this hypothesis: (1) the same species of insect herbivores attack young and adult trees of a given plant species; (2) herbivore densities increase on adult trees during leaf production; and (3) herbivore densities in the understory rise during the course of the wet season. Censuses were conducted on adults and saplings of two tree species, *Quararibea asterolepis* and *Alseis blackiana*. Adults and saplings of both species had largely the same suite of chewing herbivore species. On adults of *Q. asterolepis*, the density of chewing herbivores increased 6–10 times during leaf production, but there was no increase in herbivore density on adults of *A. blackiana*. Herbivore densities increased 4.5 times on *A. blackiana* saplings and 8.9 times on *Q. asterolepis* saplings during the wet season, but there were no clear trends on the adults of either species. These results suggest that the potential of adult trees as a source of herbivores on saplings depends on the value of new leaves to a tree species' herbivores, which may differ across tree species.

RESUMEN

El modelo Janzen–Connell sobre la diversidad de rboles en bosques tropicales predice que plantas de semillero y rboles jvenes creciendo cerca de rboles adultos de la misma especie han de experimentar altos niveles de dao y mortalidad causada por insectos herbvoros, ya que estos ltimos son huspedes de los rboles adultos o bien, son atrados por estos. Investigaciones anteriores en un bosque de temporada mostr que este patr de dependencia herbvora de distancia ocurri al inicio de la temporada hmeda durante el auge de la produccin de hojas nuevas. Mi hiptesis fue que la dependencia herbvora de distancia puede ocurrir durante esta temporada ya que el nuevo follaje en el dosel atrae un gran nmero de herbvoros que slamente pueden alimentarse de hojas jvenes. Como consecuencia, plantas de semillero y rboles jvenes creciendo cerca de adultos tienen mayor probabilidad de ser descubiertos y daados por estos herbvoros. Al final de la temporada hmeda, cuando hay poca produccin de hojas en el dosel, el dao en las hojas se distribuye de una manera ms equitativa a lo largo de todo el bosque y la dependencia de distancia desaparece. Hice pruebas sobre tres predicciones basadas esta hiptesis: (1) las mismas especies de insectos herbvoros atacan rboles jvenes y adultos de una determinada especie de plantas; (2) la densidad de poblacin herbvora es mayor en rboles adultos durante la poca de reproduccin de hojas; y (3) la densidad de poblacin herbvora en el sotobosque crece mientras transcurre la temporada hmeda. Los censos fueron realizados en rboles jvenes y adultos de dos especies, *Quararibea asterolepis* y *Alseis blackiana*. Tanto los rboles adultos como los jvenes en ambas especies tuvieron en gran parte la misma clase de herbvoros. En rboles adultos de *Q. asterolepis*, la densidad de poblacin de herbvoros se increment de 6 a 10 veces durante la poca de reproduccin de hojas, pero no hubo incremento en la densidad de poblacin de herbvoros en adultos de *A. blackiana*. La densidad de herbvoros se increment 4.5 veces en rboles jvenes de la especie *A. blackiana* y 8.9 veces en *Q. asterolepis* durante el transcurso de la temporada hmeda, pero no hubo tendencias claras en rboles adultos de ambas especies. Estos resultados sugieren que el potencial que tienen los rboles adultos como fuente de herbvoros sobre rboles jvenes depende del valor que tengan las hojas nuevas para los herbvoros de esa especie de rbol, lo cual puede variar entre las diferentes especies de rboles.

Key words: Alseis; Barro Colorado Island; canopy; herbivores; herbivory; Janzen–Connell model; Panama; Quararibea.

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RECENT INNOVATIONS HAVE FACILITATED ACCESS to the canopies of tropical trees, and the details of plant–herbivore interactions. In particular, the levels of herbivory, now are being examined at different heights within tropical forests (Lowman & Moffett 1993, Lowman 1995). A greater understanding of how herbivory differs between the canopy and the understory may help elucidate the role that insect herbivores play in the maintenance of tropical forest tree diversity, as outlined in the model of Janzen (1970) and Connell (1971). They argued that high levels of local tree diversity in the tropics are the result of disproportionately high rates of attack by herbivores, pathogens, and seed predators on seeds, seedlings, and young trees growing close to conspecific adults. The resulting pattern of distance-dependent damage, they suggested, would cause greater juvenile mortality near adults and ultimately lead to the suppression of dominant tree species by allowing weaker competitors to persist. Tests of this model have looked largely at the mortality of seeds and seedlings at varying distances to the nearest conspecific adult and frequently have supported the prediction of greater mortality near the adult trees (for reviews, see Clark & Clark 1984, Coley & Barone 1996).

Herbivory to leaves, however, also may show this distance dependence, but few studies have tested the possibility. Clark and Clark (1985) found that *Dipteryx panamensis* (Leguminosae: Papilionidae) seedlings growing in a dense group within 15 m of a conspecific adult lost more of their original leaf area than did isolated seedlings. Denslow (1980) examined damage to mature leaves of seedlings belonging to an unidentified tree species (Bombacaceae) and determined that herbivory did not differ with seedling proximity to the parental tree.

In the seasonal forest on Barro Colorado Island, Panama, Barone (1996) found distance-dependent herbivory to newly expanded leaves, but only in three of the six species examined and only during the early wet season. Because young leaves are a critical resource for many insect herbivores (Lowman 1985, Basset 1991, Barone 1998a), Barone (1996) suggested that the presence of distance dependence in the early wet season was due to an increase in new leaf production. Canopy leaf production peaks during the early wet season in this forest (Leigh & Windsor 1982), and Barone (1996) hypothesized that the abundance of young leaves attracts herbivores into the canopy. This concentration of herbivores in the canopy means that saplings near adult trees would be more likely to

be discovered, resulting in distance-dependent leaf damage. Later in the wet season, when there are fewer new leaves in the canopy (Leigh and Windsor 1982) but many insects (Smythe 1982), herbivores specializing on young leaves would be forced to search more broadly through the forest to find young leaves; thus distance-dependent herbivory on young leaves would not occur.

This hypothesis, like the Janzen–Connell model, assumes that insect herbivores have narrow host ranges. Generalist herbivores can attack many of the tree species they encounter, and thus should not cause distance-dependent herbivory. For this reason, knowing the degree of specialization and the amount of damage caused by specialist and generalist herbivores is critical to demonstrating the role of insect herbivores in maintaining tree diversity.

In this study, I tested three predictions based on the hypothesis that distance-dependent herbivory in saplings is related to new leaf production in the canopies of the adults. First, the same species of insect herbivores would attack juvenile and adult trees of a given species and be responsible for similar amounts of damage. Second, for tree species showing distance-dependent herbivory in the early wet season, herbivore densities would increase on the adult trees during leaf production. Third, in the understory, herbivore densities would rise during the wet season.

To test these predictions, I conducted insect censuses and measured herbivory on saplings and adults of two Panamanian tree species, *Quararibea asterolepis* Pitt. (Bombacaceae) and *Alseis blackiana* Hemsl. (Rubiaceae). These species were chosen because *Q. asterolepis* saplings that were growing near conspecific adults experienced greater leaf damage in the early wet season compared to those saplings growing farther away from adults (Barone 1996). In addition, Wong *et al.* (1990) found that during a caterpillar outbreak during the early wet season, large saplings of *Q. asterolepis* growing near infested adults were more likely to be damaged by the outbreak caterpillars. For *A. blackiana* saplings, however, leaf damage never varied with distance to the nearest conspecific adult regardless of the time of year (Barone 1996). Thus, for *Q. asterolepis*, the density of herbivores on adults was expected to increase during new leaf production, and the same herbivore species were predicted to attack juvenile and adult trees. *Alseis blackiana* on the other hand was expected to differ from *Q. asterolepis*, either by showing no increase in herbivore densities on the adults during the early wet season leaf flush, by

having a different suite of herbivore species in the canopy than in the understory, or both. On saplings of both species, herbivore densities were expected to increase during the wet season.

METHODS

STUDY SITE AND SPECIES.—This study was conducted on Barro Colorado Island (BCI; 9°09'N, 79°51'W), which is part of the Barro Colorado Nature Monument in the Republic of Panama. The vegetation on BCI can be classified as moist or semi-deciduous lowland tropical forest (Holdridge *et al.* 1971, Croat 1978, Foster & Brokaw 1982). About two-thirds of the forest on BCI is considered mature and at least 300–400 years old, but the northeastern portion of the island is secondary forest and has been regenerating since ca 1880 (Foster & Brokaw 1982). Annual precipitation averages 2600 mm, with a single, long dry season typically stretching from mid-December until mid-April (Windsor 1990). More details on the climate and natural history of BCI can be found in Leigh *et al.* (1982) and Gentry (1990).

Leaf production on BCI peaks twice annually, at the beginning of both the wet season (May–June) and the dry season (December–January). During these periods, canopy trees and understory saplings produce new leaves, although the flush during the early wet season is more extensive in terms of both the number of individuals and species making new leaves (Leigh & Windsor 1982; Aide 1988, 1993). In the late wet season (October–November), there is usually another flush that is limited largely to the understory, when saplings of fewer species, including those used in this study, produce additional leaves (Leigh & Windsor 1982, Aide 1993).

Alseis blackiana (Rubiaceae) and *Q. asterolepis* (Bombacaceae) are shade tolerant canopy tree species, both of which are among the 20 most abundant woody plant species on the 50-ha Forest Dynamics Plot on BCI (Condit *et al.* 1996). Hereafter, I will refer to both species by their generic names. Saplings and adults of *Alseis* are annually deciduous, exchanging their leaves in the early wet season. Large *Quararibea* adults shed leaves slowly at the end of the dry and wet seasons, becoming leafless for brief periods (Wright & van Schaik 1994). Small adults and saplings of *Quararibea* are not deciduous, although their peaks in leaf production coincide with those of the canopy adults (Barone 1998b).

HERBIVORE CENSUSES ON ADULTS.—Leaves of the adult trees were reached using single rope climbing techniques (Perry 1978). Adults were chosen primarily on the basis of their accessibility and apparent sturdiness. To reach the canopy leaves of *Alseis* trees, a species with weak wood, the rope was placed in adjacent, emergent trees (either *Pseudobombax septenatum* or *Ficus* sp.) and positioned so that the *Alseis* leaves could be reached. Of the four *Alseis* adults that were censused, three were in the mature forest on the plateau in the center of the island and one was in the younger forest near Donato Trail. Three *Quararibea* adults were censused, two in the mature forest south of the plateau along Armour Trail and the third on the plateau.

Herbivores were censused on the adults every 10 to 14 days, depending on the weather. I climbed in the morning to avoid the afternoon rain showers that are common on BCI. The same branches were inspected at each census, but when a branch broke or died, a new branch was added. All were between 12 and 15 m above the ground for *Quararibea* and 12 to 20 m for *Alseis*. Their accessibility determined the total number of branches that were marked in each tree. For *Quararibea*, I marked 13 branches on two of the trees and 8 branches on the third. For *Alseis*, two adults had 14 marked branches, one tree had 9 marked branches, and the fourth tree had 8 marked branches. All of the leaves were in the shade, although the degree of shading varied from branch to branch and tree to tree. Sampling was restricted to shade leaves because the architecture of both tree species made reaching the sun leaves difficult. The number of leaves that were censused on each adult differed, based on how many could be reached and the time of year, but averaged 243 leaves (a total of 2.0 m²) for each *Quararibea* adult and 120 leaves (1.0 m²) for each *Alseis* adult.

The top and the bottom of each leaf was inspected visually and the number and morphospecies of each herbivore present was recorded, as was the number of new leaves. Every attempt was made to avoid disturbing herbivores. Ropes were positioned to minimize contact with the leaves and were tied back when not in use. These efforts appeared to be largely successful since herbivores rarely were seen flying or falling off the leaves. Censuses of one adult each of *Quararibea* and *Alseis* began in September 1994, and the other adults were added in January and February 1995. The censuses ended in October 1995. The results reported here are from February to October 1995.

In the early wet season of 1995, caterpillars of

the genus *Eulepidotis* (Noctuidae) reached outbreak levels on *Quararibea* adults at BCI. These caterpillars, which also experienced outbreaks in 1985 (Wong *et al.* 1990) and 1993 (J. Barone, pers. obs.), specialize on young *Quararibea* leaves (Wong *et al.* 1990). Two of the three adults in this study suffered from the outbreaks and were defoliated completely. These two *Quararibea* adults each flushed a second set of leaves later in the wet season (July and September). The impact of new leaf production on herbivore densities was tested using this second flush instead of the first, because the outbreak caterpillars would have biased the test. I report the results for both leaf-chewing herbivores, which are the main focus of this study, as well as for Homoptera, because studies of plant-herbivore interactions in the tropics largely have ignored the impact of sucking insects (Coley & Barone 1996).

HERBIVORE CENSUSES ON SEEDLINGS.—Weekly censuses of saplings (0.2–2.0 m tall) of both *Alseis* and *Quararibea* began in early September 1994 and lasted one year, with three additional censuses conducted during September and October 1995. Fifty saplings of *Alseis* and 36 of *Quararibea* were censused. All the saplings were initially in the shaded understory, although by the end of the censuses three *Alseis* were in small gaps. The saplings were spread out along lesser-used trails on BCI and located in both the mature and secondary forest. The proximity of the saplings to the nearest conspecific adult was not measured.

During each census, the upper and lower surfaces of every leaf on each sapling were inspected by hand in a manner identical to that used for the adults. I recorded the number and morphospecies of herbivores and the number of new leaves. As with the adults, I minimized disturbance of the herbivores. For each census, an average of 1780 *Quararibea* leaves (11.9 m²) and 540 *Alseis* leaves (5.2 m²) were examined.

MEASUREMENTS OF HERBIVORY.—During the early wet season, leaf damage was measured on adults and saplings of both species. Herbivory was measured on young expanding leaves, because in tropical forests, the majority of a leaf's lifetime damage typically occurs during this vulnerable stage (Coley 1980, 1983; Lowman 1985). On the adults, the new leaves on each branch marked for the herbivore censuses were counted as soon as the leaves had broken bud. When new leaves reached full size and toughened (*ca* 4 wk), the amount of damage they had experienced was measured in place by us-

ing a small transparent plastic grid (100 squares/in²). To estimate the average area of a leaf without any damage, I removed 25–50 leaves from each adult (from branches not used in the herbivore censuses) and measured their area with a Li-Cor LI-3050A leaf area meter (Li-Cor, Lincoln, Nebraska). For each tree, an average leaf size was calculated and the amount of damage to each leaf was expressed as a percentage of this area. Damage to leaves that were completely eaten was scored as 100 percent. In the analysis of leaf damage, an average damage to each branch was calculated because there was little evidence that herbivores moved from branch to branch.

Leaf damage to saplings was measured in a comparable fashion. As soon as a new leaf broke bud, I marked its position by winding a small piece of colored wire on a neighboring mature leaf or a twig. After the new leaf had matured, both the area of any damage and the total leaf area were measured using the plastic grid. For any leaves that had been rolled up by a herbivore, the leaf was unrolled gently and then measured. Leaf damage again was expressed as a percentage of total leaf area.

During this study, I became quite familiar with the herbivores on these two tree species and the types of damage they made. Indeed, one reason that these particular species were chosen was because their herbivore faunas left distinctive patterns of damage on leaves. Furthermore, by the beginning of this study, I had already 19 months of experience working with the herbivores on these tree species during other research (Barone 1996, 1998a). Therefore, when marked leaves were not eaten completely, I usually was able to assign the damage to a particular herbivore morphospecies. In addition, I conducted extensive feeding trials on the most common herbivores to determine their diet range (Barone 1998a). Forty-six species were used in these trials, including 13 species that eat *Quararibea* and 10 species that eat *Alseis*. For the trials, the herbivores were fed the young and mature leaves of: (1) congeners of their known host plant species (although no congeners of *A. blackiana* were present on BCI); (2) two or three congeneric species; and (3) ten of the most abundant species on BCI. For *Alseis*, the five most common herbivore species restricted their feeding to this host species, while for *Quararibea*, five of the most common herbivore species restricted their feeding to this plant genus and four were limited to feeding on the family Bombacaceae (Barone 1998a).

Based on these feeding trials, I report the amount of damage caused by herbivores with dif-

ferent diet breadths. The cause of leaf damage was assigned during the measurements based on the pattern of damage to the leaves. In addition, because of the herbivore censuses, I often had a record of a particular herbivore species eating a particular leaf. Such determinations were not made for leaves that had disappeared completely. Nonetheless, I believe that the same herbivore species were responsible for leaves that were completely eaten and those that were only partially damaged.

For clarity, I will use the following terms: a species-specialist is an herbivore that ate only one plant species in the feeding trials; a genus-specialist could eat only the plants in a single genus; and a family specialist was limited to feeding on plants in a single family. A generalist is any herbivore that can feed on plants in more than one family.

ANALYSIS.—A Shapiro-Wilk W -test was used to confirm that the data were normally distributed, and appropriate transformations were made when necessary. A repeated-measures ANOVA was used to examine if herbivore densities increased on saplings of both tree species through time, with season (early or late wet season) as the between-subject effect and the census as the within-subject effect. To compare herbivore densities between saplings and adults, a t -test was used on natural log-transformed data.

To determine if herbivore densities on the adult trees increased during new leaf production, a repeated-measures MANOVA was used. For *Quararibea*, branches were nested within trees for the analysis, with tree as the between-subject factor and time, either before, during, or after leaf production, as the within-subject factor. Only significant effects using Wilks' Lambda are reported. As noted above, two of the three *Quararibea* adults were damaged severely by an outbreak of caterpillars at the beginning of the wet season. Therefore, for these two adults, the density of chewing herbivores during this replacement bout of new leaf production was analyzed. For *Alseis*, the density of herbivores during leaf production was evaluated in a similar manner, except that branches were not nested within trees. New *Alseis* leaves are produced in whorls at the tips of new branches, and new leaf production invariably results in new branches. Thus, the leaves examined before leaf production were on different branches than the subsequent new leaves.

RESULTS

HERBIVORES AND HERBIVORY IN THE CANOPY AND UNDERSTORY.—The first prediction tested was that the

same species of herbivores attack juvenile and adult trees and produce similar amounts of damage. For both tree species, largely the same species of herbivores attacked the leaves of the adults and juveniles. Of the 7 species of chewing herbivores that were common (5 or more individuals were found in the censuses) on *Alseis* (6 lepidopteran larvae, 1 Coleoptera), 6 occurred in both the canopy and understory. For *Quararibea*, 11 species of chewing herbivores were common (9 lepidopteran larvae and 2 Coleoptera) and 8 species were found on both adults and saplings. Two species of caterpillars were limited to the understory, and 1 cerambycid beetle species was found exclusively in the canopy.

In the early wet season of 1995, *Alseis* saplings suffered somewhat higher levels of herbivory than adults (12.7 and 8.2% of potential leaf area, respectively). Between 82.3 and 92.6 percent of the damage to these adults by area was due to leaves that completely disappeared during leaf expansion. *Quararibea* 1, the adult that was not affected by the outbreak, experienced virtually the same amount of damage (26.3%) as the saplings (27.2%). On this adult, 76.1 percent of leaf damage was from leaves that completely disappeared during leaf expansion.

On *Quararibea* 1, leaf pathogens caused the most damage (46.1% leaf area lost), followed by an unidentified noctuid caterpillar (42.4%), which is specialized on the genus *Quararibea* (Barone 1998a; Table 1). On saplings, pathogens were responsible for only 6.0 percent of the leaf damage, but the same noctuid species was again the most destructive insect species (38.7%). Overall, there was no correlation between the amounts of damage caused by different herbivore species on the *Quararibea* adult and saplings (Spearman's coefficient of rank correlation: $r_s = 0.473$, $P = 0.166$; excluding damage by pathogens and from unknown causes: $r_s = 0.503$, $P = 0.204$). In total, insect herbivores were responsible for 92.6 percent of the damage to leaves on saplings and 51.2 percent to *Quararibea* 1. Herbivores limited to feeding exclusively on the genus *Quararibea* were responsible for 96.1 percent of the insect herbivory on *Quararibea* 1. On the saplings, genus and family specialists were responsible for 79.1 percent of the leaf damage. As noted above, in the early wet season, all of the young leaves on the other two *Quararibea* adults were eaten by *Eulepidotis* sp. caterpillars, a genus specialist.

For the *Alseis* adults, leaf-cutting ants (*Atta colombica*) were responsible for the largest proportion of the leaf area lost (32.5%; Table 2), but all of this damage was to a single tree. This tree was also

TABLE 1. Area (cm²) and, in parentheses, the percentage of leaf damage by different causes to young leaves on an adult and saplings of *Quararibea asterolepis*. *"Genus" means that in feeding trials the herbivore species fed on plants in one genus. "Family" means that the herbivores were limited to one family. A "generalist" could feed on many families. Based on 1920 cm² of damaged leaf area to adults and 250 cm² to saplings.

Cause	Adult	Saplings	Host Specificity*
Noctuidae sp. 1	814.1 (42.4)	96.8 (38.7)	Genus
<i>Eulepidotis</i> sp.	74.9 (3.9)	76.8 (30.7)	Genus
Lepidoptera sp. 1	51.8 (2.7)	0	Genus§
Cerambycidae sp. 1	3.8 (0.2)	0	Genus
Alticinae sp. 1	0 (0)	7.5 (3.0)	Family
Pyralidae sp. 1	0 (0)	2.3 (0.9)	Family
Chrysomelidae sp. 1	25.0 (1.3)	4.3 (1.7)	Generalist
Acrididae sp. 1	13.4 (0.7)	44.0 (17.6)	Generalist
Pathogen	885.1 (46.1)	15.0 (6.0)	Unknown
Unknown/Physical damage	49.9 (2.6)	3.5 (1.4)	—

§ Assessment based only on field observations.

the only adult of either species in secondary forest. Leaf-cutting ants are very rare in the mature forest on BCI (J. Barone, pers. obs.), and neither the ants nor any of their damage was ever seen on the other adults or any saplings. The *Alseis* adult in the secondary forest, however, did not have any other herbivores or damage types that were not found also on the other adult *Alseis*.

Leaf pathogens were the second most important cause of leaf damage to *Alseis* adults, responsible for 25.6 percent of the overall leaf area lost. On the saplings, pathogens caused only 6.6 percent of the leaf damage. After leaf-cutting ants, the most destructive insect herbivores on the adults were *Adelpha* sp. caterpillars (Nymphalidae; A. Aiello, pers. comm.). Although this species did occur on the saplings, it was rare, particularly in the early wet season. In contrast, the most damaging herbivore on the saplings was a leaf-rolling caterpillar in

the family Pyralidae. Again, although this species was observed on the adults, it was more abundant on saplings. As with *Quararibea*, there was no correlation between the amount of damage due to different causes on the adults and saplings of *Alseis* ($r_s = -0.318$, $P = 0.404$; excluding damage by pathogens, leaf-cutting ants, and unknown causes: $r_s = -0.527$, $P = 0.179$). Overall, 42.2 percent of the leaf damage on the adults (excluding leaf-cutting ants) and 73.9 percent on saplings was caused by insect herbivores. Of this damage, 46.7 percent on the adults and 94.3 percent on the saplings were due to species-specialist herbivores.

HERBIVORE DENSITIES DURING FLUSHING.—The second prediction was that for *Quararibea*, the tree species that showed distance-dependent herbivory in the early wet season, herbivore densities would increase during leaf production. This prediction

TABLE 2. Area (cm²) and, in parentheses, percentage of leaf damage by different causes on adults and saplings of *Alseis blackiana*. Based on 464 cm² of damaged leaf area on adults and 150 cm² on saplings.

Cause	Adults	Saplings	Host Specificity*
<i>Adelpha</i> sp.	61.2 (13.2)	0	Species
Curculionidae sp. 2	39.4 (8.5)	15.6 (10.4)	Species
Oecophoridae sp. 1	26.4 (5.7)	9.5 (6.3)	Species
Gracillariidae sp. 1	5.6 (1.2)	0.3 (0.2)	Species§
Pyralidae sp. 2	0	79.2 (52.8)	Species
Leaf-cutting ants (<i>Atta</i> sp.)	150.8 (32.5)	0	Generalist
Limacodidae sp. 1	0	3.8 (2.5)	Generalist
Acrididae sp. 1	0	2.6 (1.7)	Generalist
Pathogen	118.8 (25.6)	9.9 (6.6)	Unknown
Physical damage	45.9 (9.9)	12.5 (8.3)	—
Unknown	16.2 (3.5)	16.8 (11.2)	—

§ Assessment based on field observations.

* See Table 1 for definitions.

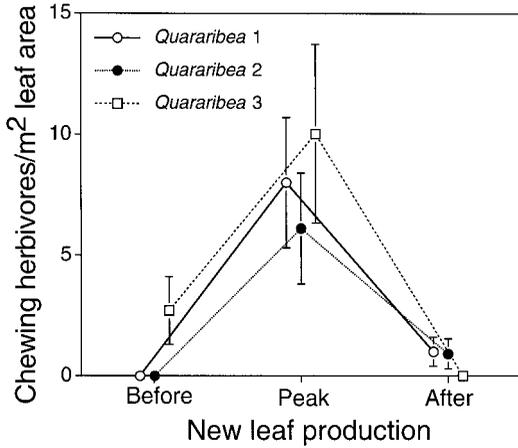


FIGURE 1. Mean number of chewing herbivores (Lepidoptera, herbivorous Coleoptera, and Orthoptera) per m² of leaf area (SE) on *Quararibea* adults. Data are from individual leaves. Before refers to the latest census prior to the onset of leaf flushing, peak refers to the census during the peak of leaf production, and after refers to the first census after the leaves had matured fully.

was tested by comparing herbivore densities before, during, and after leaf production. For all three *Quararibea* adults, the density of chewing herbivores was significantly higher during the period of leaf flushing than before or after, regardless of seasonal timing in leaf production (Fig. 1; repeated measures MANOVA for time effect: $F_{4,27} = 5.39$, $P = 0.011$; the tree effect was not significant). In contrast, the density of chewing herbivores did not differ significantly during the course of leaf expansion for the *Aleis* adults ($P > 0.30$ for time and tree effects). In a comparable test with the saplings of *Quararibea* and *Aleis* (using saplings as replicates), no short-term increase was observed in the density of chewing herbivores during leaf production in the early wet season ($P > 0.30$).

HERBIVORE DENSITIES IN UNDERSTORY AND CANOPY.— Leaf size differed significantly among adults of both *Quararibea* (one-way ANOVA: $F_{2,144} = 9.27$, $P < 0.001$) and *Aleis* ($F_{3,144} = 40.93$, $P < 0.001$). Leaves on saplings of *Quararibea* were much smaller than the leaves on adults ($\bar{x} = 54.7$ cm² and 88.1 cm², respectively; $F_{1,179} = 32.6$, $P < 0.0001$). *Aleis* saplings had somewhat larger leaves than the adults on average (94.7 and 84.6 cm², respectively), although the difference was not significant ($P = 0.081$). Because of these variations in leaf size, comparisons of herbivore abundance

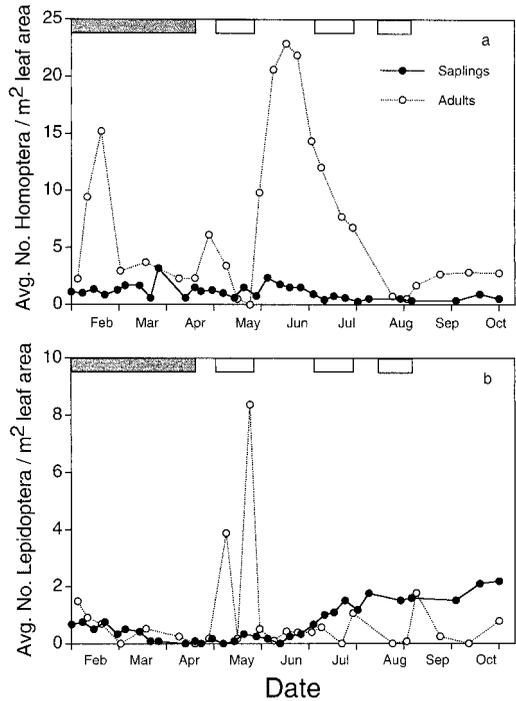


FIGURE 2. Seasonal changes in the mean number of (a) Homoptera and (b) Lepidoptera on leaves of *Quararibea*. The filled circles are for saplings, and the open circles for adults. The dark bars mark the dry season, and the open bars indicate the periods of leaf production by the adults. Note that the vertical scales are different. In (b) the first sharp peak in Lepidoptera numbers represents the increase in chewing herbivore densities during young leaf production in *Quararibea* 1. The second large peak in (b) is the result of the caterpillar outbreak on the other two *Quararibea* adults.

on adults and saplings were made on a leaf area basis, with leaves considered as one-sided.

The numbers of herbivorous insects per leaf area varied considerably during the censuses (Figs. 2 and 3). Overall, saplings of *Aleis* had significantly higher densities of both lepidopteran larvae and chewing insects in general than did the adults (Table 3). *Quararibea* adults and saplings showed neither of these differences, although adults did have higher densities of all herbivores, due to higher densities of Homoptera in the canopy.

The third prediction I tested was if chewing herbivores became more abundant during the wet season in the understory. The densities of lepidopteran larvae, Orthoptera, and herbivorous Coleoptera were compared during two periods of leaf production for the saplings: the first two months of the early wet season (mid-April to mid-June

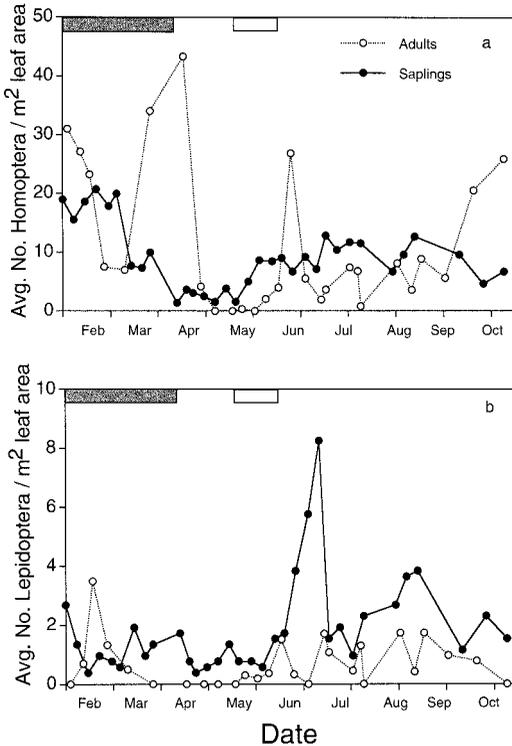


FIGURE 3. Seasonal changes in the mean number of (a) Homoptera and (b) Lepidoptera on leaves of *Alseis*. Symbols follow Figure 1. Note that the vertical scales are different. The large peak in (b) reflects an increase in the abundance of one caterpillar species on the saplings after leaf production had ended.

1995) and the last two months of the late wet season (October and November 1994). For both *Alseis* and *Quararibea* saplings, the density of chewing herbivores was lower in the early wet season than in the late wet season (repeated measures ANOVA: for the seasonal effect, *Alseis*, $F_{1,11} = 11.16$, $P = 0.007$; *Quararibea*, $F_{1,15} = 10.33$, $P = 0.006$). On

average, *Alseis* saplings had 0.96 and 4.3 herbivores/m² leaf area in the early and late wet season, respectively. For *Quararibea* saplings, herbivore densities were 0.18 and 1.6 herbivores/m² in the early and late wet season, respectively. The densities were also higher in the three censuses conducted in the late wet season (September and October) of 1995. For *Alseis* saplings, there were 3.58 herbivores/m² leaf area and 2.66 herbivores/m² for *Quararibea*.

DISCUSSION

HERBIVORES AND HERBIVORY.—The first prediction tested by the herbivore censuses was that the adults and saplings would share the same herbivore species. Of the common chewing herbivore species, 86 percent were shared between the canopy and understory for *Alseis* and 73 percent for *Quararibea*. The herbivores not shared between the adults and saplings were the least common of these species, suggesting that they may exist in both locations but simply were not found. Other rare herbivore species also may be limited to the canopy or understory, but their rarity implies that they probably have little impact on the dynamics of the plant populations. Thus, the assumption that adult trees are a potential source of herbivores attacking nearby juveniles is supported for both tree species.

Alseis exhibited similar levels of leaf damage in the canopy and understory, showing that there is little vertical stratification in the total amount of herbivory for these two species. This was also true for *Quararibea*, but only for the one adult that was not defoliated by the outbreak. Since outbreaks of *Eulepidotis* appear to happen every few years (1985, 1993, and 1995) on BCI, long-term average damage may be higher in the canopy for this tree species. Regardless, the causes of leaf damage in the canopy and understory were not correlated be-

TABLE 3. Mean number of individuals per m² of leaf area (SE) from all censuses on adults and saplings of *Quararibea asterolepis* and *Alseis blackiana*.

	<i>Quararibea</i> adults	<i>Quararibea</i> saplings	Sign [‡]	<i>Alseis</i> adults	<i>Alseis</i> saplings	Sign
Homoptera	7.0 (1.4)	1.1 (0.11)	***	11.4 (2.4)	5.5 (1.0)	NS
Lepidoptera	0.91 (0.35)	0.69 (0.12)	NS	0.69 (0.15)	1.9 (0.29)	***
Coleoptera	0.66 (0.14)	0.37 (0.04)	NS	0.59 (0.14)	0.65 (0.11)	NS
Chewing herbivores [§]	1.8 (0.37)	1.6 (0.17)	NS	1.6 (0.22)	2.8 (0.31)	*
All herbivores	9.6 (1.5)	4.0 (0.25)	**	14.2 (3.0)	11.8 (0.96)	NS

[§] The chewing herbivores category includes Lepidoptera, Coleoptera, and Orthoptera.

[‡] Significance was determined by using *t*-tests on natural log-transformed data. * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$. $N = 3$ *Quararibea* adults and 36 saplings, 4 *Alseis* adults and 50 saplings.

tween the adults and saplings of either species. Still, it is worth noting that for *Quararibea*, the two most damaging insect species were the same in the adults and saplings, and that these two species were responsible for the vast majority of damage by insects in both the canopy and the understory. *Quararibea* was the species that showed distance-dependent herbivory in the previous study (Barone 1996). Although the causes of leaf damage were not identified in that study, it is possible that these two species alone were largely responsible for the occurrence of distance dependence. In contrast, the single most damaging herbivore species of *Alseis* saplings caused no damage to the adults, and the most damaging species of herbivore in the adults (after leaf-cutting ants) caused no damage to the saplings. Herbivory to *Alseis* saplings was never distance-dependent, perhaps reflecting this difference in the identity of the most damaging herbivores in the canopy and understory.

For practical reasons, all of the censuses in this study, of both adults and saplings, were conducted during daylight. This limitation means that a second nocturnal fauna could have been present on these species and would not have been detected. If such herbivores do exist, they probably do not cause much damage. Tables 1 and 2 show that for leaves that were not eaten completely, the majority of damage in both the canopy and understory was attributable to known species. Nonetheless, the possibility that unseen herbivores consumed young leaves whole and for that reason went undetected cannot be ruled out.

HERBIVORE DENSITIES IN THE CANOPY.—The second prediction tested was that for tree species showing distance-dependent herbivory in the early wet season, such as *Quararibea*, herbivore densities would increase during leaf production. For all three *Quararibea* adults, this was indeed the case, as the densities of chewing herbivores were about eight times higher during leaf flushing than either before or after. This short-term increase in herbivore densities was not apparent on the *Alseis* adults during their leaf flush, and *Alseis* never showed any distance-dependent herbivory (Barone 1996).

One explanation for this difference between *Quararibea* and *Alseis* may lie in the feeding specialization of their herbivores. On *Quararibea*, the most damaging herbivores are not only specialized on the genus *Quararibea*, but they also are limited to feeding on young leaves, either exclusively or for the first three or four instars (Barone 1998a). In contrast, all of the chewing herbivore species that

attack *Alseis* leaves are able to grow and mature on either young or mature leaves, although they are specialized to feeding on this tree species at BCI (Barone 1998a). Mature *Alseis* leaves were the softest and had the second highest nitrogen content of the 21 shade tolerant species on BCI examined by Coley (1983). With such palatable food, the herbivores on *Alseis* are not confined to feeding on young leaves, and thus may not be attracted into the canopy of the adults during the early wet season leaf flush. Without the concentration of herbivores in the canopy, distance-dependent herbivory on young leaves would not be expected, and indeed, it was never observed on *Alseis* (Barone 1996).

HERBIVORE DENSITIES IN THE UNDERSTORY.—The third prediction, that herbivore densities would increase during the course of the wet season, was supported, with densities increasing 4.5 times on *Alseis* saplings and 8.9 times on *Quararibea* saplings. Similar trends were not observed on the adults of either species, suggesting that populations of insect herbivores build up in the understory of this forest during the wet season; this may be why distance-dependent herbivory is absent in the late wet season. Any new leaf in the understory is much more likely to be discovered, regardless of its distance to the nearest conspecific adult.

TREE DIVERSITY AND HERBIVORY.—The results of this study substantiate two critical assumptions of the Janzen–Connell model with respect to insect herbivores (Janzen 1970, Connell 1971). First, the presence of the same herbivore species on the adults in the canopies and on the saplings in the understory supports the contention that adult trees can act as the source of natural enemies that can attack nearby juvenile trees in the understory. If adults and juveniles were eaten by different herbivore faunas, then the Janzen–Connell model would be unlikely to work. Second, Janzen and Connell assumed that most natural enemies feeding on trees in tropical forests have rather narrow diets. Combined with feeding trial data (Barone 1998a), the damage data presented here show that specialized herbivores caused most of the insect herbivory on these species, as assumed.

At least on the two tree species in this study, most of the leaf damage to both the saplings and the adults was by no more than 11 common herbivore species. The number of pathogen species attacking these trees was not evaluated; however, there was only one common type of pathogen damage on each tree species and it was the same

on both saplings and adults (J. Barone, pers. obs.). These results suggest that when distance-dependent damage to leaves does occur, it is driven largely by a few species of herbivores. If some of these herbivores were absent in a forest, due to local extinction for example, it could have a profound impact on the density of their host plants.

The two species in this study were chosen because of the differences that I had found previously in the presence of distance-dependent herbivory. Other work in the same forest (Condit et al. 1992) suggests that some, but not all, species of tropical trees show evidence of distance dependence in recruitment and mortality. Why this variation exists is not clear, but the results of this study suggest that at least part of the variation may be attributable to differences in the herbivore faunas of different tree species or in the palatability of their young leaves. Future work on how herbivores influence local tree diversity should focus on under-

standing this variation across tree species. Any such work, however, needs to look at patterns of herbivore densities and herbivory across seasons, and if possible, at different sites across a tree species range, since variations in tree densities across sites may be due in part to differences in their herbivore faunas.

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