

Levels of Herbivory in Two Costa Rican Rain Forests: Implications for Studies of Fossil Herbivory¹

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ABSTRACT

We measured changes in insect herbivore intensity and guild structure in two tropical forests of Costa Rica over a three-year period. We estimated herbivory levels using discrete leaf litter samples to account for factors that influence the types of leaves most likely to be preserved in the fossil record. We found that leaf area removed by insect herbivores did not vary significantly between years within the two sampled forests, but differed across years between forests. The lack of variation in herbivore intensity within forests suggests that estimates of herbivore damage from fossil assemblages may reflect levels of herbivore intensity typically experienced by a given forest, at least over a short ecological timescale. The differences in herbivore intensity between similarly categorized forests suggest that simple one-to-one comparisons between fossil and modern sites can be problematic. The distribution of functional feeding groups also differed on an interannual basis both within and between forests. As guild structure can be highly variable, caution should be taken when comparing modern herbivore guild structures with those from fossil assemblages. Studies of herbivory in fossil assemblages have yielded much lower levels of damage than those found in this study as well as those measured from other modern forests. Leaf fossil preservation, environmental differences, and changes in plant–insect associations through time may account for these differences.

RESUMEN

En este estudio medimos durante un período de tres años los cambios en la intensidad de herbivoría y la estructura de la comunidad de insectos herbívoros en dos bosques tropicales en Costa Rica. Estimamos los niveles de herbivoría usando muestras discretas de hojarasca teniendo en cuenta los factores que influyen sobre el tipo de hojas que tienen una mayor probabilidad de ser preservadas en el registro fósil. El área de la hoja removida por insectos herbívoros no cambió significativamente entre años dentro de los bosques muestreados, pero era diferente entre años entre bosques. La falta de variación en la intensidad de herbivoría dentro de un mismo bosque, sugiere que la estimación del daño por herbivoría en las comunidades fósiles puede reflejar los niveles de intensidad de herbivoría que se presentan típicamente en bosques actuales por lo menos en cortos periodos de tiempo ecológico. La diferencia en la intensidad de herbivoría entre bosques de categoría similar sugiere que las comparaciones simples uno a uno entre sitios fósiles y sitios modernos puede llegar a ser problemática. La distribución de grupos funcionales difieren año a año tanto entre como dentro de bosques. Ya que la estructura de la comunidad puede ser altamente variable, debe tenerse precaución al comparar las estructuras de la comunidad de herbívoros actuales con la comunidad fósil. Los estudios de herbivoría en comunidades fósiles han encontrado niveles de daño mucho menores que las encontradas en nuestro estudio al igual que en otras estudios en bosques actuales. La preservación de hojas fósiles, las diferencias en el ambiente y cambios en la asociación de plantas e insectos a través del tiempo pueden ser la causa de estas diferencias.

Key words: annual variation; discrete vs. long-term measurement; fossil herbivory; rates of herbivory; tropical wet forests.

MODERN LEVELS AND PATTERNS OF HERBIVORE DAMAGE have been examined in a variety of forest types, which include temperate, subtropical, and tropical forests (reviewed in Landsberg & Ohmart 1989 and Coley & Barone 1996). In tropical forests, many of these studies have focused on the analysis of foliar herbivory in the understory and canopy, on persistent and pioneer plants, and on trees at different growth stages (Barone 2000). Among the

patterns that have emerged from these studies, it appears that in the tropics, young leaves are preferentially attacked by herbivores (Lowman 1985, Basset 1991); canopy leaves experience a lower incidence of herbivory than subcanopy leaves (Lowman 1985, Lowman & Heatwole 1992); and shade tolerant species experience lower rates of herbivory (due to their greater investment in defenses) than fast-growing gap colonizers (Kursar & Coley 2003). From a compilation of studies, it also appears that tropical dry forests may experience higher rates of herbivory than tropical wet forests and foliar herbivory may be higher in tropical forests

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than temperate forests (Coley & Barone 1996). Although these studies have added to our understanding of plant–herbivore dynamics in tropical forests, many patterns still remain to be investigated (such as how herbivore abundance and diversity and climatic factors correlate with insect damage levels). Much work is also needed to understand the mechanisms behind these emerging patterns.

In addition to the research being conducted on herbivory in modern forests, there has been a growing amount of work on herbivory in fossil forests. These studies have focused on the evolution of plant–insect interactions and the identification of specialized interactions (Opler 1973, Hickey & Hodges 1975, Hickey & Doyle 1977, Larew 1986, Upchurch & Dilcher 1990, Labandeira *et al.* 1994, Wilf *et al.* 2000) or have tracked community-level patterns of change in insect feeding damage through time (Scott & Taylor 1983, Ash 1997, Beck & Labandeira 1998, Wilf & Labandeira 1999, Smith 2000a, Wilf *et al.* 2001, Labandeira *et al.* 2002). These studies have demonstrated that specialized interactions can be especially long-lived, climatic factors may be important determinants of insect feeding intensity, and modern plant defensive strategies may have been in place as early as 50 million years ago. In addition, many of the studies that have looked at herbivore dynamics in fossil environments have concentrated on what are believed to have been ancient tropical forests (Wilf & Labandeira 1999, Smith 2000a, Wilf *et al.* 2001, Labandeira *et al.* 2002).

While paleobiology provides us with an opportunity to examine community-level patterns of insect feeding damage over an evolutionary timescale, modern methods of estimating herbivore intensity and feeding patterns do not provide us with estimates that are most analogous to the types of leaves often preserved in fossil assemblages. From the extensive literature on the preservation potential of plants, we know that fossil leaf assemblages tend to be dominated by “sun” leaves derived from the forest canopy and that these assemblages are relatively depauperate in understory taxa (Spicer 1981, Ferguson 1985, Greenwood 1992). We also know that fossil lake environments tend to preserve the leaves of plants from the local environment (Spicer & Wolfe 1987, Burnham *et al.* 1992) and that the relative abundance of leaves tends to be proportional to the abundance of trees in the original forest (Spicer 1981, Ferguson 1985, Burnham *et al.* 1992). Finally, a fossil flora preserved in a lake environment is also thought to represent an accu-

mulation of leaf material over a single season to a few years (Behrensmeier *et al.* 2000).

While fossil leaf assemblages tend to be dominated by canopy leaves, much of the work on modern herbivory has been conducted on the more accessible understory leaves. Lowman and Heatwole’s work (1992) comparing canopy and understory herbivory in Australian *Eucalyptus* forests suggests, however, that canopy leaves may have lower levels of herbivory than understory leaves (Lowman 1985). If so, studies that use modern herbivory levels determined from understory leaves for comparison with fossil floras may always find herbivory levels from modern assemblages that are greater than levels of herbivory in fossil floras (Beck & Labandeira 1998, Smith 2000a).

Several researchers who study modern forests have commented on the benefits of utilizing long-term sampling methods as opposed to discrete sampling methods (Lowman 1986, Filip *et al.* 1995). By marking leaves and tracking herbivory through time, one can gain a better estimate of true herbivory because this method accounts for leaves that are completely consumed by insects. Leaves that were completely eaten by insects, however, are not preserved as fossils. Therefore, herbivory estimates using long-term sampling methods, while useful for understanding modern ecosystems dynamics, are not comparable to those from fossil assemblages. As canopy leaves are more likely to be preserved as fossils and because leaf litter samples contain a large proportion of canopy leaves (Burnham 1994, 1997), herbivory data that are collected using discrete sampling methods from modern leaf litter may be most appropriate for comparison with fossil leaf data.

The goals of this study were to (1) document the levels and patterns of insect herbivore damage in two modern tropical forests in a manner that would allow for comparison with herbivory data from fossil assemblages; (2) determine the degree to which insect damage levels and feeding guild structure fluctuate over a three-year ecological timescale (to help us understand the degree to which fossil assemblages might reflect variation in insect damage and guild structure for assemblages that have been preserved over short timescales); and (3) determine the degree to which two lowland tropical forests differ in their patterns of herbivory. If the two forests have similar levels of herbivory, paleontologists will find it easier to identify analogous modern forests with which to compare to their fossil forests. We also provide a brief summary of herbivory data from fossil assemblages and com-

pare these data to trends seen in modern assemblages.

METHODS

STUDY SITES.—Leaves were collected from two sites within two tropical lowland forests in Costa Rica. In each of the forests, the dry season begins in January and ends in mid-April (Herrera 1985). The first site was at La Selva Biological Station in Heredia Province (10°26'N, 83°59'W). This lowland tropical wet forest has a mean annual temperature of 25.9°C and a mean annual precipitation of 400 cm (Holdridge 1967, McDade & Hartshorn 1994). La Selva does not have a true dry season, as it never becomes completely dry—mostly due to the condensation drip that occurs almost nightly. In March, the driest month of the year at this site, La Selva typically receives 15 cm of rainfall (Sanford *et al.* 1994). Approximately 1744 plant species have been described at La Selva (Hartshorn & Hammel 1994). Leaf litter samples were collected from two sites in the primary forest. The first site was located perpendicular to the Camino Experimental Sur, at the 500 m marker. The second site was located perpendicular to the Camino Circular Lejano, just west of the Quebrada El Salto. Approximately 150 leaves were collected from each site for a total of 300 leaves from La Selva in April 1998, April 1999, and February 2000.

The second study site was in the Parque Nacional Corcovado on the Osa Peninsula, Puntarenas Province (8°30'N, 83°35'W). This tropical wet forest has a mean annual temperature of *ca* 25.5°C and a mean annual precipitation of *ca* 550 cm (Kappelle *et al.* 2003). Unlike La Selva, Corcovado has a distinct dry season that usually lasts for one to two months (Kappelle *et al.* 2003). The 1998 El Niño year had an especially long dry season that lasted five months (L. Gilbert, pers. comm.). Approximately 845 plant species have been identified around the Sirena Field Station, although nearly 2695 species have been described from the Osa Peninsula overall (Kappelle *et al.* 2003). In all years, leaf litter samples were collected from two sites in the primary forest. In 1999, the first collection site was located parallel to the Espervales trail, beginning near tree seven, on the self-guided tree path. The second site was located in the primary forest behind the Gilbert Laboratory. In 1999 and 2001, we collected leaves from the Espervales trail, as above, but due to difficulties accessing the laboratory sites, the second collecting site was located

perpendicular to the Ollas trail, 7 m below the top of the ridge. We collected 150 leaves from each site for a total of 300 leaves from Corcovado in March 1998 and March 1999. Approximately 100 leaves were collected from each site for a total of 199 leaves from Corcovado in March 2001.

SAMPLING.—Leaf litter samples were collected in the dry season because many of the trees in both forests drop their leaves during this time of the year. As many of the species in Corcovado are also semi-deciduous, collecting in the dry season allowed us to take into account the herbivory levels experienced by leaves during their yearly cycle. Leaf litter samples did not include leaf fall from previous years, as the decomposition of the leaf litter is fairly rapid (less than one year) in Neotropical rain forests (Parker 1994), and we only collected newly fallen leaves in each sample that were typically green, yellow, or orange, still retained water, and were relatively pliable. Samples consisting of 30 dicotyledonous leaves were collected haphazardly from 1 m² sampling quadrats, at 10 m intervals along a 50 m transect, for a total of five samples (150 leaves) from each site; however, we collected only 20 leaves at each of the five sampling points from Corcovado in 2001. Leaf margins and all insect damage on leaves were traced onto thin tracing paper within three days of collection.

The taxonomic identity of leaves was not determined. Many of the studies on herbivory in modern forests give damage estimates for the entire forest and are not broken down by taxonomic group. This is also true of most paleontological studies on herbivory, which have emphasized the overall amount of leaf area consumed from the entire fossil assemblage.

We counted the number of leaves that had some form of insect damage and documented and measured the type of damage found on each leaf. The commonly used criteria to distinguish the damage patterns made by herbivores from detritivores on fossilized leaves were used to distinguish between herbivore damage and detritivore damage on the modern leaves (Beck & Labandeira 1998, Labandeira 1998). The most important characteristics for identifying herbivore damage were the presence of plant reaction tissue around the damaged area and signs of an insect's presence such as larval or pupal chambers, frass trails, and/or the presence of exit holes. Because we collected only recently fallen leaves, damage due to detritivory was minimal in our samples. Damage due to detritivory and fungus were not included in this study.

TABLE 1. Mean original leaf area and mean leaf area damaged for La Selva and Corcovado during 1999–2001.

Locality	Sample Size	Leaves Damaged (%)	Original Leaf Area (mm ²)		Leaf Area Damaged (mm ²)		
			\bar{x}	SE	\bar{x}	SE	%
La Selva 98	300	92	5124.82	139.09	462.70	31.78	8.9
La Selva 99	298	89	5307.29	270.06	553.19	63.85	9.9
La Selva 2000	300	88	5265.72	223.29	521.63	42.43	9.7
Corcovado 98	300	83	4336.44	240.23	153.46	16.83	4.1
Corcovado 99	300	62	5402.76	302.84	300.20	37.41	4.9
Corcovado 01	199	77	6790.62	429.02	532.32	88.34	6.2

We categorized damage as belonging to one of the following five functional feeding groups: (1) hole feeding—external foliage feeding in which an insect feeds through the leaf leaving behind a hole; (2) margin feeding—external foliage feeding in which an insect feeds on the margins of the leaf; (3) skeletonizing—external foliage feeding in which an insect feeds on the soft tissues of the leaf but does not feed on the veins; (4) galling—internal feeding in which an insect feeds and lives between the leaf layers and the plant responds by building up leaf tissue around the site; and (5) leaf mining—internal feeding in which an immature insect lives and feeds within the leaf layers, leaving behind a blotch or serpentine-shaped mine.

All leaf tracings were scanned into a computer using a flatbed scanner. All leaves and insect damage were measured using NIH Image software for the Macintosh or Scion Image for PCs. Measurements of the leaf area removed by insects, the area of each type of damage, and the total original (pre-damaged) leaf area were made.

STATISTICAL ANALYSIS.—For all parametric comparison of percent data, percent data were arcsine

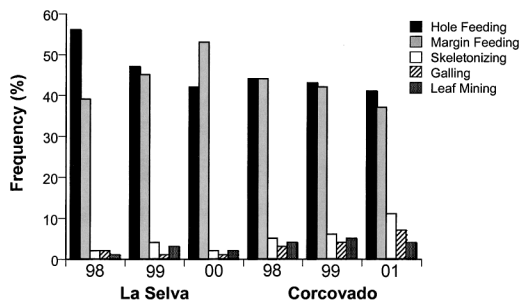


FIGURE 1. Histogram showing the relative distribution of functional feeding groups in each of the six samples. Functional feeding group distributions differed within and between forests (see text). Hole feeding was the most common type of insect damage in all samples except the 2000 La Selva collection.

transformed to meet the assumptions of normality although untransformed values are presented throughout the text. Analysis of variance tests were used to compare differences in leaf sizes and percent leaf area removed both within and between sites. The frequency of leaves that contained insect damage and the distribution of functional feeding types within and between sites were compared using contingency tables. All statistical analyses were performed with JMP 4.0.2 (SAS 2000).

RESULTS

BETWEEN-YEAR VARIATION IN HERBIVORY.—Over the three years surveyed for La Selva, we detected no significant difference in the mean area of leaves collected each year ($F_{2, 895} = 0.19$, $P = 0.82$) or in the percentage of leaves that showed signs of insect damage ($\chi^2 = 3.170$, $P = 0.205$). At this site, 88–92 percent of the leaves showed signs of insect damage during the three-year study (Table 1). The mean percent area removed by insects did not differ among years ($F_{2, 894} = 0.29$, $P = 0.75$) (Table 1). An average of 9.5 percent (8.8–10.2%, 95% CI) \pm SE 0.003 of the leaf area was removed or damaged by insects during the three-year study.

At La Selva, the relative frequency of functional feeding groups found among the sampled leaves was not similar across all years (Fig. 1). While the frequency of the functional feeding groups among leaves did not differ between the 1998 and 1999 samples ($\chi^2 = 9.65$, $P = 0.05$), the frequency in the sample collected in 2000 was significantly different from that collected the two previous years ($\chi^2 = 25.79$, $P = 0.001$). Hole-feeding insects attacked leaves in the 1998 and 1999 samples most often, while margin-feeding insects more commonly attacked leaves in the 2000 sample.

Over the three years surveyed for Corcovado, we measured a significant difference in the mean area of leaves collected in each sample ($F_{2, 798} = 13.91$, $P < 0.0001$), with an increase in average

leaf size during each of the subsequent collecting years (Table 1). The percentage of leaves that showed signs of insect damage did not differ between the 1998 and 2001 samples in which 83 and 77 percent of leaves, respectively, were found to have signs of insect damage ($\chi^2 = 2.54$, $P = 0.111$). Significantly fewer leaves, however, showed signs of insect damage in 1999 (62%) than those collected in 1998 and 2001 ($\chi^2 = 33.39$, $P < 0.0001$). While the average leaf size and frequency of damaged leaves differed across years, the percent mean area removed estimated for each sample did not differ significantly ($F_{2, 796} = 1.03$, $P = 0.35$; Table 1). On average, 4.9 percent (4.4–5.4%, 95% CI) \pm SE 0.003 of the leaf area was removed or damaged by insects over the three-year study period. Interestingly, the increase in the mean size of leaves within the Corcovado samples over time was associated with an increase in the average leaf area removed by insects on damaged leaves ($F_{2, 798} = 14.91$, $P < 0.0001$; Table 1).

At Corcovado, the relative frequency of the different functional feeding groups found among the sampled leaves also varied across years (Fig. 1). The frequency of functional feeding groups was not significantly different between the 1998 and 1999 leaf samples ($\chi^2 = 1.895$, $P = 0.755$), but the 2001 sample had a distribution that was significantly different from both the 1998 and 1999 samples ($\chi^2 = 22.08$, $P = 0.0048$). Damage made by hole-feeding insects was the most common type of damage in all samples from Corcovado (Fig. 1).

BETWEEN-SITE VARIATION IN HERBIVORY.—Despite similarities in the original mean leaf area of leaves collected from La Selva and Corcovado ($F_{1, 1695} = 0.28$, $P = 0.68$; Table 1), the mean leaf area damaged or removed between these sites was significantly different ($F_{1, 1695} = 117.94$, $P < 0.0001$; Table 1). The leaf area removed or damaged by insects was nearly twice as high for La Selva than it was for Corcovado (4.9 vs. 9.5%). The frequency of damaged to undamaged leaves differed between Corcovado and La Selva for the two comparable years of 1998 ($\chi^2 = 11.81$, $P = 0.0006$) and 1999 ($\chi^2 = 57.61$, $P < 0.0001$). The distribution of functional feeding groups was also significantly different between La Selva and Corcovado ($\chi^2 = 115.79$, $P < 0.0001$).

DISCUSSION

BETWEEN-YEAR VARIATION IN HERBIVORY.—During the three years surveyed, the mean percent leaf area

removed by insect herbivores remained relatively stable within both Corcovado and La Selva. This significant lack of yearly variation was impressive for several reasons. First, both sites experienced an extremely dry wet season during the El Niño year of 1998. The dry conditions in the El Niño year would have affected the leaves that were flushed during the beginning of the 1998 wet season and collected in 1999. Although the percent leaf area removed did not appear to differ as a result of the El Niño, there were significantly fewer leaves with insect damage (62 percent) at Corcovado in the 1999 sample relative to the proportion of leaves damaged in 1998 and 2001 (83 and 77%, respectively). As insects in Corcovado removed significantly more leaf tissue, on a per leaf basis, during each of the respective sampling periods, the leaf area removed by insect herbivores appeared to remain constant, however (Table 1). This suggests that El Niño events may impact herbivore–plant dynamics within tropical forests in ways other than by affecting the total area removed by herbivores, which is the measure commonly reported in the modern herbivory literature.

Although the mean area removed remained constant over the three years surveyed at both sites, significant differences were found in the frequency to which leaves were damaged by insects from different functional feeding groups during the same time period. Yearly fluctuations in the distribution of functional feeding groups may reflect fluctuations in the diversity and abundance of insect herbivores on an interannual basis (Fig. 1). Alternatively, given that we did not account for the taxonomic origin of the leaves in each sample, differences in guild structure may (especially in Corcovado, where there were yearly differences in the average size of leaves collected in each sample) reflect differences in the species of plants sampled and their specific interactions with insect herbivores. Finally, although hole feeding was the most common feeding type associated with leaves collected during most sampling periods, the differences in the overall guild structure, both between and within modern forests, suggest that paleontologists must be cautious in how they interpret community-level interactions and their stability in fossil forests (Smith 2000a, Wilf *et al.* 2001, Labandeira *et al.* 2002).

Despite yearly differences in the distribution of functional feeding groups at both La Selva and Corcovado and differences in both the proportion of leaves damaged and the average size of leaves sampled at Corcovado, the mean area removed by

TABLE 2. A summary of herbivory data from paleontological herbivory studies. Some of the data was not available (NA) in the manuscripts. The dominant feeding guild (DFG) in all of the assemblages, when recorded, was hole feeding (HF). Abbreviations for the age of the time periods are as follows: Perm = Permian, Cret = Cretaceous, E Paleo = Early Paleocene, Paleo = Paleocene, E Eocene = Early Eocene, M Eocene = Middle Eocene, and L Eocene = Late Eocene. Abbreviations for forest type are as follows: NAngio = non-angiosperm, Trop = predominantly tropical, DTr-Temp = transitional dry tropical to temperate, and Temp = temperate.

	Age of Assemblage Studied							
	Perm ¹	Cret ²	E Paleo ²	Paleo ³	E Eocene ³	M Eocene ⁴	M Eocene ⁵	L Eocene ⁵
Forest Type	NAngio	Trop	Trop	Trop	DTr-Temp	DTr-Temp	DTr-Temp	Temp
Area damaged (%)	3.30	NA	NA	NA	NA	NA	2.5	1.4
Leaves damaged (%)	31.6	16	4	28	35	19.4	34	23
DFG	HF	NA	NA	NA	NA	NA	HF	HF

¹ Beck & Labandeira 1998.

² Labandeira *et al.* 2002.

³ Wilf & Labandeira 1999.

⁴ Wilf *et al.* 2001.

⁵ Smith 2000a.

insects within each site remained relatively constant. A few studies that have used discrete sampling methods over three to eight years have also found herbivory levels to remain relatively constant over time (Reichle *et al.* 1973, Filip *et al.* 1995). As fossil plant assemblages in lakes are thought to represent leaf material accumulated over a single season to a few years (Behrensmeyer *et al.* 2000), our study suggests that herbivory levels (*e.g.*, the proportion of leaf area removed by insect herbivores) measured from these fossil assemblages may provide an accurate estimate of herbivory levels typical for a given site, at least over an equivalent ecological timescale. Studies that examine seasonal changes in herbivory levels and damage levels over greater timescales (5, 10, 50, or 100 yr) are needed.

BETWEEN-SITE VARIATION IN HERBIVORY.—While herbivory levels within La Selva and Corcovado remained rather constant over the three years surveyed, herbivory levels differed between forests. In Corcovado, an average of 4.9 percent of leaf area was lost to insect herbivores while La Selva experienced nearly double that amount (9.5%). The mean area damaged in all of the La Selva samples and the 2001 Corcovado sample were well within the range of herbivore levels found in other studies of Neotropical forests that used discrete sampling to estimate understory herbivory levels: 5.5–10.5 percent (Odum & Ruiz-Reyes 1970, Johnstone 1981, Hendrix & Marquis 1983, Dirzo 1984, Newberry & de Foresta 1985, de la Cruz & Dirzo 1987, Sterck *et al.* 1992, Filip *et al.* 1995). The mean area removed during 1998 and 1999 in Corcovado (4.1 and 4.9%, respectively) was lower than

the range typically found in other discretely sampled Neotropical forests. It appears that understory herbivory levels may indeed be higher than those found in the canopy, and therefore, discrete samples collected from the leaf litter may be most appropriate for comparison with fossil assemblages.

For the two comparable years of 1998 and 1999, the two forests differed not only in the amount of leaf area removed by insect herbivores, they also differed in the frequency of leaves that showed signs of insect damage (92 and 89% for La Selva and 83 and 62% for Corcovado, during the years 1998 and 1999, respectively) and in their distributions of functional feeding groups. It is not apparent whether the differences between these forests are the result of abiotic factors such as differences in seasonality, rainfall, or even slight differences in temperature; biotic factors such as differences in herbivore diversity and/or abundance; or a combination of these factors. The yearly differences between these two forests suggest that choosing appropriate modern forests to compare with fossil forests may be more difficult than previously thought, especially given that taxonomically comparable forests are not readily available. The methods used for estimating mean annual temperature and mean annual precipitation of fossil floras (Wolfe 1978, Wing & Greenwood 1993, Wilf *et al.* 1998, Kowalski & Dilcher 2003) have improved, but it is still difficult to interpret the seasonality of a fossil assemblage; further, estimating the abundance or true diversity of insect herbivores associated with fossil forests, even when insect body fossils are present (Smith 2000b), is nearly impossible to do. As such, it may be best to compare

levels of insect herbivory in fossil tropical forests to those from a variety of modern tropical forests that have been sampled discretely from the leaf litter to determine the degree to which herbivory in modern and fossil forests differ. In addition, as herbivore intensity and frequency of attack differed between similarly categorized forests, we suggest that estimates of leaf area removed by insects from a few fossil assemblages should not be combined and taken as global means for particular forest types as some authors have suggested (Labandeira *et al.* 2002).

HERBIVORY IN THE FOSSIL RECORD.—Levels of herbivore damage from warm temperate to tropical fossil assemblages are consistently lower than those from discretely sampled modern forests (Table 2). The differences in herbivory levels between modern and fossil assemblages may be due to a variety of factors. First, the process of leaf fossilization may explain the differences in fossil and modern herbivory levels, as fossilization may somehow exclude insect-damaged leaves; however, one study of plant preservation showed that leaves with damage become waterlogged and sink more quickly than undamaged leaves, leading to a greater potential for fossilization of damaged leaves (Ferguson 1985). Second, the differences in herbivore damage between the modern and fossil assemblages may be due to environmental differences. While our study

suggests insect damage levels can differ significantly among similarly categorized “tropical” forests, the levels found in fossil assemblages (1.4–3.3% leaf area removed) appear to be much lower than the range of estimates collected from our study (4.1–9.9%) and other modern tropical forests (5.5–10.5%, discrete sampling only). This suggests that modern forests may in fact experience herbivory levels greater than those experienced in ancient tropical and warm temperate forests. It is possible that these differences are due to evolutionary change through time and that insect damage levels were indeed lower in the fossil record. This may be due to a variety of reasons, including lower insect diversity in the past (Labandeira & Sepkoski 1993, Farrell 1998) and coevolutionary dynamics, that is, the reciprocal evolution of diversifying plant and insect clades (Ehrlich & Raven 1964).

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LITERATURE CITED

- ASH, S. 1997. Evidence of arthropod–plant interactions in the Upper Triassic of the southwestern United States. *Lethaia* 29: 237–248.
- BARONE, J. A. 2000. Comparison of herbivores and herbivory in the canopy and understory for two tropical tree species. *Biotropica* 32: 307–317.
- BASSET, Y. 1991. The spatial distribution of herbivory, mines, and galls within an Australian rain forest tree. *Biotropica* 23: 271–281.
- BECK, A. L., AND C. C. LABANDEIRA. 1998. Early Permian insect folivory on a gigantopteroid-dominated riparian flora from north–central Texas. *Palaeog. Palaeoclimatol. Palaeoecol.* 142: 139–173.
- BEHRENSMEYER, K., S. M. KIDWELL, AND R. A. GASTALDO. 2000. Taphonomy and paleobiology. *Paleobiology* 26: 103–147.
- BURNHAM, R. J. 1994. Patterns in tropical leaf-litter and implications for angiosperm paleobotany. *Rev. Palaeobot. Palynol.* 81: 99–113.
- . 1997. Stand characteristics and leaf litter composition of a dry forest hectare in Santa Rosa National Park, Costa Rica. *Biotropica* 29: 384–395.
- , S. L. WING, AND G. G. PARKER. 1992. The reflection of deciduous forest communities in leaf litter—Implications for autochthonous litter assemblages from the fossil record. *Paleobiology* 18: 30–49.
- COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27: 305–335.
- DE LA CRUZ, M., AND R. DIRZO. 1987. A survey of the standing levels of herbivory in seedlings from a Mexican rain forest. *Biotropica* 19: 98–106.
- DIRZO, R. 1984. Insect–plant interactions: Some ecophysiological consequences of herbivory. *In* E. Medina, H. A. Mooney, and C. Vasquez-Yanes (Eds.). *Physiological ecology of plants of the wet tropics*, pp. 209–224. Dr W. Junk, The Hague, The Netherlands.
- EHRlich, P. R., AND P. H. RAVEN. 1964. Butterflies and plants: A study in coevolution. *Evolution* 18: 586–608.

- FARRELL, B.D. 1998. "Inordinate fondness" explained. Why are there so many beetles? *Science* 281: 555–559.
- FERGUSON, D. K. 1985. The origin of leaf-assemblages—new light on an old problem. *Rev. of Palaeobot. and Palynol.* 46: 117–188.
- FILIP, V., R. DIRZO, J. M. MAASS, AND J. SARUKHAN. 1995. Within-year and among-year variation in the levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. *Biotropica* 27: 78–86.
- GREENWOOD, D. R. 1992. Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. *Rev. Palaeobot. Palynol.* 71: 149–190.
- HARTSHORN, G. S., AND B. E. HAMMEL. 1994. Vegetation types and floristic patterns. *In* L. McDade, K. Bawa, H. Hespeneheide, and G. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 73–89. University of Chicago Press, Chicago, Illinois.
- HENDRIX, S. D., AND R. J. MARQUIS. 1983. Herbivore damage to three tropical ferns. *Biotropica* 15: 108–111.
- HERRERA, W. 1985. *Clima de Costa Rica: Vegetacion y clima de Costa Rica*, volumen 2. Editorial Universidad Estatal a Distancia, San Jose, Costa Rica.
- HICKEY, L. J., AND J. A. DOYLE. 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Bot. Rev.* 43: 3–104.
- , AND R. W. HODGES. 1975. Lepidopteran leaf mine from Early Eocene wind river formation of northwestern Wyoming. *Science* 189: 718–720.
- HOLDRIDGE, L. R. 1967. *Life zone ecology*, 2nd edition. Tropical Science Center, San Jose, Costa Rica.
- JOHNSTONE, I. M. 1981. Consumption of leaves by herbivores in mixed mangrove stands. *Biotropica* 13: 252–259.
- KAPPELLE, M., M. CASTRO, H. ACEVEDO, L. GONZALEZ, AND H. MONGE. 2003. *Ecosystems of the Osa Conservation Area (ACOSA)*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
- KOWALSKI, E. A., AND D. L. DILCHER. 2003. Warmer paleotemperatures for terrestrial ecosystems. *Proc. Nat. Acad. Sci.* 100: 167–170.
- KURSAR, T. A., AND P. D. COLEY. 2003. Convergence in defense syndromes of young leaves in tropical rainforests. *Biochem. Syst. Ecol.* 31: 929–949.
- LABANDEIRA, C. C. 1998. Early history of arthropod and vascular plant associations. *Annu. Rev. Earth Planet. Sci.* 26: 329–377.
- , D. L. DILCHER, D. R. DAVIS, AND WAGNER, D. L. 1994. Ninety-seven million years of angiosperm–insect association—Paleobiological insights into the meaning of coevolution. *Proc. Nat. Acad. Sci.* 91: 12,278–12,282.
- , K. R. JOHNSON, AND P. WILF. 2002. Impact of the terminal Cretaceous event on plant–insect associations. *Proc. Nat. Acad. Sci.* 99: 2061–2066.
- , AND J. J. SEPKOSKI. 1993. Insect diversity in the fossil record. *Science* 261: 310–315.
- LANDSBERG, J., AND C. OHMART. 1989. Levels of insect defoliation in forests—Patterns and concepts. *Trends Ecol. Evol.* 4: 96–100.
- LAREW, H. G. 1986. The fossil gall record: A brief summary. *Proc. Entomol. Soc. Wash.* 88: 385–388.
- LOWMAN, M. D. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Aust. J. Ecol.* 10: 7–24.
- . 1986. Insect herbivory in Australian rain forests—Is it higher than in the tropics? *Proc. Ecol. Soc. Aust.* 14: 109–119.
- , AND H. HEATWOLE. 1992. Spatial and temporal variability in defoliation of Australian Eucalypts. *Ecology* 73: 129–142.
- MCDADE, L., AND G. HARTSHORN. 1994. *La Selva Biological Station*. *In* L. McDade, K. Bawa, H. Hespeneheide, and G. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 6–14. University of Chicago Press, Chicago, Illinois.
- NEWBERRY, D. M., AND H. DE FORESTA. 1985. Herbivory and defense in pioneer gap and understory trees of tropical rain forest in French Guiana. *Biotropica* 17: 238–244.
- ODUM, H. T., AND J. RUIZ-REYES. 1970. Holes in leaves and the grazing control mechanism. *In* H. T. Odum and R. F. Pigeon (Eds.). *A tropical rainforest*, pp. 169–180. Atomic Energy Commission, Rio Piedras, Puerto Rico.
- OPLER, P. A. 1973. Fossil Lepidopterous leaf mines demonstrate age of some insect–plant relationships. *Science* 179: 1321–1323.
- PARKER, G. 1994. Soil fertility, nutrient acquisition, and nutrient cycling. *In* L. McDade, K. Bawa, H. Hespeneheide, and G. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 54–64. University of Chicago Press, Chicago, Illinois.
- REICHEL, D. E., R. A. GOLDETEL, R. I. CANHOOK, AND G. J. DODSON. 1973. Analysis of insect consumption in a forest canopy. *Ecology* 54: 1076–1083.
- SANFORD, R. L. JR., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology and aquatic systems. *In* L. McDade, K. Bawa, H. Hespeneheide, and G. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 54–64. University of Chicago Press, Chicago, Illinois.
- SAS 2000. JMP 4.0.2. SAS, Cary, North Carolina.
- SCOTT, A. C., AND T. N. TAYLOR. 1983. Plant animal interactions during the Upper Carboniferous. *Bot. Rev.* 49: 259–307.
- SMITH, D. M. 2000a. The evolution of plant–insect interactions: Insights from the Tertiary fossil record. PhD dissertation, University of Arizona, Tucson, Arizona.
- . 2000b. Beetle taphonomy in a recent ephemeral lake, southeastern Arizona. *PALAIOS* 15: 152–160.

- SPICER, R. A. 1981. The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. *Geol. Surv. Prof. Pap.* 1143: 1–77.
- , AND J. A. WOLFE. 1987. Plant taphonomy of Late Holocene deposits in Trinity (Clair Engle) Lake, northern California. *Paleobiology* 13: 227–245.
- STERCK, F., P. VANDERMEER, AND F. BONGERS. 1992. Herbivory in two rain forest canopies in French Guyana. *Biotropica* 24: 97–99.
- UPCHURCH, G. R. JR., AND D. L. DILCHER. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, Southeastern Nebraska. *USGS Surv. Bull.* 1915: 1–55.
- WILF, P., AND C. C. LABANDEIRA. 1999. Response of plant–insect associations to Paleocene–Eocene warming. *Science* 284: 2153–2156.
- , ———, K. R. JOHNSON, P. D. COLEY, A. D. CUTTER. 2001. Insect herbivory, plant defense, and Early Cenozoic climate change. *Proc. Nat. Acad. Sci.* 98: 6221–6226.
- , ———, W. J. KRESS, C. L. STAINES, D. M. WINDSOR, A. L. ALLEN, AND K. R. JOHNSON. 2000. Timing the radiation of leaf beetles: Hispines on gingers from latest Cretaceous to recent. *Science* 289: 291–294.
- , S. L. WING, D. R. GREENWOOD, AND C. L. GREENWOOD. 1998. Using fossil leaves as paleoprecipitation indicators: An Eocene example. *Geology* 26: 203–206.
- WING, S. L. AND D. R. GREENWOOD. 1993. Fossils and fossil climate—the case for equable continental interiors in the Eocene. *Philosophic. Trans. R. Soc. Lond., B* 341: 243–252.
- WOLFE, J. A. 1978. Paleobotanical interpretation of Tertiary climates in northern hemisphere. *Am. Sci.* 66: 694–703.
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