

Leaf damage in tropical rain forest canopies

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SUMMARY

- 1 Leaf damage levels of three comparable tropical rain forest canopies were examined in relation to three questions: what is the level of herbivore damage in a tropical rain forest canopy, does it vary between sites or between plant categories, and when does the damage occur?
- 2 Between-site variation in leaf damage levels and damage type was very low despite major contrasts in plant species composition, plant diversity, herbivore species and herbivore type.
- 3 Levels of damage to leaves from vines were lower than those from trees.
- 4 Apparent damage levels (excluding those leaves which have abscised) were higher than previously reported, and actual damage levels (taking abscission levels into account) may be considerably higher.
- 5 Most apparent and actual leaf damage occurs when the leaves are young.
- 6 The similarities in leaf damage levels between sites and the differences in leaf damage levels between plant categories are discussed.

INTRODUCTION

Insects are probably the most important arboreal herbivores; the larger herbivores (e.g. apes, iguanas, etc.) seem to consume relatively little of the available foliage (Leigh & Smythe 1978; Nagy & Milton 1979). Published evidence suggests that chewing insects take about 7–10% of the leaf area (J. Procter, pers. comm.; Bray 1964; Nielsen 1978; Leigh & Smythe 1978), though much less—perhaps 1%—in terms of primary production. However, indirect effects of phytophagous insects are widespread both on the scale of the habitat (e.g. Chew 1974; Owen & Wiegert 1976; Golley 1977) and of a single plant, branch or leaf (Haukioja 1980; Varley 1967; McGregor 1968; Rhoades 1979).

Many of these effects are likely to be general ones caused by all herbivores rather than due to the action of particular herbivore species, so it is necessary to have some idea of the overall levels of insect grazing in order to assess the importance of herbivore impact on their food plants. This is particularly true of tropical rain forests (TRF) about which there is little information on herbivore impact. Further, the facts which are available are largely based on litter or understorey samples, and it is in the TRF canopy that the majority of herbivore–plant interactions are thought to occur.

The present paper describes a preliminary attempt to fill some of these gaps by looking at herbivore impact as represented by leaf damage in the canopies of three comparable rain forest sites. Three questions are examined:

- (i) What is the level of insect herbivore damage in a tropical rain forest canopy?
 (ii) Does herbivore damage vary between sites and/or between broad categories of plant such as trees and epiphytes?
 (iii) When does the damage occur?

Study sites

Samples were taken from three sites: one in the San Blas region of coastal Panama ($8^{\circ} 48' N$, $77^{\circ} 40' W$); and two neighbouring areas on the Eastern coast of Papua New Guinea, south of Lae ($7^{\circ} 25' S$, $147^{\circ} 16' E$). All three sites consisted of seasonal lowland evergreen rain forest, with similar climatic regimes, and were sampled during their respective dry seasons. The three sites were structurally similar—each with fairly distinct understorey (particularly rich in palms in Panama), a more or less continuous leaf layer at 25–30 m and emergent species reaching 40–50 m.

Despite this overall similarity between sites, there were several important differences, beyond the obvious contrast in species composition, between the Panama and Papua New Guinea (PNG) sites (summarized in Table 1). The most outstanding of

TABLE 1. Some differences between study sites

	Panama	PNG North	PNG South
Terrain	Flat	Flat	Sloping
Drainage	Good	Poor	Good
Dominant emergents	Many spp.	<i>Anisoptera thurifera</i>	<i>Anisoptera thurifera</i> and others
Mean tree density \bar{x} 100 m ² S.E.	4.24 0.11	5.46 0.45	6.92 0.15
Transect length (m)	90	50	40
Number of samples			
trees	33	34	26
vines	—	23	27
Number of spp. sampled			
trees	23	7	23
vines	—	11	20

these were soil and drainage, plant species diversity and mean tree density. The Panama site had a lower mean tree density/100 m² than PNGS (South) or PNGN (North) ($d=2.75$, 55 d.f., $p < 0.01$ and $d=2.39$, 55 d.f., $P < 0.05$, respectively), due largely to a higher number of small trees which were more clumped. This was reflected in the number of canopy samples collected per meter of transect. Furthermore, tree diversity was high in PNGS and Panama sites and the drainage good, while in the PNGN site, tree diversity was considerably lower and the drainage poor.

METHODS

Sample collection

Leaf samples were collected from each site along transect lines at the level of the continuous leaf layer (CLL), some 25–30 m above ground level, using a series of specially built aerial walkways. These are catwalk bridges suspended from emergent trees so as to rest at canopy level (Sugden *et al.*, in press). The resultant transect lengths were *c.* 90 m in Panama, 50 m in PNG North and 40 m in PNG South. Leaves were collected by means of telescopic pruners which gave a reach of 8 m either side of the walkways as well as above and below them.

The samples consisted of at least 100 sun leaves from the outer layers of the tree crowns. Samples of both CLL and emergent trees were taken from the same height range (20–30 m), the actual choice of branches being determined by accessibility. In PNG, samples were taken from vine species as well as tree species.

Immediately after collection, the branches were examined for insect herbivores, scored for frequency of damage types and % leaf damage levels, then oven dried and pressed.

Scoring for damage level

One hundred randomly selected mature leaves from each branch sample were scored for % leaf damage on a scale of 0–5, with an additional class for undamaged ('perfect') leaves in the PNG samples. The score classes corresponded to: 0=0–5%, 1=6–30%, 2=31–50%, 3=51–70%, 4=71–90% and 5=91–100% leaf area removed. In addition to this scoring, the types of damage other than leaf area removal were recorded—selectivity eaten or skeletonized, mined, rolled, galled, and diseased—as were the scars left by leaves which had abscised. Young (not fully expanded) and semi-mature leaves (fully expanded but different in colour or texture to mature leaves) were also examined and scored separately.

The mean damage level of each branch sample was calculated by multiplying the number of leaves within each damage score class by the mean of that score class ($P=0$, 0=2.5%, 1=15%, 2=40%, 3=60%, 4=80% and 5=95% leaf area removed). This provided a % leaf damage for each sample based on visual scoring. The accuracy of these estimates was assessed by comparing the visual estimates of twenty branch samples (10 from PNG and ten from Panama) with 'mechanical' estimates obtained using a leaf area meter. A leaf area meter is unable to measure % damage caused by, e.g. miners and skeletonizers which were included, though not separately, in the visual estimates. It also relies on the reconstruction of the original shapes of heavily damaged leaves—those within score classes 4 and 5—which is likely to be very inaccurate. To compensate for these errors, the leaf area meter was used on leaves in score classes P–3, and the damage due to miners etc. and heavily damaged leaves added on. Thus, a full statistical comparison between visual and 'mechanical' estimates is not possible as the two sets of data are not fully independent. However, a plot of the two estimates (Fig. 1) suggests that the visual scores give rise to overestimates of % leaf area removal, and that the data from each country is biased differently. To compensate for this, the % leaf

damage figures quoted in the results section have been corrected from the visual estimates using the relationships given (Fig. 1) for the samples from each country.

Throughout, the number of missing leaves—as indicated by leaf scars—has been excluded from the calculations of % leaf damage, as the cause of leaf abscission was not known. Their inclusion as herbivore damaged leaves is therefore uncertain. The % leaf damage levels used are therefore apparent damage levels, rather than actual leaf damage levels, the latter being applicable only if the levels of herbivore induced abscission are known and included in the damage estimates.

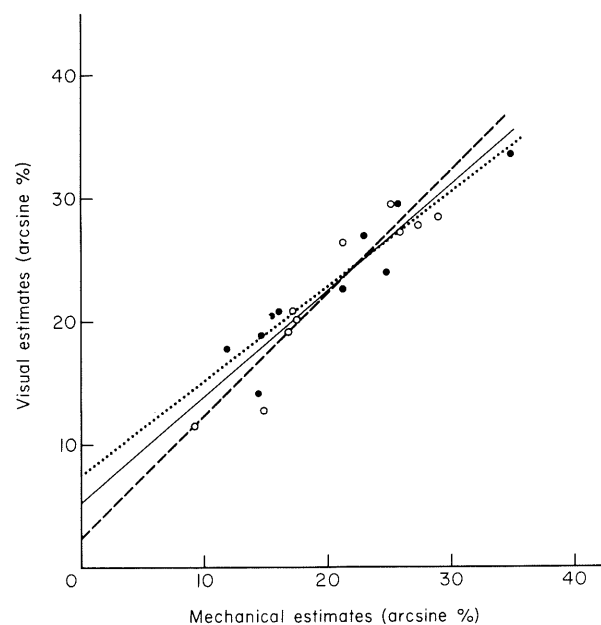


FIG. 1. Calibration curve for leaf damage estimates (●) PNG, $N=10$; (○) Panama, $N=10$: (---) Panama, $y=2.44+0.98x$, $r=0.89$, $P<0.01$; (·····) PNG, $y=7.5+0.76x$, $r=0.87$, $P<0.01$; (—) Both, $y=4.10+0.98x$, $r=0.87$, $P<0.01$.

Damage development

Selected branches of four tree species were tagged and the leaves mapped so that each leaf was individually identifiable. Every week for up to 9 weeks thereafter the leaves were scored for presence/absence, and if present then for damage level and type and leaf length. New leaves were included in the study as they appeared on the tagged branches. These new leaves were used to establish a relationship between leaf age and leaf length for each species, which was then used to age those growing leaves of which the emergence time was not known. Samples of untagged leaves, adjacent to the tagged foliage, and of known age, were examined when possible for leaf toughness using a penetrometer (Wint 1979). Leaf toughness, like leaf length, increases rapidly when the

leaves are young and stabilizes at maximum levels when the leaves are mature (Wint 1979). These maxima were used as a further indicator of leaf maturity.

RESULTS

Herbivore types

Panama and PNG rain forests support markedly different types of herbivore. In Panama, casual observation suggested that as much as 80% of the Apparent leaf damage may be due to leaf-cutter ants (*Atta* sp.). Mammalian and reptilian herbivores were also seen, though in small numbers. In PNG there are neither leaf-cutter ants nor large vertebrate herbivores, and the majority of leaf damage was probably caused by Lepidoptera, Coleoptera and Orthoptera.

In all three sites, the largest component (approx. 95%) of the Apparent leaf damage was caused by animals which left gaps or in holes in the leaves ('chewers'). Of the other damage categories (Fig. 2), skeletonizing ('selective eating') was most frequently recorded, the mean site frequencies ranging from *c.* 2–8%, while of the remaining four damage types only miners were recorded on more than an average of 2% of the leaves counted at any site. Statistically significant differences in the proportions of these secondary damage types can be found between habitats (e.g. between miners in

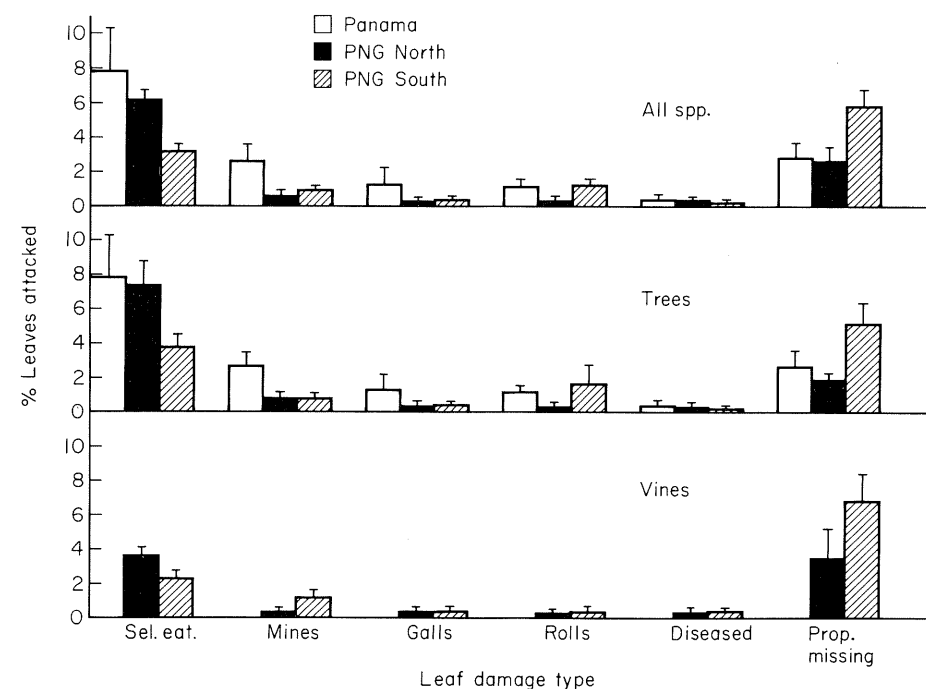


FIG. 2. Frequencies of leaf damage types (excluding 'chewed') in three rain-forest canopies (Sel. eat = skeletonized; prop. missing = proportion missing; others as stated).

Panama and PNG trees) but such a small area of the leaves was damaged that relative to the 'chewers' they are of little importance.

Leaf damage levels

Branch samples, each containing at least 100 leaves, were collected from 133 canopy plants: thirty-three from Panama, forty-seven from PNG North and fifty-three from PNG South. Of these twenty-three samples from PNG North and twenty-seven from PNG South were vine species, and the rest were trees. No vines were collected from Panama. The mean Apparent damage levels for the individual branch samples ranged from 2.02% to 76.8% in Panama, 1.4 to 31.5% in PNG North and 0 to 35.4% in PNG South.

The majority of samples were taken from separate species though several species replicates were obtained, particularly from the PNG North site. The Apparent damage levels of these species replicates (Fig. 3) suggest that each species suffers a characteristic level of Apparent leaf damage with relatively little variation within species, so that it is possible to demonstrate significant separation between species damage levels that differ by as little as 8%. This also lends support to the validity of point sampling for apparent herbivore impact.

A third measure of leaf damage levels is the mean Apparent damage level for each site. When all species examined within each site are considered together, the habitat means range from *c.* 9% to *c.* 12.5% (Fig. 4), and do not differ significantly from each

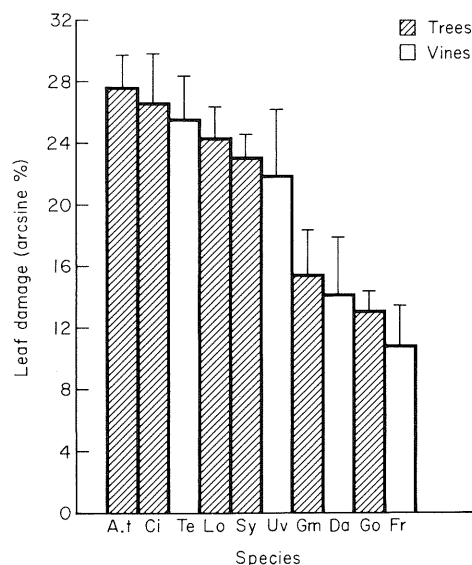


FIG. 3. Mean (and standard error) apparent leaf damage levels of some canopy species. (A.t. = *Anisoptera thurifera*, *n* = 5; Ci = *Cinnamomum* sp., *n* = 4; Te = *Tetracera* sp., *n* = 4; Lo = *Lophopetalum* sp., *n* = 6; Sy = *Syzygium* sp1, *n* = 4; Uv = *Unidentified* vine, *n* = 5; Gm = *Gmelina* sp., *n* = 4; Da = *Dahlbergia* sp., *n* = 4; Go = ? *Gonostylus* sp., *n* = 3; Fr = *Freycinetia* sp., *n* = 3.)

other, ($d < 1.89$, $P > 0.1$), though this may be due to high within-sample variation. However, these figures are surprisingly similar in view of the major differences in site characteristics and herbivore type described earlier. The figures are somewhat higher than have been found by other workers (e.g. Leigh & Smythe 1978; Bray 1964), and illustrate the value of collecting leaf samples directly from the canopy rather than using litter samples which may overlook the more heavily damaged or more rapidly decomposed leaves.

If the tree and vine samples are considered separately, the similarity between sites becomes more striking. The site means for the tree samples from Panama, PNG North and PNG South are 12.7%, 12.5% and 13.7%, respectively. The equivalent figures for the vines from PNG North and PNG South (no vines were sampled in Panama) are

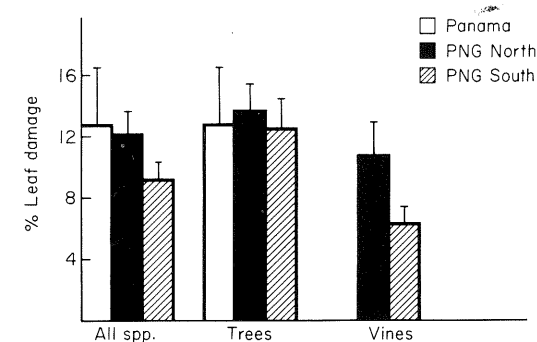


FIG. 4. Apparent mean (+95% c. level) leaf damage levels (% leaf area) in three rain forest canopies.

10.7% and 6.2%, respectively (Fig. 4). The tree figures are all statistically indistinguishable ($d < 0.49$, NS) but are all significantly greater than those from the vine samples of PNG South ($d > 2.99$, $P < 0.01$), but not from the PNG North vine samples ($d < 1.17$, NS).

It is likely that these figures are underestimates of the % leaf area removed by herbivores. The habitat means for the % of missing leaves range from approximately 3% to 6%, of which a proportion are likely to be due to herbivore activity. Further, the damage caused by sucking insects may reduce photosynthetic area. The figures are, however, likely to be accurate estimates of the % area removed in those leaves examined as it is thought that holes expand at the same rate as the lamina during leaf growth (Coley 1979; Reichle *et al.* 1973). Therefore, the % leaf area removed remains constant irrespective of when the damage occurred. The timing of the damage must have a major effect on the biomass of leaf material removed and thus the point sampling used in this study reveals little about herbivore load.

Damage development

The timing of herbivore damage was examined in two ways: by point sampling of the young foliage collected with the branch samples, and by continuously monitoring the damage levels of the growing leaves of selected species.

The young leaves collected on the branch samples of mature leaves were generally

less damaged than was the mature foliage. The habitat mean Apparent damage levels for the immature foliage were 5.8%, 4.3% and 3.6% for the Panama, PNG North and PNG South sites, respectively. These are from approximately 30–50% of the levels found in old leaves. As leaves mature in a relatively short period relative to leaf life, this suggests that the rate of herbivory on young leaves much exceeds that on old leaves.

Damage levels were monitored in the growing leaves of four species, two from Panama (*Eschweilera* sp. and *Swartzia panamensis* Benth) and two from PNG (*Anisoptera thurifera* BL. subsp. *polyandra* (Bl.) Ashton and *Syzygium* sp.).

In three of the species (*Eschweilera*, *Swartzia* and *Anisoptera*) the Apparent damage levels (i.e. with the missing or abscised leaves ignored) stabilize when the leaves become mature. Leaf maturity was indicated by maximum leaf length or maximum leaf toughness (Fig. 5). This is unlikely to be a hole expansion phenomenon for the

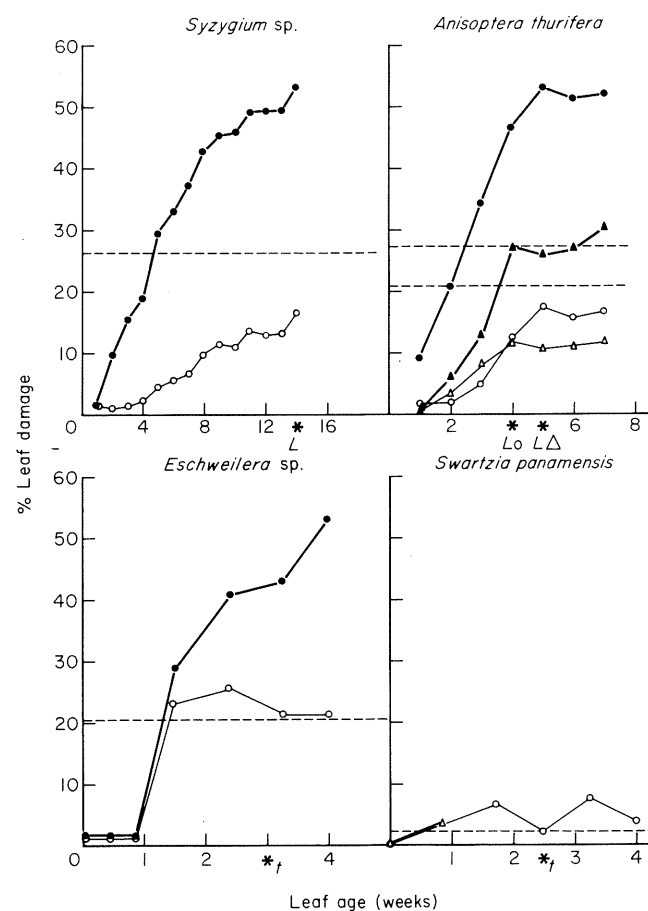


FIG. 5. Development of leaf damage levels with leaf age: closed symbols (●, ▲) % damage including missing leaves; open symbols (○, △) % damage excluding missing leaves (each symbol refers to a specific individual); * maximum length (*L*) or toughness (*t*); (---) apparent damage level of mature leaves.

reasons mentioned earlier, which suggests that the majority of herbivore damage occurs in these species when the leaves are young. In the fourth species—*Syzygium*, which in contrast to the other three, is a continuously flushing species—Apparent leaf damage appears to increase linearly with time. However, extrapolation of the data shown suggests that even in this species, the Apparent damage levels of the younger leaves would reach that of the surrounding mature foliage (which shows a fairly constant damage level) within about 20 weeks of leaf flush. Published information concerning leaf longevity is very sparse, though it is likely that, as an evergreen species, *Syzygium* retains its leaves for a year or more (M. Swaine, pers. comm.). Here again the majority of herbivore damage occurs in the young leaves.

During this monitoring programme limited observations revealed that those leaves which abscised during the study period were those which were heavily damaged. This suggests that much of the abscission was herbivore-induced. If these missing leaves are incorporated into the damage level figures (Fig. 5) to give 'Actual' damage levels, the results from three species (all except *Eschweilera*) suggest substantially similar conclusions to those reached above, in that the rate of herbivore damage is lower in mature than young leaves. However, though in *Swartzia*, Actual and Apparent % leaf damage was identical (as there were no missing leaves recorded from this species), in *Syzygium* and *Anisoptera* Actual damage levels are approximately three times the Apparent damage levels. Thus, Apparent leaf damage estimates may be considerable underestimates of the actual damage levels.

The data from *Eschweilera* also indicates that Actual leaf damage may markedly exceed Apparent damage but, in contrast, suggests that Actual damage levels may continue to increase after Apparent levels have stabilized. This in turn suggests that abscission (which may be herbivore-induced) continues after the leaves have become mature, and that the stable Apparent leaf damage levels may reflect a damage level at which the leaf abscission occurs.

CONCLUSIONS

The results of this preliminary study suggest that, in comparable tropical rain forest canopies during the dry season, the Apparent herbivore pressure on vines is less than that on trees; there is little variation in the Apparent damage levels or damage type between trees in widely separated sites despite major contrasts in plant species composition, plant diversity, herbivore species and in herbivore type; the Apparent damage levels are somewhat higher than previously reported, and the Actual damage levels may be considerably higher; and finally that the majority of Apparent and Actual leaf damage occurs when the leaves are young.

The reasons for the striking quantitative similarities between habitats remain unclear, especially as Apparent herbivore damage levels were measured in a way that says little about herbivore load in absolute terms, and ignores the effects of sucking insects completely. The similarities may be coincidental given the low number of sites examined, but this would not be consistent with relatively constant and species-specific Apparent damage levels between sites, nor with the significant differences that were

found between trees and vines. Both these factors suggest deterministic rather than stochastic processes are operating to produce the observed levels of leaf damage.

Should the quantitative similarity between sites be real rather than coincidental, then it may be due to similarities in either herbivore load or in the plants' response to herbivore damage. Information of the type presented here can contribute little definite to estimates of herbivore load unless the proportion of missing leaves is constant across species so that Apparent leaf damage bears a fixed relationship to Actual leaf damage. Also, it would be necessary to know when the damage occurred. However, if the thresholds for herbivore-induced abscission of the type found in *Eschweilera* are widespread, then such a process might contribute to quantitative similarities in Apparent leaf damage between sites, especially if it operates via physiologically determined thresholds.

However, as the mean proportion of missing leaves in each site is similar, it seems that the Actual damage levels within the different areas are closely comparable. This argues that herbivores utilize a constant proportion of the foliage in a tropical rain forest.

The differences in Apparent damage levels between tree and vine species in PNGS may also reflect differences in herbivore load or plant response to damage. Perhaps the herbivore load on vines is lower in association with their reduced apparency (sensu Feeny 1976); or perhaps photosynthetic area is at less of a premium in vines than trees so that the vines' response to herbivore damage occurs at a lower Apparent damage level than that of the canopy trees.

Such speculations are well beyond the scope of this paper, and answers can only be provided by more and repeated sampling of different sites to provide accurate estimates of herbivore load, damage they cause and the plants' response.

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