Selbyana 19(2): 162–171

FOLIVORY LEVELS OF SEEDLINGS AND CANOPY TREES IN TROPICAL AND SUBTROPICAL RAINFORESTS IN AUSTRALIA

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ABSTRACT. Folivory levels were measured for seedlings and canopy trees of seven rainforest tree species (five in subtropical rainforest and two in tropical rainforest) in Queensland, Australia. Leaf damage was found, on average, to be higher for the subtropical species than for their confamilial tropical counterparts. Higher levels of damage than those reported here occur in neotropical rainforests, which suggests that high productivity may not mask folivore pressures in those systems. The latitudinal pattern of folivory established in this study, may consequently be unique to Australia. Comparisons of damage levels between seedlings and canopy trees (of the same species) indicate that in most cases seedlings suffer higher levels of damage. This result is presumably due to the longer leaf lifetimes of seedlings and the accumulation of damage over long periods of time. For subtropical tree species, measurements of leaf damage levels were taken twice, once in spring (November 1995) and once in autumn (March 1996). Observational evidence indicates that changes in leaf damage levels were related to species-specific leaf phenological patterns. The production of new leaves generally led to a reduction in the recorded measurements of leaf area lost, because the samples consisted of greater numbers of young leaves that had little opportunity to accumulate damage.

INTRODUCTION

FOLIVORY AS AN ECOLOGICAL PROCESS. Studies of the abundance and diversity of insect folivores (Southwood *et al.* 1983, Stork 1987, Basset 1991a, 1991b, 1991c, 1996) and the levels of insect folivory indicate that folivory is a major consumptive process in forest ecosystems (Odum & Ruiz-Reyes 1970, Coley 1983a, 1983b, Lowman 1984, 1985a, Clark & Clark 1985, de la Cruz & Dirzo 1987). In Australia, folivory research has focused on sclerophyllous forests and plantations (Fox and Morrow 1983, Journet 1986, Lowman & Heatwole 1987, Lowman & Heatwole 1992, Heatwole *et al.* 1997), and results suggest that the level of folivory in these systems is greater than in similar forests outside Australia (Lowman 1985b, Ohmart 1985, Lowman 1997).

THE SIGNIFICANCE OF UNDERSTORY AND CANOPY STUDIES OF FOLIVORY. Fewer studies of folivory have been made in Australian rainforests than in other rainforests, especially the neotropics. Australian studies to date have focussed on either seedlings (Lowman 1982a, 1982b) or canopy trees, with Lowman (1984, 1985a, 1987, 1992) studying folivory and Basset (1991a, 1991b, 1991c, 1992, 1993, 1996) studying folivores; yet comparisons between seedling and canopy life stages of the same tree species have been absent. Comparisons of folivory levels of seedlings and canopy trees promise to provide a greater understanding of the differences in exploitable resources available to folivores living in these distinct understory and canopy habitats.

Leaf longevity is one of the major factors that influences folivore feeding patterns (Lowman & Box 1983, Basset 1991a, 1992, Lowman 1992). Recent studies have shown that leaf lifetimes in rainforest canopies can be much greater than previously thought (Basset 1991a, 1992, Lowman 1992), although it is generally accepted that leaf longevity is greatest in the understory as a consequence of the growth-limiting conditions of low light experienced beneath the dense rainforest canopy (Bentley 1979, Chabot & Hicks 1982). The quality of long-lived leaves on seedlings is likely to be poor relative to the quality of younger leaves in the canopy (where primary productivity is higher). Understory leaves are protected from folivores by production and accumulation of digestibility-reducing compounds and the proliferation of microepiphytic cover (Bentley 1979, Chabot & Hicks 1982). Heatwole *et al.* (1997), through their work on eucalypt saplings, also noted that newly produced sun leaves maintained their quality as forage for insects longer than did leaves produced in the understory, indicating that the best foliage for insect consumption is likely to occur in the upper canopy. Despite providing seemingly poor resources, folivores may prefer to live in the understory habitat, because it is shielded from the harsh abiotic conditions that characterize the canopy (Basset *et al.* 1992). Folivores are consequently faced with a trade-off situation in which access to high quality foliage in the can-

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TABLE 1. Rainforest tree species: summary of phenological characteristics (from Williams *et al.* 1984, Cronin 1989, Floyd 1989, Wrigley & Fagg 1989, McDonald & Thomas 1990).

Species	Plant family	Leaf phenology (period of leaf flushing)
Subtropical tree species		
Orites excelsa	PROTEACEAE	November–February
Argyrodendron actinophyllum	STERCULIACEAE	November–February
Argyrodendron trifoliolatum	STERCULIACEAE	July–September
Stenocarpus salignus	PROTEACEAE	September–November
Stenocarpus sinuatus	PROTEACEAE	September–November
Tropical tree species		
Argyrodendron peralatum	STERCULIACEAE	Periodical—responds to rain
Darlingia ferruginea	PROTEACEAE	Periodical—responds to rain

opy may be subject to physiological constraints (Basset *et al.* 1992). It has also been suggested that gaining access to high quality foliage in the upper canopy is risky, as there is commonly less structural protection from predators than there is in the highly heterogeneous understory (Basset 1991a, 1992).

PROCESSES IN SUBTROPICAL AND TROPICAL RAINFORESTS. Comprehensive comparisons of folivory levels between tropical and subtropical rainforests are yet to be undertaken, despite the fact that such studies may highlight differences in the roles that folivores play in structuring these different systems. The implicit assumption that folivores apply similar pressures in all rainforest ecosystems is yet to receive support from empirical analyses. Subtropical and tropical rainforests are distinctly different, and this difference needs to be acknowledged in all studies of the processes which shape these ecosystems.

It is reasonable to expect, based on the premise that tropical rainforests are characterised by higher productivity and higher botanical and arthropod diversity (Pianka 1966), that folivory levels in tropical rainforests may be higher than in subtropical rainforests. This implicit assumption has been based on comparisons of folivory levels from just a handful of north temperate and neotropical forests and is yet to be fully tested (particularly in the southern hemisphere).

This study aimed to quantify leaf damage levels (damage caused by folivores only) for the seedlings and canopy trees of seven (two tropical and five subtropical) rainforest tree species in Queensland, Australia. Particular interest was taken in examining the variation in damage levels of seedlings and canopy trees and in developing regional folivory patterns for Australian rainforests.

MATERIALS AND METHODS

TREE SPECIES AND SITES. Seven rainforest tree species (from two plant families) were selected for study based on their distribution, differing leaf morphologies and the availability of both seedlings and canopy individuals within study sites (TABLE 1).

Five rainforest tree species were studied in a 1 hectare site of complex notophyll vine forest (Webb 1959) at Lamington National Park (28°13′S; 153°07′E) in subtropical South-East Queensland. Field work was conducted in late spring (13–17 November 1995) and early autumn (27–31 March 1996).

Two tropical tree species, selected from the same two families as those from the subtropical site, were studied on the Atherton Tableland (17°7′S, 145°37′E) in North Queensland in one mid-summer sample period only (16–19 January 1996). According to Webb's (1959) classification, the forest at this site is complex notophyll vine forest (Type 5b).

LEAF DAMAGE ASSESSMENTS. Access to the canopy was gained using single rope techniques similar to those pioneered and described by Perry (1978). Canopy samples consisted of 20 leaves which were removed from each tree using the branch clipping technique (Majer & Recher 1988, Basset *et al.* 1997). Logistical constraints determined from where in the canopy samples could be taken. All samples were collected from the shaded exterior of the canopy, because access to these leaves was facilitated through the climbing of neighbouring trees. Some seedlings had fewer than 20 leaves in total, and sample sizes were consequently smaller in these instances.

A total of 25 seedlings (5 individuals of 5 tree species) and 25 trees (5 individuals of the same 5 tree species) were sampled in the subtropical

TABLE 2. Average percent (±SD) of leaf area lost to folivores.

	1995 Samples		1996 Samples	
Tree species	Seedlings %	Canopy trees %	Seedlings %	Canopy trees %
Subtropical species				
A. actinophyllum	20.4 (±19.3)	14.9 (±21)	11.8 (±13.7)	5.4 (±5.2)
A. trifoliolatum	12.5 (±14.9)	11.8 (±10.8)	10.7 (±11.8)	12.8 (±11.4)
S. sinuatus	11.3 (±11.2)	14.3 (±13.9)	25.4 (±20.7)	21.2 (±17.4)
S. salignus	14.4 (±19.9)	9.3 (±10.2)	12.9 (±14)	10.7 (±15.4)
O. excelsa	10.3 (±11.7)	3.6 (±5.7)	12.5 (±10.9)	2.3 (±5.3)
Subtropical averages	13.8 (±3.6)	10.8 (±4.1)	14.6 (±5.4)	10.5 (±6.5)
Tropical species				
A. peralatum	*	*	11.1 (±10.5)	8.9 (±13.8)
D. ferruginea	*	*	6.4 (±10.4)	3.9 (±8.4)
Tropical averages	*	*	8.8 (±2.4)	6.4 (±2.5)

* The tropical rainforest tree species were collected during a January 1996 sampling period only.

site. Five seedlings and five canopy trees of both tree species were sampled at the tropical site. Leaf samples were placed within plastic bags and cold stored for transportation to limit dehydration and subsequent wilting. In the laboratory, leaves were kept frozen until their leaf areas were measured.

Leaf area and the percentage of leaf area lost to folivores were measured by tracing each leaf onto graph paper and counting 1 mm squares. In instances where leaf margins had been destroyed, they were approximated (based on species specific leaf shape characteristics) and drawn onto the graph paper. As Landsberg (1989) noted, the loss of leaf margins results in some inevitable error and inaccuracy. To reduce this error, W.L. Hadwen processed all of the samples, thereby standardizing the measurements made in this study.

Percentages were used to account for leaf size changes that occurred after defoliation, based on the assumption that as a leaf grows, so do the holes caused by folivores (Reichle *et al.* 1973, Coley 1983a, Fox & Morrow 1983, Lowman 1984, Southwood *et al.* 1986, but also see Lowman 1987, Landsberg 1989, Coleman & Leonard 1995).

STATISTICAL ANALYSIS. Leaf area measurements (% leaf area lost) for seedlings and canopy trees were compared using analysis of variance (ANOVA) models within the SAS computer package (SAS Institute Inc. 1989).

For the subtropical rainforest trees, the ANOVA model was a split plot design. The main plot tested the effect(s) of developmental stage (seedling vs. canopy) and the subplot tested for the effect of time (i.e., comparing damage levels recorded in November 1995 with those from March 1996) and the interaction of time with the developmental stages.

For the significant terms identified in each ANOVA model, post hoc analyses were conducted on the samples that contributed to the significance, using the LSMEANS (least significant difference) statement within SAS (SAS Institute Inc. 1989).

For the tropical tree species, a one-way ANOVA model was designed to test for significance between the seedling and canopy developmental stages.

RESULTS

Variation in leaf damage levels among species was substantial, with average damage levels ranging from 6.4% to 25.4% in the seedling samples and from 2.3% to 21.2% in the canopy samples (TABLE 2).

The average damage levels determined for the subtropical and tropical tree species were 14.2% and 8.8% respectively for seedlings and 10.6% and 6.4% respectively for canopy trees (FIGURE 1). When the data for seedlings and canopy trees are pooled, the average percentage of leaf area lost to folivores for the five subtropical trees was 12.2%, compared to an average of 7.8% calculated for the two tropical tree species.

For four species (*Darlingia ferruginea, Orites excelsa, Argyrodendron actinophyllum* and *Argyrodendron peralatum*), levels of leaf damage were higher in seedlings than in canopy trees (TABLE 2). A combination of factors, including longer leaf life spans, lower rates of leaf turnover and accumulation of damage through time may account for these results (Bentley 1979, Chabot & Hicks 1982, Clark & Clark 1985, Lowman 1984).

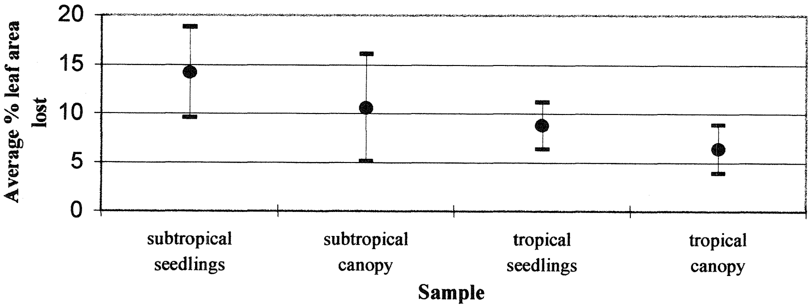

FIGURE 1. Average damage levels (±SD) for subtropical and tropical tree species calculated for seedlings and canopy trees.

For the remaining three species (*Argyrodendron trifoliolatum, Stenocarpus sinuatus* and *Stenocarpus salignus*), leaf damage levels did not vary markedly between seedling and canopy samples. The effects that differences in leaf lifespans have on folivore feeding preferences may account for this result (Odum & Ruiz-Reyes 1970, Coley 1983a, Cooke *et al.* 1984, Lowman 1985a, Basset 1991a).

O. excelsa exhibited lower leaf damage levels than did the other tree species studied. This finding was expected as this species has tougher and longer lived leaves than do the other species sampled (M.F. Olsen pers. obs.), and these traits are known to reduce damage by facilitating the development of physical and chemical palatability-reducing features (Feeny 1975, Cates 1980, Lowman & Box 1983, Feeny 1992).

The relationship between damage levels and time was species specific. Two of the species studied (*A. trifoliolatum* and *S. salignus*) showed no significant change in the level of leaf damage between the late spring (November 1995) and early autumn (March 1996) sampling periods.

A. actinophyllum showed a trend towards a reduced level of defoliation over the course of the study. This species was observed to produce new leaves throughout the course of the study (November to February), and leaf damage levels presumably dropped because the young leaves being sampled in March 1996 had little time to accumulate damage.

S. sinuatus showed an increase in the level of leaf damage through the course of the study. This was not unexpected, as the trees produced no new leaves after the spring (November 1995) sampling period. The leaf damage levels recorded for the autumn (March 1996) sampling period therefore represent the accumulation of folivore feeding activities over the preceding months.

For *O. excelsa,* damage levels increased on seedling leaves with time but decreased on canopy leaves. This relates to the highly variable nature of leaf phenology, with higher leaf turnover (and subsequent lower damage levels) expected (and observed) for the canopy leaves because of the higher levels of solar radiation intercepted in this microhabitat (Niklas 1989).

ANOVA RESULTS—SUBTROPICAL RAINFOREST. TABLE 3 summarizes the results from ANOVA analysis of leaf damage levels for the five tree species collected from the subtropical rainforest.

As identified by the error margins presented in TABLE 1, the damage levels recorded within samples were highly variable. For *A. actinophyllum, A. trifoliolatum* and *S. salignus,* this variation was highly significant ($P = 0.0001$) and confounded further analysis of differences in damage levels between developmental stages and seasons.

For *S. sinuatus,* the significant variation in damage levels between seasons ($P = 0.0076$), highlights the pattern of increasing leaf damage levels for seedling and canopy leaves evident throughout the course of the study. FIGURE 2 presents the mean damage levels (±SD) for *S. sinuatus* from samples in spring and autumn. A notable increase in damage levels occurred for both seedling and canopy samples throughout the course of the study.

For *O. excelsa,* the damage levels recorded in spring and autumn were not significantly different. Significant variation ($P = 0.0004$) existed, however, in damage levels between individuals within both the seedling and the canopy developmental stages, therein prohibiting the examination of differences in leaf damage levels between these stages.

ANOVA RESULTS—TROPICAL RAINFOREST. TABLE 4 presents a summary of results from the ANOVA conducted on leaf damage levels for the two tropical tree species studied in North Queensland.

As was the case for its southern congeners,

TABLE 3. Summary of statistically significant values from ANOVAs conducted on leaf damage levels for subtropical rainforest tree species. (df = Degrees of Freedom, Type III SS = Sums of squared deviates from mean, Mean square = Variance = Sums of Squares/Degrees of Freedom, F value = Expected variance from F distribution, Pr > F = the probability of a greater F value through chance alone.)

Species	Significant term	df	Type III SS*	Mean square	F value	Pr > F
A. actinophyllum	Interaction between season and variation within developmental stages	8	87.43	10.93	16.77	0.0001
A. trifoliolatum	Interaction between season and variation within developmental stages	8	77.84	9.73	11.37	0.0001
S. sinuatus	Variation between the 1995 and 1996 sampling periods	1	14.48	14.48	12.52	0.0076*
S. salignus	Interaction between season and variation within developmental stages	8	57.47	7.18	5.00	0.0001
O. excelsa	Variation within developmental stages	12	36.96	3.08	3.09	0.0004

* Type III SS of the interaction between time and the variation among individuals within developmental stages was used as the error term to calculate the F value.

significant variation ($P = 0.0001$) occurred in damage levels among individuals within developmental stages for *A. peralatum.* On the other hand, *D. ferruginea* exhibited a statistically significant difference in leaf damage levels ($P = 0.0406$) between stages, with seedling leaves suffering significantly higher levels of defoliation than the leaves of canopy trees.

DISCUSSION

DO FOLIVORY LEVELS IN AUSTRALIAN RAINFORESTS DIFFER FROM THOSE RECORDED ELSEWHERE? In this study, the levels of folivory for subtropical tree species (12.2%) are higher than the levels reported by Lowman (1984) (3–10%; see TABLE 5). Other studies using long-term sampling strategies (such as Lowman 1982a and 1984) to account for total defoliation (i.e., the loss of an entire leaf as a consequence of folivore activities), however, have identified greater leaf area losses for subtropical rainforest species. Because the sampling techniques used here differ significantly from those adopted in long-term sampling strategies, comparing the results obtained from these different methodological approaches would be inappropriate. For the tropical tree species sampled, the damage levels were lower than those reported for neotropical rainforests, but higher than those reported for studies in French Guyana (see TABLE 5).

Despite these general trends, variation in the accuracy of sampling techniques erodes the confidence with which comparisons of leaf damage levels can be made among studies conducted at different times and different locations (Reichle *et al.* 1973, Lowman 1984, Landsberg 1989, Waller & Jones 1989, Coley & Aide 1991).

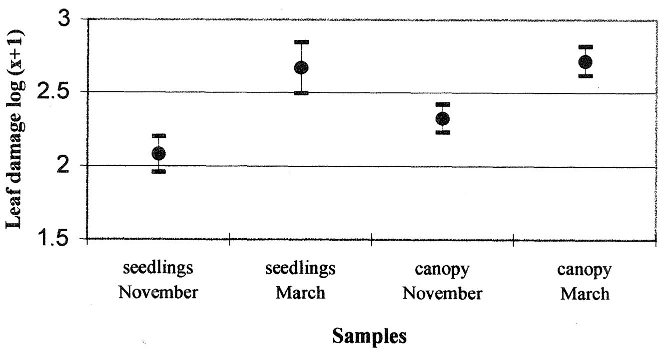

FIGURE 2. Mean leaf damage levels (±SD) for *Stenocarpus sinuatus* seedlings and canopy trees in November 1995 and March 1996.

TABLE 4. Summary of the statistically significant values from the ANOVAs conducted on leaf damage levels for tropical rainforest tree species. (df = Degrees of Freedom, Type III SS = sums of squared deviates from mean, Mean square = Variance = Sums of Squares/Degrees of Freedom, F value = Expected variance from F distribution, Pr > F = the probability of a greater F value through chance alone.)

Species	Significant term	df	Type III SS*	Mean square	F value	Pr > F
A. peralatum	Variation within developmental stages	8	27.41	3.42	4.61	0.0001
D. ferruginea	Variation between seedlings and canopy trees	1	10.37	10.37	5.95	0.0406*

* Type III SS for the variation among individuals within developmental stages was used as the error term.

Potential methodological inconsistencies aside, the results from this study suggest that Australian subtropical rainforests suffer relatively high levels of leaf damage. This finding reinforces Lowman's suggestion that Australian systems suffer higher folivory levels than do forest systems overseas (Lowman 1985b, 1997). However, the tropical rainforest tree species in this study do not support this pattern, and were found to suffer lower levels of folivory than reported in other tropical rainforests (particularly in the canopy tree samples—see TABLE 5). These inconsistencies suggest that the pattern suggested by Lowman (1985b, 1997), which was based on Australian temperate and subtropical data, may be an artifact of latitudinal patterns of folivory within Australia, rather than providing evidence of distinct continental differences. This area deserves further research attention, as elucidation of patterns on both regional and global scales will provide us with information that will enable the development of improved rainforest management and forestry initiatives. However, before the pattern of folivory described by Lowman (1985b) can be fully examined, more subtropical datasets are required for comparative purposes.

As is often the case in folivory studies (Clark & Clark 1985, Lowman 1985a, Basset 1991a, Soumela & Ayres 1994), huge variation was recorded in leaf damage levels among individual samples in this study. The ubiquity of this result (among species and among studies) suggests that this variability is a real phenomenon, rather than simply being an artifact of insufficient replication.

WHAT EFFECT DOES DEVELOPMENTAL STAGE HAVE ON FOLIVORY LEVELS? Evidence from this study suggests that seedlings are usually more heavily

TABLE 5. Comparisons of the leaf damage levels determined in this study with levels of damage reported for other rainforests.

Folivory study Author(s) and location	Seedlings & saplings Subtropical rainforest	Seedlings & saplings Tropical rainforest	Canopy trees Subtropical rainforest	Canopy trees Tropical rainforest
This study—Q, A	14.2%	8.8%	10.6%	6.4%
Aide and Zimmerman (1990)—BCI, P		10.9%		10.9%
Coley (1982)—BCI, P		21%		
de la Cruz and Dirzo (1987)—LT, M		10%		
Leigh and Smythe (1978)—BCI, P				8%
Leigh and Windsor (1982)—BCI, P				15%
Lowman (1982)*—NSW, A	21.3%			
Lowman (1984)●—NSW, A			3–10%	
Lowman (1984)●*—NSW, A			14.6%	
Newbery and de Foresta (1985)—FG		5.5%		
Odum and Ruiz-Reyes (1970)—RP, PR				8%
Sterck *et al.* (1992)—FG				5%
Wint (1983)—NG				9–12%

(Locations: Q, A = Queensland, Australia; BCI, P = Barro Colorado Island, Panama; LT, M = Los Tuxtlas, Mexico; NSW, A = New South Wales, Australia; FG = French Guyana; RP, PR = Rio Piedras, Puerto Rico; NG = New Guinea) ● These results came from the same study but used different methodologies. * Leaf damage levels were calculated using a long-term sampling methodology that accounts for whole-leaf losses. All other results presented used discrete sampling methods similar to those used for this study.

damaged by folivores than are leaves sampled from the canopy. A number of possible explanations for this pattern warrant further attention. First, leaves in the understory tend to have both longer leaf life times and slower turnover rates than do those in the canopy (Bentley 1979, Chabot & Hicks 1982). Evidence of damage may, therefore, accumulate on the leaves of seedlings to a greater degree than it can on canopy leaves. Second, evidence suggests that because the abiotic conditions prevailing in the rainforest canopy are harsh (Basset 1991a, Moffett 1993), more folivorous insects may live in the relatively stable environment nearer the forest floor to feed on the leaves of seedlings. Third, terrestrial folivorous mammals may consume large quantities of leaf material from seedlings (W.L. Hadwen pers. obs.). Of course arboreal mammals may exert similar pressures on leaves in the rainforest canopy, and more research is required to quantify the effects that mammals have on folivory levels in rainforests. Because mammals are more likely to consume entire leaves than are insect folivores, only long-term studies will be able to adequately quantify the effects of mammals as folivores. Fourth, the chemical composition of seedling and canopy tree leaves may differ substantially (Coley 1988, Coley & Barone 1996). For example, the young leaves of seedlings generally contain higher levels of nitrogen and water and lower levels of digestibility-reducing phenolics than do mature leaves (Coley 1983b). As a consequence of the differential growth rates of leaves in the canopy and near the forest floor (Chabot & Hicks 1982), canopy leaves may be rendered less attractive than seedling leaves as food resources for folivores (but see Heatwole *et al.* 1997). Finally, the holes caused by folivores when leaves are young may not grow in direct proportion to the leaf, particularly in the understory where growth may be indeterminant and slow (Lowman 1987, Landsberg 1989, Coleman & Leonard 1995). If such disproportionality exists, discrete measurements, even when percentages are used, may overestimate the amount of leaf material consumed by folivores.

ARE SUBTROPICAL FOLIVORY LEVELS **REALLY** HIGHER THAN TROPICAL FOLIVORY LEVELS? Results from studies in the northern hemisphere (Bray 1964, Aide & Zimmerman 1990) suggest that folivory levels increase from the poles to the equator. However, as Lowman (1985b) noted, the reverse trend may exist in Australia. In long-term studies of folivory in three rainforest areas in Australia, Lowman (1985b) found that leaf damage levels decreased with latitude (cool temperate rainforests 26%, warm temperate rainforests 22%, subtropical rainforests 14.6%). In view of Lowman's findings it is not surprising that the results from our study supported this trend, with subtropical folivory levels being much higher than those recorded for tropical trees. Unfortunately Lowman's results were obtained using different sampling methodologies from those adopted in this study, so direct comparisons of folivory levels across latitudes is not possible.

An understanding of the phenological patterns of the species studied, the productivity levels within tropical and subtropical rainforest ecosystems and the abundance and trophic dynamics of the fauna of these regions may help to explain these results (Lowman 1985b). Subtropical rainforests characteristically support a lower diversity and productivity than do tropical rainforests (Pianka 1966), and, although this feature does not necessarily suggest high levels of folivory, Basset *et al.* (1992) reported that arthropods can be found in greater densities in subtropical forests than in tropical rainforests. The higher abundance (yet lower relative diversity) of subtropical rainforest arthropods might enable common folivores to consume vast quantities of leaf matter; hence the high folivory levels reported here.

Tropical systems, with their higher biological diversity, may be less susceptible to similar levels of resource exploitation. Insect folivores in tropical rainforests are likely to be competing for resources with many more species, and, at the same time, trying to avoid more predator species. These consequences of increased diversity, in the form of increased competition and predation pressures (and subsequent reduced dominance by common folivore species), might explain the reduced levels of folivory measured for the two tropical species in this study.

If the dynamics hypothesised above exist, then similar latitudinal patterns of reduced folivory in highly productive ecosystems should be observed elsewhere. However, before rigorous testing of the relationship between productivity and folivory levels is possible, a greater number of comparable subtropical datasets is required (the paucity of folivory data in subtropical regions is presented in TABLE 5).

Furthermore, the sampling methodologies employed in folivory research will continue to influence the results and comparability among studies (Lowman 1985b, 1997). If patterns of leaf longevity and leaf turnover are responsible for lower measurements of folivory in tropical rainforests, then only long-term sampling strategies will appropriately describe the dynamics of folivory in these systems (Lowman 1984, 1985a). These potential differences in the dynamics of ecological processes between subtropical and tropical rainforests, suggest that comparisons between these ecosystems using discrete sampling techniques, may be flawed.

An ecosystem level approach is required to further our understanding of the complexities of folivory in rainforest ecosystems. Folivory levels are likely to be responsive to a large number of biotic and abiotic variables. One of the key questions to be answered regarding folivory in rainforest ecosystems may be: Are folivory levels regulated by pressure from primary productivity and plant palatability (bottom-up control) or competition, predation and/or parasitism (top-down control)?

Both of these processes undoubtedly operate in tropical and subtropical ecosystems, but the relative strengths of each may account for the trends presented here. Future research efforts need to adopt a broader, ecosystem-level approach to analyses of folivory levels in forests, for it is only through this holistic approach that significant inroads will be made in our understanding of folivory processes in rainforest systems.

ACKNOWLEDGMENTS

The authors express their gratitude to Michael Arthur for assisting with statistical analyses and to all of the people who assisted W.L. Hadwen with climbing trees and sampling in the field. The study, conducted as part of W.L. Hadwen's B.Sc (Hons) research project at Griffith University, was supported in part by facilities and equipment provided by the Cooperative Research Centre for Tropical Rainforest Ecology and Management.

LITERATURE CITED

AIDA T.M. 1991. Synchronous leaf production and folivory in juveniles of *Gustavia superba.* Oecologia 88: 511–514.

———. 1993. Patterns of leaf development and folivory in a tropical understorey community. Ecology 74 (2): 455–466.

——— AND J.K. ZIMMERMAN. 1990. Patterns of insect folivory, growth and survivorship in juveniles of a tropical liana. Ecology 71 (4): 1412–1421.

BASSET Y. 1991a. Influence of leaf traits on the spatial distribution of insect folivores associated with an overstorey rainforest tree. Oecologia 87: 388–393.

———. 1991b. The seasonality of arboreal arthropods foraging within an Australian rainforest tree. Ecol. Ent. 16: 265–278.

———. 1991c. Leaf production of an overstorey rainforest tree and its effects on the temporal distribution of associated insect folivores Oecologia 88: 211–219.

———. 1992. Influence of leaf traits on the spatial distribution of arboreal arthopods within an overstorey rainforest tree. Ecol. Ent. 17: 8–16.

———, H.-P. ABERLENC AND G. DELVARE. 1992. Abundance and stratification of foliage arthropods in a lowland rainforest of Cameroon. Ecol. Ent. 17: 310–318.

———. 1993. Patterns in the organization of the arthropod community associated with an Australian rainforest tree: How distinct from elsewhere? Selbyana 14: 13–15.

———. 1996. Local communities of arboreal folivores in Papua New Guinea: Predictors of insect variables. Ecology 77 (6): 1906–1919.

———, N.D. SPRINGATE, H.-P. ABERLENC AND D G. DELVARE. 1997. A review of methods for sampling arthropods in tree canopies. Pp. 27–53 *in* N.E. STORK, J. ADIS AND R.K. DIDHAM, eds., Canopy arthropods. Chapman & Hall, London.

BENTLEY B.L. 1979. Longevity of individual leaves in a tropical rainforest understory. Annals of Botany 43: 119–121.

BRAY J.R. 1964. Primary consumption in three forest canopies. Ecology 45: 165–167.

CATES R.G. 1980. Feeding patterns of monophagous, oligophagous and polyphagous insect folivores: the effect of resource abundance and plant chemistry. Oecologia (Berlin) 46: 22–31.

CHABOT B.F. AND D.J. HICKS. 1982. The ecology of leaf life spans. Ann. Rev. Ecol. Syst. 13: 229–259.

CLARK D.B. AND D.A. CLARK. 1985. Seedling dynamics of a tropical tree: impacts of folivory and meristem damage. Ecology 66 (6): 1884–1892.

COLEMAN J.S. AND A.S. LEONARD. 1995. Why it matters where on a leaf a folivore feeds. Oecologia 101: 324–328.

COLEY P.D. 1982. Rates of folivory on different tropical trees. Pp. 123–132 *in* E.G. LEIGH JR, A.S. RAND AND D.M. WINDSOR, eds., The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington D.C.

———. 1983a. Folivory and defensive characteristics of tree species in a lowland tropical forest. Ecol. Mono. 53(2): 209–233.

———. 1983b. Intraspecific variation in folivory on two tropical tree species. Ecology 64 (3): 426–433.

———. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia (Berlin) 74: 531–536.

——— AND T.M. AIDA. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pp 25–49 *in* P.W. PRICE, T.M. LEWINSOHN, G.W. FERNANDES AND W.W. BENSON, eds., Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, Inc., London.

——— AND J.A. BARONE. 1996. Herbivory and plant defenses in tropical forests. Ann. Rev. Ecol. Syst. 27: 305–335.

COOKE F.P., J.P. BROWN AND S. MOLE. 1984. Folivory, foliar enzyme inhibitors, nitrogen and leaf structure of young and mature leaves in a tropical forest. Biotropica 16(4): 257–263.

Cronin L. 1989. The concise Australian flora. Reed Books, New South Wales.

de la Cruz M. and R. Dirzo. 1987. A survey of the standing levels of folivory in seedlings from a Mexican rainforest. Biotropica 19(2): 98–106.

Feeny P. 1975. Plant apparency and chemical defense. Pp. 1–40 *in* J.W. Wallace and R.L. Mansell, eds., Biochemical interaction between plants and insects: recent advances in phytochemistry, Vol. 10 (Proceedings of the Fifteenth Annual Meeting of the Phytochemical Society of North America held on the campus of the University of South Florida, Tampa, Florida.) Plenum Press, New York.

———. 1992. The evolution of chemical ecology: Contributions from the study of herbivorous insects. Chapter 1 Pp. 1–45 *in* G.A. Rosenthal and M.R. Berenbaum, eds., Folivores: their interactions with secondary plant metabolites, 2nd ed. Vol. 2: ecological and evolutionary processes, Academic Press, New York.

Floyd A.G. 1989. Rainforest trees of mainland southeastern Australia. Forestry Commission of New South Wales, Inkata Press, Sydney.

Fox L.R. and P.A. Morrow. 1983. Estimates of damage by herbivorous insects on *Eucalyptus* trees. Aust J. Ecol. 8: 139–147.

Heatwole H., M.D. Lowman, C. Donovan and M. McCoy. 1997. Phenology of leaf-flushing and macroarthropod abundances in canopies of *Eucalyptus* saplings. Selbyana 18(2): 200–214.

Journet A.R.P. 1986. Insect folivory on the Australian woodland eucalypt, *Eucalyptus blakelyi* M. Aust. J. Ecol 6: 135–138.

Landsberg J. 1989. A comparison of methods for assessing defoliation, tested on eucalypt trees. Aust. J. Ecol 14: 423–440.

Leigh E.G. and N. Smythe. 1978. Leaf production, leaf consumption, and the regulation of folivory on Barro Colorado Island. Pp. 33–50 *in* G.G. Montgomery, ed., The ecology of arboreal folivores. Smithsonian Institution Press, Washington, DC.

——— and D.M. Windsor. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. Pp. 109–123 *in* E.G. Leigh, A.S. Rand, and D.M. Windsor, eds., The ecology of a tropical forest. Smithsonian Institution Press, Washington, DC.

Lowman M.D. 1982a. Effects of different rates and methods of leaf area removal on rain forest seedlings of Coachwood (*Ceratopetalum apetalum*). Aust J. Bot. 30: 477–483.

———. 1982b. Seasonal variation in insect abundance among three Australian rain forests, with particular reference to phytophagous types. Aust J. Ecol. 7: 353–361.

———. 1984. An assessment of techniques for measuring folivory: is rainforest defoliation more intense than we thought? Biotropica 16(4): 264–268.

———. 1985a. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. Aust. J. Ecol. 10: 7–24.

———. 1985b. Insect herbivory in Australian rain forests—is it higher than in the Neotropics? Proc. Ecol. Soc. Aust. 14: 109–119.

———. 1987. Relationships between leaf growth and holes caused by folivores. Aust. J. Ecol. 12: 189–191.

———. 1992. Leaf growth dynamics and herbivory in five species of Australian rainforest canopy trees. J. Ecol. 80: 433–447.

———. 1997. Herbivory in forests—from centimetres to megametres. Pp. 135–149 *in* A.D. Watt, N.E. Stork, and M.D. Hunter, eds., Forests and insects. Chapman and Hall, London.

——— and J.D. Box. 1983. Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. Aust. J. Ecol. 8: 17–25.

——— and H. Heatwole. 1987. The impact of defoliating insects on the growth of Eucalyptus seedlings. Aust. J. Ecol. 12: 175–181.

——— and H. Heatwole. 1992. Spatial and temporal variability in defoliation of Australian Eucalypts Ecology 73(1): 129–142.

Majer J.D. and H.F. Recher. 1988. Invertebrate communities on Western Australian eucalypts: a comparison of branch clipping and chemical knockdown procedures. Aust. J. Ecol. 13: 269–278.

McDonald W.J.F. and M.B. Thomas. 1990. Flora of Lamington National Park, 2nd ed. Queensland Department of Primary Industries, Brisbane.

Moffett M.W. 1993. The high frontier: exploring the tropical rainforest canopy Harvard University Press, London.

Newbery D.McC. and H. De Foresta. 1985. Herbivory and defense in pioneer, gapand understory trees of tropical rainforest in French Guiana. Biotropica 17(3): 238-244.

Niklas K.J. 1989. The effect of leaf-lobing on the interception of direct solar radiation. Oecologia 80: 59–64.

Odum H.T. and J. Ruiz-Reys. 1970. Holes in leaves and the grazing control mechanism. Pp. 69–80 *in* H.T. Odum and R.F. Pigeon, eds., A tropical rain forest. U.S. Atomic Energy Commission, Rio Piedras.

Ohmart C.P. 1985. Is insect defoliation in eucalypt forests greater than that in other temperate forests? Proc. Ecol. Soc. Aust. 14: 121.

Perry D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10 (2): 155–157.

Pianka E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100: 33–46.

Reichle D.E., R.A. Goldstein, R.I. Van Hook and G.J. Dodson. 1973. Analysis of insect consumption in a forest canopy. Ecology 54: 1077–1084.

SAS Institute Inc. 1989. SAS/STAT User's Guide. Version 6, 4th ed. Vol. 1, SAS Institute Inc., Cary North Carolina.

Soumela J. and M.P. Ayres. 1994. Within-tree and among-tree variation in leaf characteristics of mountain birch and its implications for folivory. Oikos 70: 212–222.

Southwood T.R.E., V.K. Brown and P.M. Reader. 1983. Continuity of vegetation in space and time:

a comparison of insects' habitat templet in different successional stages. Research in Population Ecology—Supplement 3: 61–74.

———, V.K. Brown and P.M. Reader. 1986. Leaf palatability, life expectancy and folivore damage. Oecologia (Berlin) 70: 544–548.

Sterck F., P. van der Meer and F. Bongers. 1992. Herbivory in two rainforest canopies in French Guyana. Biotropica 24(1): 97–99.

Stork N.E. 1987. Guild structure of arthropods from Bornean rain forest trees. Ecol. Ent. 12: 69–80.

Waller D.A. and C.G. Jones. 1989. Measuring herbivory. Ecol. Ent. 14: 479–481.

Webb L.J. 1959. A physiognomic classification of Australian rain forests. J. Ecol. 47: 551-570.

Williams J.B., G.J. Harden and W.J.F. McDonald. 1984. Trees and shrubs in rainforests of New South Wales and southern Queensland. University of New England Printery, Armidale.

Wint G.R.W. 1983. Leaf damage in tropical rainforest canopies. Pp. 229–240 *in* S.L. Sutton, T.C. Whitmore and A.C. Chadwick, eds., Tropical rain forest: ecology and management. Blackwell, Oxford.

Wrigley J.W. and M. Fagg. 1989. Banksias, Warratahs and Grevilleas, and all other plants in the Australian Proteaceae family. Collins Australia, Sydney.