Chapter 29
Ontogeny of Herbivory on Leaves in a Tropical Rain Forest in Madagascar

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Keywords Canopy • Epiphyllae • Galls • Herbivory • Madagascar • Ontogeny

Summary

This study was undertaken to ascertain the extent to which damage inflicted by different agents to foliage in a tropical rain forest in Madagascar varied during the flushing and maturation of leaves. There was an ontogenetic sequence in which agents attacked leaves. New, tender foliage was attacked primarily by grazing insects, and by the time the leaf had hardened, it had already suffered a high proportion of the total loss of leaf area it would sustain from grazers throughout its life. As grazing waned, other agents, such as fungi, skeletonizing insects, and galls, came into play. The last agent was epiphyllae; it started late and gradually accumulated over the life of the leaf.

1 Introduction

Leaves undergo ontogenetic changes in their toughness, chemical composition, and texture, all of which affect their palatability to herbivores and pathogens and their resistance to physical agents (Lowman and Box 1983; Lowman 1995; Coley and

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M. Lowman et al. (eds.), *Treetops at Risk: Challenges of Global Canopy Ecology and Conservation*, DOI 10.1007/978-1-4614-7161-5_29,

Kursar 1996; Coley et al. 2006). Consequently, rates of herbivory and other damage would be expected to change during the life of the leaf, and hence, there may be temporal as well as spatial dimensions to the vicissitudes of leaves. The present study was carried out to ascertain the changes in vulnerability of leaves to damage by various agents as the leaves undergo ontogeny.

2 The Study Area

Fieldwork was conducted from 31 October to 13 November 2001 in the Masoala National Park on Masoala Peninsula in northeastern Madagascar. The park includes an elevational gradient spanning habitats from lowland, humid, evergreen rain forest near sea level to montane thicket and cloud forest at >1,200 m. With an area of 211,230 ha, this park is larger than all other forest reserves in Madagascar combined (Kremen et al. 1999). Since the park was gazetted in 1997, disturbance by humans had been minimal and, at the time of the study, consisted mainly of hand felling a few trees and processing them by pit sawing (Kremen et al. 1999). At one time, cinnamon was grown in the vicinity of the research encampment, and there was some incursion by cinnamon trees (*Canella winterana*) into the edges of the forest, but otherwise the forest appeared relatively undisturbed.

The study was carried out in lowland to mid-elevation humid evergreen forest from a base of operations at the Tampolo Field Station (15° 43′ 48″ S; 49° 57′ 34″ E) (Monte-Alegre et al. 2005). There was a closed upper canopy at 15–22 m and a less complete mid-canopy at 10–13 m. Scattered "emergent" trees, up to 37 m tall, protruded above the upper canopy. Branches and trunks at all levels supported a profuse growth of epiphytes, lianas, vines, and parasitic plants. The ground layer consisted of a sparse cover of seedlings, saplings, and shrubs.

3 Materials and Methods

The study consisted of three parts: (1) a comparison of damage to mature leaves of different relative ages by a variety of agents, including fungi, grazing insects, skeletonizing insects, leaf miners, galls, mechanical forces, and epiphyllae; (2) a comparison of damage by grazing and skeletonizing insects to recently flushed versus mature leaves on the same twigs; and (3) measurement of the weekly rate of damage by various agents to newly flushed leaves. Because the data obtained were not normally distributed, nonparametric tests were used throughout.

3.1 Damage by Various Agents to Hardened, Mature Leaves of Different Relative Ages

The effect of relative age of mature leaves upon the extent of grazing by insects was ascertained for one canopy liana and for branches from 36 saplings or shrubs from the ground layer. Samples from the ground layer were taken by walking a service path through the forest, and at 10-m intervals, the shrub or sapling nearest the path was selected for sampling, choosing the plant to the right of the transect at odd-numbered stations and to the left at even-numbered stations. For the liana, a given branch of a shrub, or for an entire sapling, leaves were numbered, beginning apically (relatively youngest leaves) and progressing toward the base (oldest leaves). All leaves were mature (hardened and deep green).

Method of assessment of damage varied depending on the agent. Leaves were individually scored for mechanical breakage, incrustation by epiphyllae, attack by fungi, and attack by leaf miners, as follows: nil (no damage), + (damage present, but inconsequential), and slight, moderate, or heavy. The number of galls on each leaf was recorded. In comparisons of incidences by chi-square analyses, the actual values (rather than percentages), including the "nil" category, were used. When expected values fell below five, categories were lumped until this minimum criterion was met.

For assessing damage by insect grazers and skeletonizers, the outline of each leaf was traced on paper and the extent of damage traced within the original (before damage) outline of the leaf, separately for these two trophic groups. The tracings were cut out with manicure scissors and the total undamaged area of each leaf was measured to the nearest 0.01 cm^2 by a Li-Cor area meter, model LI-3100. Then, the area eaten by insect grazers was excised and a second reading taken. Finally, the area eaten by skeletonizers was excised and a final measurement made. Subtraction of the various leaf areas allowed separate calculation of the percentage of the total leaf surface eaten by grazers and skeletonizers. Insects, bite marks were easily distinguished from mechanical damage by the nature of the broken surfaces.

The prediction of a direct, positive relationship between leaf age and extent of grazing damage was tested by the Spearman Rank Correlation test; since the direction of the result could be predicted a priori, the test was considered one-tailed, with a rejection level of 2.5 %.

3.2 Damage to Recently Flushed Versus Mature Foliage by Grazing and Skeletonizing Insects

Recently flushed leaves were distinguished from mature leaves by color, sclerophylly, and texture (Lowman 1985). New leaves were flimsy and light green, red, or light brown, depending on the species, compared to the deep green of older, thicker, and less flexible leaves. Nine twigs from the crown of a *Uapaca* sp. (Euphorbiaceae) canopy tree containing an apical cohort of newly flushed leaves and a more basal one of mature ones were collected by single-rope climbing techniques

(Montgomery 1977). Damage by grazing and skeletonizing insects to these leaves was assessed as described above, and the rejection level of statistical testing was 2.5 %.

3.3 Weekly Rate of Damage to Newly Flushed Leaves

Using a motor-powered, hot-air dirigible (Montgomery 1977; Hallé et al. 2000; Hallé 2002; Mitchell et al. 2002; Heatwole et al. 2009), an 800-m rope transect was laid across the upper canopy of the forest and fixed at intervals to tree limbs. A helium-filled balloon, harnessed to a single investigator and attached by jumars to the transect rope, was used to follow this transect to find branches with newly flushed leaves. Whenever such a branch was encountered, it was flagged and leaves already suffering damage were pinched off and discarded. One week later, the transect was revisited and the marked branches collected for measuring the damage sustained since the original visit, using the methods described for assessing damage to mature leaves of different ages. Even if leaves continued to grow during the interval of study, proportional extent of grazing can be directly compared as Lowman (1987) showed that the holes in leaves caused by herbivores increase in size in proportion to the growth of the leaf itself.

4 Results

4.1 Damage by Various Agents to Hardened, Mature Leaves of Different Relative Ages

It was predicted that among mature leaves, the oldest, most basal, ones would have suffered a greater incidence of damage or infestation than would have the youngest, more apical, ones. This was true only for coverage by epiphyllae (Table 29.1). Only 15 % of the youngest leaves had epiphyllae, whereas 47 % of the oldest leaves were infested. The difference was significant, and thus, even after maturing, leaves clearly continued to accumulate epiphyllae. All the other agents had slightly higher incidences for the two oldest leaves, as opposed to the two youngest ones, except for incidence of damage by skeletonizing insects in which the incidence on older leaves was slightly lower than on younger ones; none of these differences, however, were significant (Table 29.1). It would appear, then, that the incidence of these agents does not increase markedly with further ageing once the leaf has matured, hardened, and changed color.

The extent of damage by grazing insects could be treated in more detail than could incidence. Extent of grazing damage was positively correlated with relative leaf age, as determined by its location on the apical-to-basal scale (leaf number), in 19 (51 %) of the 37 tests, negatively correlated in 17 (46 %), and identical in one (2.7 %) (Table 29.2). These correlations were significant in only eight samples

Table 29.1 Comparison of incidences of different kinds of damage to the two youngest and two oldest of mature leaves on 36 saplings, shrubs, and vines from the ground layer of a Madagascaran rain forest. All tests are one-tailed; **boldface** indicates significance at a rejection level of 2.5 %. For taxonomic identification of these plants, see Table 29.2

	Number of leaves			
Kind of damage	Damaged	Undamaged	Chi-squared	P
Fungus				
Youngest	34	38	0.02	0.45>P>0.40
Oldest	42	30		
Leaf miners				
Youngest	21	51	0.11	0.40>P>0.35
Oldest	24	48		
Epiphyllae				
Youngest	11	61	15.64	**P<0.0005**
Oldest	34	38		
Mechanical damage				
Youngest	9	63	0.06	0.40>P>0.35
Oldest	11	61		
Galls				
Youngest	1	71	0.83	0.25>P>0.15
Oldest	4	68		
Insect grazing				
Youngest	49	23	0.03	0.99>P>0.98
Oldest	50	22		
Insect skeletonizing				
Youngest	4	68	0.15	0.95>P>0.90
Oldest	3	69		

(six positive, two negative). There did not seem to be any taxonomic consistency in the occurrence of significant positive correlations except that perhaps they tended to be more prevalent in the family Rubiaceae than in the Euphorbiaceae. In summary, there is seldom a significant increase in grazing damage with age in leaves after they are already hardened and mature.

4.2 *Damage to Recently Flushed Versus Mature Foliage by Grazing and Skeletonizing Insects*

Newly flushed leaves had lower incidence of attack and less damage by grazing insects than did mature leaves (Table 29.3). Wilcoxon Matched-Pairs Signed-Ranks tests, pairing by twig, gave overall significance to both measures (in both cases, $T=0$; $P<0.005$). The same was true for skeletonizers (Wilcoxon test: $T=0$; $P<0.005$). Despite these expected differences, the most striking result was the amount of grazing already sustained by new leaves. The incidence of attack on newly flushing leaves by grazing insects averaged 14 % that on mature, hardened leaves, with values for individual twigs reaching as high as 47 %. The proportion of the area consumed

Table 29.2 Relation of relative age of mature, hardened leaves to their extent of damage by grazing insects. Values in **boldface** indicate significance at the 2.5 % rejection level (one-tailed Spearman Rank Correlation test). *N* number of leaves

Plant type/taxon/plant no.	N	r	P
Canopy liana			
Menispermaceae	26	−0.033	0.873
Ground-layer plants (saplings, shrubs, vines)			
Arecaceae, *Dypsis* sp.	5	0.900	0.072
Canellaceae, *Canella* sp.[a]	16	−0.563	**0.029**
Clusiaceae sp. 1	7	0.083	0.838
Clusiaceae, *Garcinia* sp.			
Tree 1	13	−0.630	**0.029**
Tree 2	10	−0.124	0.709
Dioscoreaceae, *Dioscorea* sp.	6	0.507	0.257
Ebenaceae, *Diospiros* sp.			
Tree 1	14	−0.064	0.818
Tree 2	15	0.269	0.315
Euphorbiaceae, *Uapaca* sp. 1			
Tree 1	10	−0.220	0.510
Tree 2	16	−0.381	0.141
Tree 3	4	0.316	0.584
Tree 4	18	0.244	0.315
Tree 5	7	−0.793	0.052
Tree 6	11	−0.364	0.250
Tree 7	8	−0.383	0.311
Tree 8	10	−0.267	0.422
Euphorbiaceae, *Uapaca* sp. 2	26	−0.322	0.108
Menispermaceae			
Tree 1	14	0.607	**0.029**
Tree 2	21	0.369	0.099
Monimiaceae, *Tambourissa* sp.	10	−0.203	0.542
Moraceae, *Bosqueia* sp.	8	0.082	0.827
Myrsinaceae	14	−0.020	0.943
Myrsinaceae, *Oncostemum* sp.	10	0.365	0.273
Oleaceae	11	−0.073	0.818
Rubiaceae			
Tree 1	10	0.038	0.909
Tree 2	4	0	>0.999
Tree 3	12	0.387	0.199
Tree 4	10	0.766	**0.022**
Tree 5	10	0.730	**0.029**
Tree 6	5	0.264	0.598
Tree 7	13	0.699	**0.015**
Tree 8	7	0.808	**0.048**
Tree 9	7	−0.506	0.215
Rubiaceae, *Coffea* sp.	8	−0.172	0.649
Rubiaceae, *Ixora* sp.	9	0.693	**0.050**
Violaceae, *Rinorea* sp.	6	0.698	0.118
All ground-layer plants	385	0.058	0.256

[a]Escaped domestic tree

Table 29.3 Comparison of damage by grazing and skeletonizing insects between new and mature foliage on twigs of a *Uapaca* sp. tree (Euphorbiaceae). Note that means are presented for descriptive purposes, but all statistical tests are nonparametric (Mann–Whitney *U* test). Leaves per twig=2–18 for new foliage and 5–39 for mature foliage. **Boldface** indicates significance at the 2.5 % rejection level

	Mean number of attacks per leaf				Mean percent of total leaf area consumed			
Twig no.	Old foliage	New foliage (% of old)	Z	P	Old foliage	New foliage (% of old)	Z	P
Grazing insects								
1	1.29	0.60 (47)	−0.46	**0.048**	7.42	2.02 (27)	−0.27	0.787
2	1.00	0.29 (29)	−1.45	0.146	18.30	0.54 (3)	−1.84	0.066
3	2.17	0.50 (23)	−0.86	0.390	8.05	2.95 (37)	−1.03	0.306
4	2.00	0 (0)	−3.31	**0.0009**	12.48	0 (0)	−3.30	**0.001**
5	4.00	0.14 (4)	−3.93	**0.001**	12.37	1.63 (13)	−3.44	**0.0006**
6	2.00	0 (0)	−3.04	**0.002**	1.70	0 (0)	−3.03	**0.003**
7	1.76	0 (0)	−3.70	**0.002**	7.27	0 (0)	−3.69	**0.002**
8	3.79	0.50 (13)	4.47	**<0.0001**	6.06	4.78 (79)	−3.02	**0.003**
9	1.60	0.14 (9)	−3.13	**0.0018**	10.23	0.61 (6)	−2.76	**0.0058**
Skeletonizing insects								
1	0.14	0	−0.85	0.398	0.14	0	−0.85	0.398
2	0.20	0	−1.18	0.237	0.20	0	−1.18	0.237
3	0.17	0	−0.58	0.564	0.17	0	−0.58	0.564
4	0.11	0	−1.05	0.292	0.11	0	−1.05	0.292
5	0.17	0	−1.53	0.127	0.17	0	−1.53	0.127
6	0	0	–	–	0	0	–	–
7	0	0	–	–	0	0	–	–
8	0	0	–	–	0	0	–	–
9	0	0	–	–	0	0	–	–

of leaves still in the unhardened state had already reached as high as 79 % (mean = 18 %) of the cumulative levels in mature foliage on the same branch.

Incidences and damages by skeletonizers were much lower; none of the new foliage had suffered any damage from skeletonizers, whereas 56 % of the older leaves had. Thus, grazing occurs on leaves earlier than does skeletonizing.

4.3 *Weekly Rate of Damage to Newly Flushed Leaves*

Neither time nor resources were available for tracking the damage by insect herbivores throughout the entire lifetime of leaves as was done by Lowman and Heatwole (1992). The harvesting of new foliage from individual branches a week after previously damaged leaves had been excised did, however, allow a short-term assessment of rates of herbivory on new, succulent foliage.

On average, the newly flushing leaves of all tree species collectively lost 1.6 % of their total area to insect grazers per week, whereas the accumulated damage to

Table 29.4 Comparison of damage caused by one week of grazing by insects on new growth of the canopy with cumulative grazing damage to mature leaves throughout the canopy of a Madagascaran rain forest. Statistical testing by Mann–Whitney *U* test, one-tailed. **Boldface** indicates significance at a rejection level of 2.5 %

Family (N)	Mean % of leaf area grazed (New as % of old)	Z	P
Trees			
Clusiaceae			
New growth (6)	0 (0)	−2.05	**0.041**
Mature leaves (90)	5.0		
Euphorbiaceae			
New growth	1.9 (65)	−3.55	**0.0004**
Mature leaves	2.9		
Meliaceae			
New growth	3.2 (17)	−8.71	**<0.0001**
Mature leaves	18.5		
Myrtaceae			
New growth	2.3 (54)	−5.12	**<0.0001**
Mature leaves	4.3		
Rubiaceae			
New growth	0.8 (16)	−0.66	0.503
Mature leaves	4.9		
Mean for all tree families			
New growth	1.6 (23)	–	–
Mature leaves	7.1		
Epiphytes			
Asclepiadaceae			
New growth (13)	0 (0)	−0.86	0.123
Mature leaves (30)	3.9		
Loranthaceae			
New growth	3.4	–	–
Mature leaves	No data on old growth		

mature foliage was 7.1 % (Table 29.4). The mean damage by grazing insects to new leaves was 23 % of the mean accumulated damage to mature leaves, and values for individual branches reached as high as 65 %. After one week, all the new leaves were still in the immature state and did not appear to be beginning to harden. Consequently, it is likely they would sustain considerably more damage before assuming mature texture and color.

No skeletonization was observed in leaves that were still tender and with their young coloration and no leaf miners, epiphyllae, or galls were seen; only a few small of spots of fungi were detected. Thus, there seems to be an ontogenetic sequence with grazing occurring first, followed by fungal attack and then by other kinds of damage.

5 Discussion

Although a tropical rain forest is commonly perceived as providing an equable and benign environment, in reality it presents a kaleidoscope of spatial and temporal challenges, emanating especially from the biotic component of the ecosystem. Damage inflicted by various agents on leaves in a tropical rain forest in Madagascar is vertically stratified (Heatwole et al. 2009). Attack by grazing insects and fungi is a major challenge for seedlings at ground level, but with increasing height of saplings above the ground as the tree grows, fungal attack on leaves becomes more prevalent, while attack by grazing insects diminishes. Thus, the optimal adaptive strategy for a tree may change throughout its life. It not only needs to balance its defenses to meet multiple threats at a particular time within a given stratum, but it also must adapt to a series of different suites of challenges as it develops from a seedling into a sapling and finally into a mature tree while growing upward through different strata.

At least part of such adaptation occurs via physiological adjustments to immediate conditions. Attack may induce a response in the plant that counters that particular stress. For example, Haukioja and Niemelä (1979) and Haukioja and Neuvonen (1985) showed that birch trees respond to mechanical simulations of light grazing by elevating the levels of defensive chemicals in their leaves. Such responses may exhibit spatial resilience and selectively direct the response to local sites where grazing is greatest, rather than wasting resources by mobilizing antidotes in parts of the tree not subject to high intensities of grazing. For example, Lowman and Heatwole (1987) found that branches of eucalypt saplings subject to attack by grazing insects produce lower levels of autochthonous defensive chemicals than do branches on the same tree and at the same time that had been sprayed with insecticides and thus were protected from attack by grazers.

In addition to temporal shifts in responses by an entire tree, or some part thereof, in adjusting to its changing milieu as it grows through different strata, individual leaves in a given stratum face sequential shifts in challenges during their own ontogeny. They are first subject mainly to grazing by insects, then to attack by fungi, then skeletonizers and leaf miners, and finally to a gradual accumulation of epiphyllae. During flushing, young leaves suffer a more rapid and extensive damage from grazing insects than they do for the rest of their lives (Lowman 1985; Selman and Lowman 1983; Coley and Kursar 1996). Supporting evidences from the present study are as follows: (1) on most branches of ground-layer plants, the relatively older, mature leaves seldom showed a significant increase in grazing damage over that suffered by younger mature leaves, and (2) newly flushed leaves had high rates of grazing upon them, in only 1 week suffering an average loss of leaf area of 23 % of the cumulative loss by mature, hardened leaves. In contrast to their relative immunity to attack by grazing insects, hardened leaves are more subject to fungal infections and the blocking of their leaves' photosynthetic surfaces by epiphyllae.

The interaction of challenges and adaptive response is complex, with the severity of damage serving both as a cause and a consequence of a leaf's attributes. As noted above, the intensity of grazing by insects can induce adaptive defensive responses. It also transpires that a leaf's character, independent of induced responses, has an influence on intensity of attack. For example, young leaves are selectively targeted by grazing insects probably because flushing leaves are mechanically easier to chew than are hardened ones (Lowman 1985). Thus, the pattern of grazing is a consequence of the vulnerability of young, tender leaves to grazing by insects. One would expect, then, that tender leaves would (1) maximize growth rate as a means of shortening the time spent in flushing, (2) channel available resources into production of chemical defenses of young leaves, while (3) deferring use of resources for other functions, such as photosynthesis.

Young tropical leaves are usually light brown, light green, or red; only later, after they have developed mechanical protection, do the leaves become deep green as metabolic resources are redirected from growth and chemical protection into producing chlorophyll and assembling the photosynthetic apparatus (Coley and Aide 1989). In this way resources are not wasted by producing expensive photosynthetic materials, part of which would be harvested by insects rather than benefit the plant.

In conclusion, there are spatial and ontogenetic components of a complex interaction of assaults upon leaves and of trees' physiological and evolutionary responses to them. The nature of this complexity is only beginning to be understood and constitutes an important challenge for research into canopy dynamics.

Acknowledgments We thank Pro-Natura International and Operation Canopée for financial and logistic support; Judith Thomas for use of the leaf meter; Francis Hallé for sharing his expertise; the dirigible pilots, Dany Cleyet-Marrel and Jean Drouault, for their expert flying; Giles Ebersolt, Thierry Aubert, and François Idiené, for technical support and teaching us to fly the helium balloon; the late Audry Heatwole and the late Shirley Waters for laboratory assistance; and Susan King for critical comment on the manuscript.

References

Coley PD, Aide TM (1989) Red coloration of tropical young leaves: a possible antifungal defense? J Trop Ecol 5:293–300

Coley PD, Kursar T (1996) Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological trade-offs. In: Mulkey SS, Chazdon LR, Smith AP (eds) Tropical forest plant physiology. Chapman & Hall, New York

Coley PD, Bateman ML, Kursar TA (2006) The effects of plant quality on caterpillar growth and defense against natural enemies. Oikos 115:219–228

Hallé EF (2002) The canopy raft. In: Mitchell AW, Secoy K, Jackson T (eds) The global canopy handbook, techniques of access and study in the forest roof. Global Canopy Programme, Oxford

Hallé EF, Cleyet-Marrel D, Ebersolt G (2000) Le Radeau des Cimes, exploration des canopées forestières. Editions Jean-Claude Lattès, Paris

Haukioja E, Neuvonen S (1985) Induced long-term resistance of birch foliage against defoliators: defensive or incidental? Ecology 66:1303–1308

Haukioja E, Niemelä P (1979) Birch leaves as a resource for herbivores: Seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. Oecologia 39:151–159

Heatwole H, Unsicker S, Andriamiarisoa LR, Lowman MD (2009) Vicissitudes of leaves in a tropical rain forest in Madagascar. J Trop Ecol 25:615–624

Kremen C, Razafimahatratra V, Guillery RP, Rakotomalala J, Weiss A, Ratsisompatrarivo JS (1999) Designing the Masoala National Park in Madagascar based on biological and socioeconomic data. Conserv Biol 13:1055–1068

Lowman MD (1985) Temporal and spatial variability in insect grazing of the canopies of five Australian rain forest tree species. Aust J Ecol 10:7–24

Lowman MD (1987) Relationships between leaf growth and holes caused by herbivores. Aust J Ecol 12:189–191

Lowman MD (1995) Herbivory as a canopy process in rain forest trees. In: Lowman MD, Nadkarni N (eds) Forest canopies. Academic, San Diego

Lowman MD, Box JD (1983) Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. Aust J Ecol 8:17–25

Lowman MD, Heatwole H (1987) The impact of defoliating insects on the growth of eucalypt saplings. Aust J Ecol 12:175–181

Lowman MD, Heatwole H (1992) Spatial and temporal variability in defoliation of Australian eucalypts. Ecology 73:129–142

Mitchell AW, Secoy K, Jackson T (2002) Global canopy handbook, techniques of access and study in the forest roof. Global Canopy Programme, Oxford

Monte-Alegre A, Rakotomalala Z, Levedgle M, Coulier F, Faure E (2005) Ecological, vertical and elevational distributions of Heteropsis (Lepidoptera, Satyrinae) in the rainforest of Masoala (NE Madagascar). J Zool Syst Evol Res 43:214–222

Montgomery N (1977) Single rope techniques, a guide for vertical cavers. Sydney Speleogical Society Occasional Papers no. 7, p. 1–122

Selman BJ, Lowman MD (1983) The biology and herbivory rates of Novacastria nothofagi Selman (Coleoptera: Chrysomelidae), a new genus and species on *Nothofagus moorei* in Australian temperate rain forests. Aust J Zool 31:179–91