Australian Journal of Ecology (1987) **12**, 189–191

Relationships between leaf growth and holes caused by herbivores

M. D. LOWMAN
Zoology Department, University of New England, Armidale, NSW 2350, Australia

Introduction

There are two approaches to the estimation of herbivory in a canopy. One is to measure the absolute amount consumed by herbivores in terms of bites of leaf tissue removed and express defoliation as metres squared of leaf surface area (or kilogram of photosynthetic tissue). This approach is useful for examining the population dynamics and feeding behaviour of the insects or, in a sense, to approach herbivory from a herbivore's perspective. The second is to measure the proportion of leaf area missing, usually expressed as a percentage of total leaf surface area. The latter approach was used for long-term studies of herbivory in Australian rainforests (Lowman 1982, 1984, 1985), and is currently in use for similar studies on eucalypt canopies (Lowman & Heatwole 1987, unpubl. data). One of the most frequently asked questions regarding defoliation measurements expressed as percentage leaf area losses is: 'Does the proportion of area of defoliation stay the same as a leaf expands?'

Many herbivores exhibit marked preference for young leaf tissue (Lowman & Box 1983; Selman & Lowman 1983; Wint 1983). A direct measurement (cm^2) of holes in mature leaves, therefore, may be an overestimation of the actual amount ingested by herbivores that fed upon young, partially expanded leaves. A proportional estimate of defoliation will remain accurate throughout the life of a leaf, however, if leaf holes expand at the same rate as leaf area. This was tested on young leaves of one species of a northern temperate forest, *Liriodendron tulipifera* L. (albeit with deciduous, and unusual tulip-shaped leaves), and its holes expanded at a rate proportional to leaf growth (Reichle *et al.* 1973). In this study, a similar test was performed for a range of Australian rainforest tree species exhibiting different leaf shapes, textures, and growth habits.

Methods

The field growth experiment was performed on five species of rainforest canopy trees, namely *Nothofagus moorei* (F. Muell.), *Doryphora sassafrass* Endl., *Dendrocnide excelsa* (Wedd.) Chew, *Ceratopetalum apetalum* D. Don, and *Toona australis* (F. Muell.) Harms. Species were selected to represent all major regions of rainforest in New South Wales: cool temperate, warm temperate and subtropical; and to include both evergreen and deciduous leaf growth patterns, and different leaf textures and shapes. More information on species and sites is listed elsewhere (Lowman 1982, 1984).

Approximately 40 leaves of each of five rainforest canopy tree species were selected at a very young age, class 1 (Fig. 1, Lowman & Box 1983), just after budburst but well before full expansion. A standard hole of 0.33 cm^2 was removed from each leaf using a paper punch in the lower region of the blade to the right of the midvein. Each leaf was numbered on the underside with a black waterproof pentel pen and its leaf length measured. Several fully expanded leaves (stages 2 and 3, Fig. 1, Lowman & Box 1983) were also punched and monitored to serve as controls for possible artefacts of the sampling technique. About 4 weeks later, or when the leaves had matured (i.e. reached stage 3 in development), they were harvested. Because mortality of young leaves is fairly high due to natural events of predation, desiccation, or physical tearing, only 15–25 of the original 40 leaves per species remained for analysis. Both leaf lengths and the expanded hole area made by the original punch were measured again, the latter with a Lambda portable area meter. The ratio of change in leaf hole size expansion was regressed against the ratio of change in leaf length.

Results and discussion

The relationships between the change in area of leaf hole and change in leaf length were very reliable, with all r^2 values above 0.76 (Fig. 1).

This confirms that leaf holes of a variety of rainforest trees expand proportionally with leaf growth, despite the fact that the area (cm^2) changes. A proportional expression of herbivory can be quantified into weights or surface areas, if the total weight or surface area of a leaf (or canopy or forest) is known. In the case of these five rainforest species, defoliation was translated from proportions to areas of holes (cm^2) in a number of sites (Table 1). The proportional data, however, provides accurate information throughout the lifespan of a leaf; whereas hole areas (cm^2) may overestimate the amount consumed by insects if the defoliation occurred while the leaf was young.

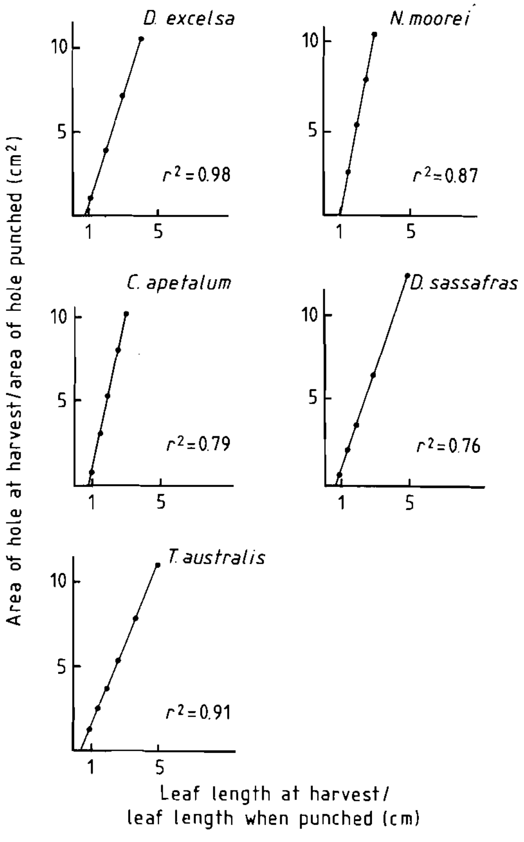

FIG. 1. Regression slopes of changes in leaf area in relation to changes in leaf length for five Australian rainforest trees. Equations are as follows: y(*D. excelsa*) = $-2.59 + 3.32x$; y(*N. moorei*) = $-5.48 + 5.41x$; y(*C. apetalum*) = $-4.04 + 4.72x$; y(*D. sassafras*) = $-2.51 + 3.07x$; and y(*T. australis*) = $-1.36 + 2.52x$, where x = change in leaf length and y = change in hole area.

In all five experimental cases, the holes retained a circular shape after leaf expansion, indicating a constant growth relationship between leaf length and width. A similar result was obtained for some colonizing, understorey species (*Solanum mauritianum* Scop. and *Omalanthus populifolius* Grah.) with rounder (not eliptical as were most leaves in this study) leaves (Neldner 1980). In some tree species (e.g. *Eucalyptus camuldulensis*), the formation of epicormic shoots may produce leaves that are longitudinally distorted as foliage matures, and insect holes are also subsequently distorted (P. B. Carne pers. obs.). In other cases of both eucalypts and rainforest trees, insect defoliation infrequently damages midveins or leaf margins in a manner that results in distortion of leaf outlines and insect holes (M. D. Lowman pers. obs.).

In studies of pest outbreaks, it may be useful to measure insect damage in mature leaves and extrapolate back to original insect bites inflicted when the leaves were young. The equations are:

$$y = ax + b$$
$$y_2/y_1 = a(x_2/x_1) + b$$

where: x_1 = average young leaf length; x_2 = length of mature leaf, y_2 = hole area in the mature leaf and y_1 = the unknown variable (i.e. hole size in young leaf). In cases of host-specific insects, short-lived herbivores, or characteristic types of defoliation where herbivores prefer young leaves, insect numbers can be estimated even after they have disappeared and the leaves fully expanded.

Acknowledgments

I am grateful to Peter Myerscough for advice throughout my years of rainforest research, to Tony Underwood for statistical advice, and to Joe Connell and Harold Heatwole for discussions of relevant ideas. Thanks to P. B. Carne and D. Lamb for their comments on the

TABLE 1. Defoliation of Australian rainforest leaves, expressed both as proportional (%) leaf area losses and as amounts (cm^2) of missing leaf surface (n = 30 leaves)

Sample	Potential leaf area (cm^2)*		Percentage missing†		Amount missing (cm^2)
	$\bar{x}$	s.e.m.	$\bar{x}$	s.e.m.	
Toona australis					
3 m shade, Atherton, N. Qld	27.6	1.3	2.6	1.1	0.7
1 m shade, Hinchinbrook Is, Qld‡	39.1	2.2	5.3	1.7	2.1
8 m shade, Dorrigo NP, NSW	23.1	1.1	14.2	2.8	3.3
1 m sun, Mt Keira, NSW	22.1	0.3	1.7	0.2	0.4
15 m sun, Mt Keira, NSW	19.9	0.5	0.9	0.5	0.2
Dendrocnide excelsa					
1 m shade, Ingham, Qld	219.7	65.0	5.0	1.8	11.0
2 m shade, Dorrigo NP, NSW	210.9	26.1	42.1	3.8	88.8
10 m sun, Dorrigo NP, NSW	54.4	4.7	25.8	2.3	14.0
1 m shade, Mt Keira, NSW	290.2	22.0	5.9	1.3	17.1
Nothofagus moorei					
1 m shade, New England NP, NSW	15.8	0.8	20.1	3.0	3.2
8 m shade, New England NP, NSW	15.2	0.4	10.9	1.5	1.7
10 m sun, New England NP, NSW	8.1	0.6	16.3	2.3	1.3
5 m shade, Mt Banda Banda, NSW	11.4	0.81	11	1.6	1.3
Ceratopetalum apetalum					
30 m sun, Dorrigo NP, NSW	19.5	1.5	9.3	2.3	1.8
5 m sun, Royal NP, NSW	12.1	1.0	1.0	0.2	0.1
5 m shade, Royal NP, NSW	60.1		6.8	2.6	4.1
2 m sun, Mt Keira, NSW	21.9	0.3	9.6	0.3	2.1
2 m shade, Mt Keira, NSW	51.6	0.7	5.9	2.6	8.2
Doryphora sassafras					
2 m shade, Dorrigo NP, NSW	19.0	0.9	9.3	2.3	0.8
3 m sun, Dorrigo NP, NSW	8.9	0.7	1.2	0.6	0.1
5 m sun, New England NP, NSW	5.9	0.4	13.9	3.1	0.8
2 m shade, Royal NP, NSW	42.3	2.1	7.3	2.3	3.0

*Potential leaf area — defined as the total amount of leaf area, had insects not defoliated any (see Lowman 1982). †Discrete herbivory measurements from a harvested sample actually underestimated true herbivory since leaves entirely eaten are not measured (see Lowman 1984). ‡*Toona albertii*. NP = national park.

manuscript. This work was completed during an ARGS postdoctoral fellowship. Sandra Higgins kindly typed the manuscript.

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(Final manuscript received July 1986)