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GRAZING ON AUSTRALIAN EUCALYPT LEAVES BY INSECTS

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ABSTRACT. Discrete samples of leaves from 28 species of eucalypts were collected from various habitats in southeastern Australia for measurement of herbivory in terms of (1) percentage of leaves damaged by folivorous insects and (2) the proportion of total leaf area consumed. There was high variation among samples in percentage of leaves damaged (range 27–100%). Proportion of leaf area consumed varied greatly from leaf to leaf and from sample to sample, even among closely located conspecifics. Mean values for different habitats, however, were remarkably similar, varying from 5.3% (urban cultivars) to 9.7% (roadsides) for a grand mean over all habitats of 7.6%. Distributions of values often were highly skewed and most median values were low. A review of the literature combined with the present data suggests that the baseline level of folivory by insects on healthy eucalypts is about 7.5%, with a secondary peak at about 15%. The latter is attributable, at least in part, to elevated folivory suffered by eucalypt seedlings, saplings and regrowth. The literature includes conclusions that chronic folivory of Australian trees is considerably higher than that on other continents. However, the values from Australian eucalypts overlap broadly with those elsewhere, and the differences, if real, are not so great as sometimes believed. An appeal is made for more process studies of the dynamics of folivory in which individual cohorts of leaves are followed separately and account taken of variation in leaf-longevity and the phenology of flushing.

Key words: *Eucalyptus,* herbivory, folivory, Australia

INTRODUCTION

Herbivory can be a potent factor in affecting plant populations. Indeed, Bigger and Marvier (1998) concluded that herbivores may exert as important an effect on plant biomass as does competition among plants. Specifically, folivory by insects has been shown to have adverse effects upon eucalypts (Landsberg & Cork 1997). Lamb (1985) reviewed insect-eucalypt interactions and concluded that although there were some particular circumstances in which herbivory may confer a nutritional advantage on a plant community through mobilizing nutrients temporarily removed from the normal cycle between trees and soil, grazing by insects usually accelerates the removal of nutrients and is detrimental to plants. Folivory by insects has been implicated as an ingredient in dieback of eucalypts in the New England district of Australia (reviewed by Heatwole & Lowman 1986), and has been shown to adversely affect tree growth (e.g., Greaves 1966, Lowman & Heatwole 1987). The impact of grazing by insects on eucalypts can be modified by other environmental factors (e.g., Stone & Bacon 1995).

There are many sources of variability in numbers of individuals and species of arthropods in Australian canopies, such as geographic location, climate, elevation, topography, weather, season, species or subgenus of tree, individual tree, young versus mature trees, fire-history, level in the canopy, phenology of the host tree, site fertility, and age and nutrient status of leaves (Morrow 1977a, Ohmart et al. 1983b, Basset 1991, Kitching et al. 1993, Recher et al. 1996, Majer et al. 1992, 1997). Within-tree variation sometimes is greater than between-tree variation. Abbott et al. (1992) found dissimilarities among individual jarrah (*Eucalyptus marginata*) trees, as well as between stands, and concluded that there was neither a fixed pattern of organization nor a predictable assemblage in jarrah forests. Similarly Heatwole et al. (1997) found large differences in arthropod numbers on various species of *Eucalyptus* saplings both spatially and temporally, with adjacent conspecific plants sometimes showing greatly different levels.

Given the large variation in abundances of folivorous insects in Australian canopies, it is not

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surprising that leaf-damage by grazing insects also varies greatly. This is further compounded by the fact that the abundance of grazing insects and the leaf-area lost to them often do not correlate closely because of variation in size of folivorous species in different places and because of influxes of nocturnal grazers (Fensham 1994b). The extent of damage to the foliage of Australian trees caused by folivores is related to a large number of variables, including age of leaves, leaf nutrient levels, leaf chemistry (but see Fox & Macauley 1977), leaf texture, phenology of leaf-flushing in relation to insect emergences, individual tree, age of tree, tree health, seedlings versus mature trees, species of tree, other species of trees present, stratum or level within the canopy, height above ground, degree of canopy closure, density of trees, edge versus interior of forest, distance from grassland, habitat (urban versus rural, open areas or woodland versus forest), vegetation type, site productivity, resource availability, degree of human disturbance, previous land use, locality, elevation, climatic zone, season, year, weather, moisture conditions, whether in sun or shade, abundance and kinds of birds present, and sampling methods (Greaves 1966, Burdon & Chilvers 1974b, Carne et al. 1974, Specht & Brouwer 1975, Morrow 1977b, 1983, Journet 1981, Landsberg & Wylie 1983, Lowman 1984a, 1985a, 1992a, 1992b, 1995a, 1995b, Fox & Morrow 1986, Landsberg 1989, 1990a, 1990b, Williams 1990, Lowman & Heatwole 1992, Fensham 1994a, Landsberg & Gillieson 1995, Stone 1996, Heatwole et al. 1997, Landsberg & Cork 1997, Hadwen et al. 1998).

The intent of the present study was to assess the range of levels of folivory encountered by eucalypts over a wide spectrum of locations, conditions, and tree species in Australia for use as a baseline for comparison of grazing on eucalypts introduced into other parts of the world. This baseline rests on a review of previously published information and on new data obtained from southeastern Australia.

MATERIALS AND METHODS

Sampling consisted of collecting the two oldest (most basal) leaves from each of 15 branches, for a total of 30 leaves from a given tree, the minimum sample size considered by Lowman (1997) to be adequate. On a few occasions the sample had fewer leaves for lack of sufficient accessible branches, or because one or more leaves were lost. For the sake of consistency, only branches from the lower canopy of mature trees were used. Lowman (1985a) noted that leaves in the lower canopy usually suffer somewhat heavier damage than those in the upper canopy and therefore, the values of the present study probably represent maximum values for the sampled trees.

FIGURE 1. Map of Australia showing sampling locations. Several species were sampled from some localities. Stippling indicates areas where eucalypts are prominent in the landscape. They are not entirely absent from unstippled areas, but are limited there to specialized sites, such as seasonal watercourses or rock clefts, that cannot be represented on the scale of the diagram. Map modified from Pryor (1996).

No attempt was made to select particular species. Rather, sampling was widespread in southeastern Australia (FIGURE 1) with the view of representing many species, localities, and habitats so as to encompass as great a range of conditions as possible. During trips for other purposes, sampling was carried out opportunistically by stopping at convenient intervals along the way and collecting leaves from whatever species happened to be available. In all, 51 samples from 28 species of eucalypts from 37 localities, ranging from the Tropic of Capricorn to about 35°30′S latitude, were sampled. The habitats fell into six major categories: (1) forest, (2) woodland, (3) riversides and dry streambeds, (4) roadsides, (5) cultivars in gardens or other urban situations, and (6) isolated trees in otherwise open areas such as pastures.

The surface area of each individual leaf was measured by a computerized Delta T Area Meter. Then, black electrical tape was placed over any areas suffering damage that appeared to have been caused by chewing insects, and the tape trimmed to conform to the original shape of the leaf (FIGURE 2). The surface area was measured again and the first reading (area of grazed leaf) subtracted from the second one (original, ungrazed area of leaf) to provide the

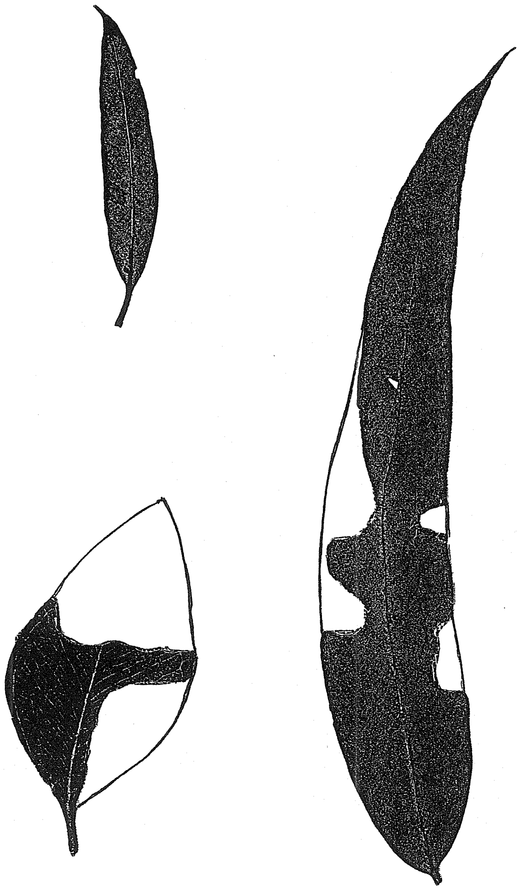

FIGURE 2. Three examples of leaves with different degrees of damage and their reconstructed shapes. Upper left: slight damage. Lower left: heavy damage. Right: moderate damage.

leaf area consumed. Damage by sucking herbivores, leaf miners, and fungi was not assessed.

All trees sampled appeared healthy and thus the measured level of herbivory excludes those high values characteristic of trees experiencing dieback (Landsberg 1988, 1990a, 1990b; Lowman & Heatwole 1992).

There are several sources of error inherent in the method: (1) The tips of some leaves had been broken off, seemingly by mechanical means other than insect grazing. Thus, the original, ungrazed area of the leaf was underestimated, and the proportional damage by grazing exaggerated accordingly; such breakages were infrequent and slight and not believed to be a serious source of error. (2) Leaves entirely consumed by insects, or those prematurely shed because of heavy grazing (Carne et al. 1974; Journet 1981, Fox & Morrow 1983) went undetected and the extent of grazing was underestimated accordingly (see the Discussion section for comparison of discrete sampling with long term monitoring of grazing). (3) Holes may expand as leaves grow (Robertson & Duke 1987, Landsberg 1989) and proportional loss of leaf-area would overestimate the weight of leafy tissue consumed if grazing took place when the leaf was younger. However, Lowman (1987) showed that the holes in leaves of a number of Australian tree species expand in proportion to leaf growth. Hence, damage expressed as proportion of leaf area missing, such as in the present study, remain accurate throughout the lifespan of the leaf. (4) The sampled leaves had not completed their lives and it is possible that they would have undergone additional herbivory had they been left on the tree. This error is believed to be slight as most herbivory is suffered by young leaves soon after flushing, with relatively little additional damage as they age (Robertson & Duke 1987, Landsberg 1988; Lowman & Heatwole 1992). However, to gain an appreciation of this source of error, some samples were duplicated by picking up 30 recently fallen leaves directly under the sampled tree and the results from the two methods compared.

For analysis, herbivory was expressed in two different ways: (1) the proportion of the leaves of a sample that had sustained at least some damage, without reference to how severe or how light that damage was, and (2) the proportion of the total surface area consumed.

RESULTS

The number of leaves suffering at least some damage varied widely among samples. There were no samples in which all leaves were completely intact whereas there was one sample (2%) in which all leaves had at least some damage (see APPENDIX). The mean for all samples was 65.9% ± SE 3.49%. However, the data were not normally distributed but were skewed to the right, with the modal decade of values being 80–90% (FIGURE 3). The median value was 73%.

The percentage of the total leaf-area consumed varied widely among leaves within a sample. FIGURE 4 shows three examples of the distribution of grazing intensities among individual leaves: the most heavily damaged sample (mean leaf-area consumed 26.2%), the most lightly grazed one (0.01%) and the sample with the median value of grazing (4.9%). The last reflects the most common pattern of distribution of grazing intensities. For most of the samples, the grazing intensities were skewed to the left, with little or no damage to most leaves and only a few leaves more heavily damaged. Only at unusually high grazing intensities did the values

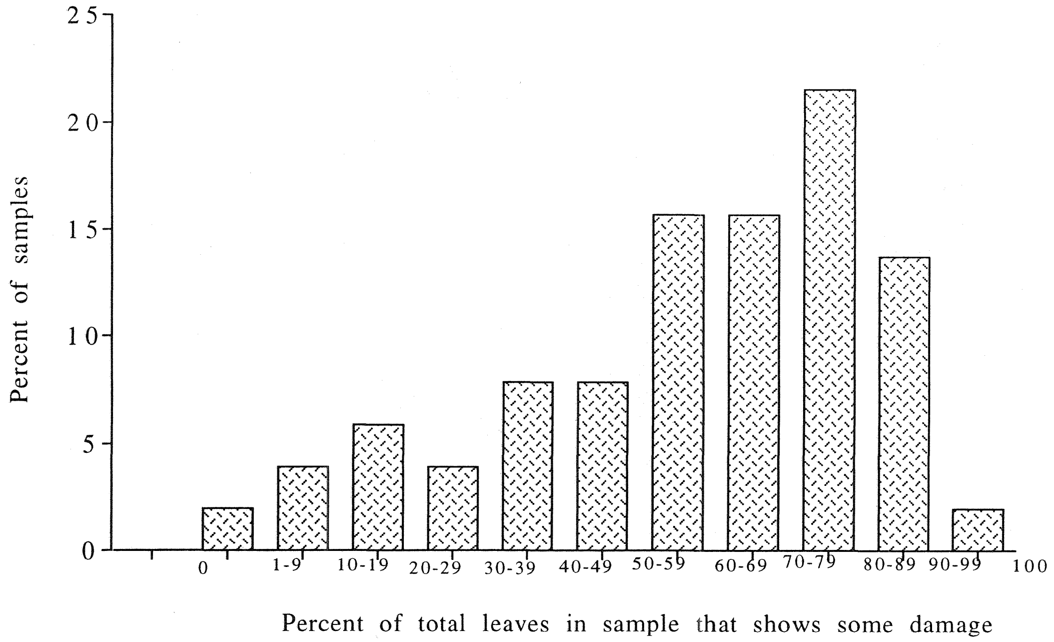

FIGURE 3. Frequency distribution of proportions of the total leaves showing at least some damage.

approach a normal distribution with lower and higher damages recorded for fewer leaves than for those of intermediate values.

The mean percentage of leaf surface area consumed also varied widely among samples. This was true even when samples came from conspecific trees located near each other (TABLE 1). The two largest categories of samples suffered an average consumption of between 4 and 5% and between 7 and 8% of total leaf surface (FIGURE 5). The frequencies were not normally distributed but were skewed somewhat to the left. By

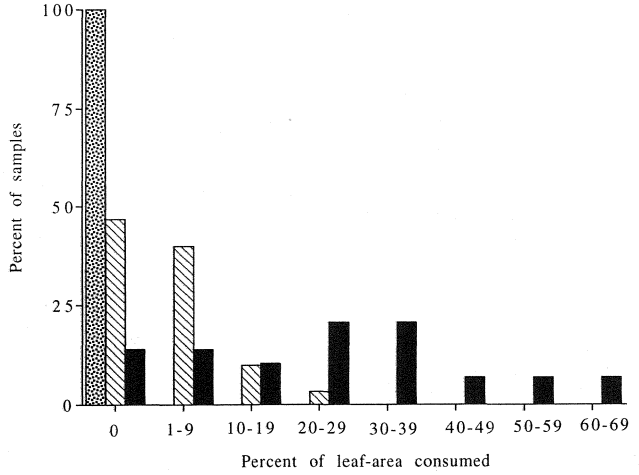

FIGURE 4. Frequency distribution of grazing intensities of three samples of leaves. Stippled histograms represent a sample of leaves from a *Eucalyptus globosa* grown as a cultivar in Cobar, NSW; it had the lightest herbivory of any sample in the study (mean 0.01%; median zero). Hatched histograms represent a sample of leaves from a *Eucalyptus cladocalyx,* from a roadside at Riverton, SA; it had moderate herbivory (mean 4.86%; median 1.4%). Black histograms represent a sample of leaves from a *Eucalyptus albens* from a roadside at Tamworth, NSW; it had suffered the heaviest herbivory in the study (mean 26.17%; median 25.5%).

TABLE 1. Folivory on leaves of pairs of conspecific, nearby trees of Australian eucalypts.

Species	*N*	% of leaf area consumed (Mean ± SE)	Range	Median	Mode	% of leaves with damage
Angophora floribunda	30	7.46 ± 2.303	0–41.0	0	0	40.0
	30	16.16 ± 2.955	0–51.3	11.6	0	83.3
Eucalyptus camaldulensis	30	4.20 ± 1.145	0–20.4	0.1	0	56.7
	30	11.60 ± 2.131	0–47.6	10.4	0	86.7
Eucalyptus populnea	30	7.44 ± 2.174	0–43.7	0.6	0	63.3
	30	1.89 ± 0.814	0–15.0	0	0	26.7
Eucalyptus socialis	29	10.15 ± 1.795	0–33.3	11.1	0	75.9
	30	4.87 ± 1.662	0–32.7	0	0	66.7

contrast, the median values were lower than the means (see APPENDIX) and were strongly skewed to the left, with most samples having a median herbivory of less than one percent, and values tailing off sharply above that value (FIGURE 5).

The two measures of folivory (proportion of leaves damaged, and proportion of total leaf area consumed) are correlated. The correlation coefficient between these variables was 0.71 with an R^2 of 0.504; an analysis of variance indicated the linear regression as significant ($F = 49.7$; $P = 0.0001$) (FIGURE 6). From the scatter around the line, it is clear that the mean leaf-area consumed showed greater variation at the higher levels of leaf damage. In some samples consumption of leafy material and proportion of leaves damaged were both high, as one would intuitively expect. However, even when mean consumption of leafy material was low, many leaves were damaged, i.e., many leaves attacked, but few, if any, of them suffered more than minor damage.

For each of the three paired-samples available, estimates of leaf damage based on harvesting the oldest leaves from the tree gave higher values than those based on picking up fallen leaves from the ground (TABLE 2).

Given the great variation in levels of damage among individual leaves and from tree to tree, different habitats had remarkably similar values; the range in values was only from 5.3% to 9.7% (TABLE 3). Within that narrow range, values for woodlands and forests fell within the span of those from more open kinds of habitats. The overall mean was 7.6%.

DISCUSSION

Percentage of Leaves Sustaining Damage

In comparison to estimates of the proportion of leaf area consumed, there are few data available for Australian trees on the percentage of the leaves that are damaged by grazing. Robertson and Duke (1987) reported mean values for 25

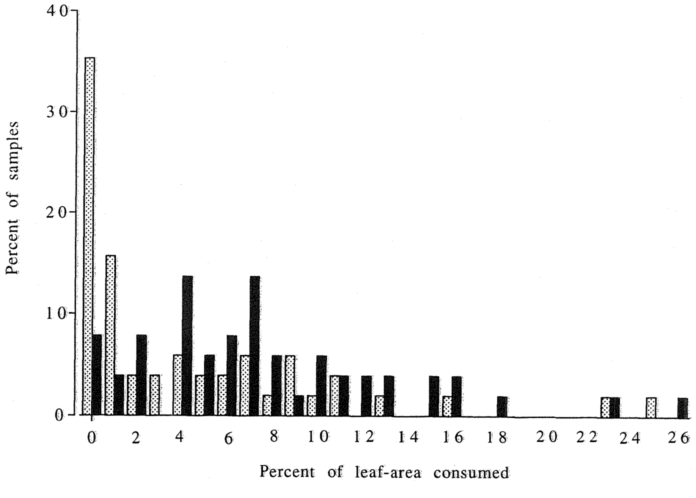

FIGURE 5. Frequency distribution of mean (black histograms) and median (stippled histograms) values of grazing intensity of eucalypt leaf samples.

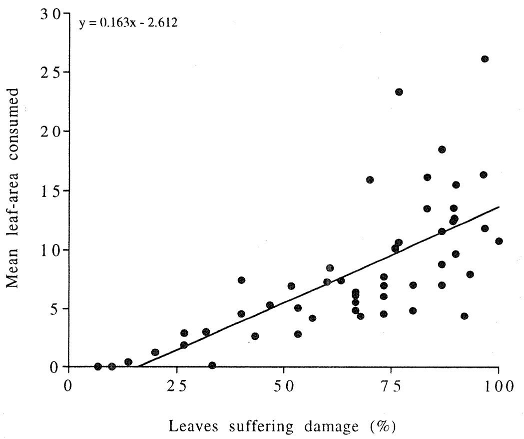

FIGURE 6. Relationship of two measures of folivory: percentage of leaves suffering damage and mean leaf-area consumed.

species of Australian mangroves ranging from 8% to 100%, depending on species and locality. Fox and Morrow (1983) reported data for eucalypts from which such information could be calculated. Twelve species from relatively undisturbed upland woodlands gave a mean of 74% of the leaves having sustained some degree of damage (range 30–95%). Corresponding values for 21 species from relatively undisturbed lowland woodlands and forests, 12 species from disturbed lowland woodlands and forests, and seven species from mallee[1] were 80% (49–98%), 86% (72–99%), and 73% (50–96%), respectively. Greaves (1966) observed that in *Eucalyptus regnans,* the proportion of leaves damaged varied with age of tree, the younger trees having a greater proportion of their leaves damaged (62–65% damaged by beetle larvae for different levels in the canopy; 23–57% damaged by adult beetles) than was true for older trees (6–9% and 4–6%, respectively). Heatwole and Preker (unpubl. data) obtained mean values of 55.6% and 39.3–69.0% for *Acacia salicina* and *Melaleuca quinquenervia,* respectively. The mean value for the samples from the present study (66%) are lower than those of Fox and Morrow but similar to those of Greaves; our range (7–100%) exceeds the overall range (30–99%) of Fox & Morrow (Greaves' ranges not specified).

The generally higher values of Fox & Morrow corresponded to a greater proportion of leaf area consumed and, as in the present study, the two measures of folivory were correlated.

Levels and Variability of Proportional Leaf-area Consumed

Individual leaves within a sample varied greatly in the proportion of leaf area consumed by folivorous insects. This had both spatial and temporal components. For example, samples from conspecific trees near each other had several-fold differences in the extent of leaf-damage (TABLE 1); similarly, the oldest leaves still on branches showed several-fold differences in folivory from newly fallen leaves from the same tree (TABLE 2), probably because the two samples represented cohorts from slightly different periods of time. Such between-tree and between-cohort differences were sometimes as great as those between localities for a given species (APPENDIX). By comparison, mean folivory between habitats (lumping all species sampled) produced remarkably consistent values. This uniformity may be by chance, or it may reflect the fact that only healthy, mature trees were sampled. It has been noted repeatedly that unhealthy trees (see Heatwole & Lowman 1986), as well as saplings and regrowth (see TABLE 4), often sustain considerably higher folivory than do healthy, older trees.

Often, damage levels were not normally distributed among leaves and the scedasticity was

TABLE 2. Comparison of leaf damage in eucalypt leaves collected by two different methods.

		% of leaf area consumed				% of leaves with
Species	Method	(Mean ± SE)	Range	Median	Mode	damage
Angophora floribunda	Oldest leaves on tree	18.47 ± 2.811	0–47.0	16.6	0	86.7
	Newly fallen leaves on ground	7.07 ± 1.667	0–35.2	4.0	0	86.7
Eucalyptus coolibah	Oldest leaves on tree	7.76 ± 2.232	0–49.3	3.5	0	73.3
	Newly fallen leaves on ground	4.39 ± 1.316	0–30.3	2.1	1	92.0
Eucalyptus populnea	Oldest leaves on tree	12.45 ± 2.789	0–52.5	7.3	0	89.3
	Newly fallen leaves on ground	7.07 ± 1.667	0–35.2	4.6	0	80.0

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[1] Mallee is a growth form of Australian woody plants, especially eucalypts and wattles, in which multiple stems, rather than a single tree trunk, arise from a lignotuber to form a thicket (Child & Child 1971).

TABLE 3. Comparison of folivory of eucalypt leaves by habitat.

Habitat	No. of: Leaves	No. of: Samples	No. of: Species	Mean % of leaf area consumed	% of leaves with damage
Forest	178	6	5	7.91	40–93
Woodland	264	9	8	7.21	46–97
Riverbanks & streambeds	120	4	1	8.95	57–87
Roadsides	582	20	12	9.66	27–100
Urban or cultivars	150	5	5	5.26	7–77
Isolated trees	201	7	6	6.61	14–96
Total	1495	51	28	7.60 (Grand Mean)	7–100

sufficiently great that transformations of the data did not produce normality. For such samples, the mean is not appropriate as a measure of central tendency or for comparison with other samples. Because our data included samples in which distribution of damage among leaves was highly skewed and those in which it was normally distributed, any parametric comparison would be tenuous at best. Landsberg (1989) also has noted markedly non-normal distribution of damage to individual eucalypt leaves in samples. She avoided the problem by expressing folivory as the ratio of total area of damage to all leaves in the sample to total potential area (before damage) summed for all leaves. However, in the present study lack of normality also occurred in the distribution of damage among samples. The data were skewed to the left, i.e., many samples had low levels of folivory and a few had high levels (FIGURE 5). Thus, a mean of these samples is not an adequate descriptor of central tendency and not appropriate for comparison with other studies or continents. Similar considerations apply to folivory as measured by the proportion of damaged leaves within a sample. Heatwole et al. (1997) also found the numbers of insects on eucalypt saplings to be highly skewed, and suggested that measures of central tendency were of less importance than an understanding of the phenology of interaction of plants and their insect grazers.

Williams (1990) also has criticized the use of means in assessing levels of herbivory on eucalypts. Because of the skewed nature of herbivory data, Wotherspoon (1998) suggested the median to be superior to the mean in comparisons of folivory. However, few studies in the literature provide median values, and at present most comparisons of necessity are made on the basis of averages, inadequate though they may be. Development of appropriate statistical treatments based on the median and accounting for scedasticity would be an advance in the study of folivory.

Wotherspoon obtained median damage levels of 4.9–8.4% in four species of eucalypts in Tasmania; the results of the present study were similar in that of the 51 samples, only 10 had a median of 10 or greater (range 0–23.7) and the average median value was 4.5 (see FIGURE 5).

Lowman (1985a) noted grazing on leaves to be extremely variable at small spatial scales (i.e., among individual leaves or between branches) but that pooling on the basis of whole canopies or geographic areas produced greater similarity. Mean folivory in the present study did not differ greatly among habitats; means from different habitats varied from 5.3 to 9.7 (grand mean 7.6%). We believe that the great variation in levels of damage, and the inconsistency in scedasticity of the distribution of damage among individual leaves and among samples, presently do not allow precise comparisons.

There are some comparisons, however, that involve orders of magnitude. There were four samples that sustained exceptionally low damage (0.01–0.41%). Two of these were from Narrabri, NSW, and were growing near cottonfields where they were subject to drift of insecticides. The remaining two were ornamentals that may have been intentionally sprayed. Thus, the damage to these trees probably was artificially reduced through application of insecticides.

We are currently undertaking a study of folivory in eucalypts introduced into other countries from Australia. Severe damage to introduced eucalypts, especially from introduced Australian insects, have been reported (review by Ohmart & Edwards 1991). However, our preliminary data suggest that folivory rates in introduced eucalypts generally are an order of magnitude lower than on eucalypts growing natively in Australia. Other comparisons of the extent of folivory, not involving such great differences, are discussed below.

Dynamics of Grazing

The present analysis allows some speculation and interpretation of the dynamics of grazing.

TABLE 4. Mean folivory by chewing insects in some Australian canopies. Values are from healthy trees only, i.e., herbivory on trees suffering from dieback is excluded. L indicates long-term monitoring; D = discrete sampling. Where a spread of values is indicated it denotes the range of means from different localities, times or situations. Brackets indicate multiple studies on the same species.

	Folivory (% of total leaf area)		
Taxon and conditions	L	D	Reference
NON-EUCALYPTS			
Acanthaceae			
Acanthus ilicifolius		6.8–9.0	Robertson and Duke (1987)
Anacardiaceae			
Buchania obovata (sprouts)			Fensham (1994a)[1]
Tall forest	5.8		
Low forest	6.3		
Avicenniaceae			
Avicennia marina		8.8–12.0	Robertson and Duke (1987)
Boraginaceae			
Argusia argentea		2–5	Lowman (1984b)
Argusia argentea		1–12	Heatwole et al. (1981)
Caesalpiniaceae			
Cymenometra iripa		19.7	Robertson and Duke (1987)
Erythryophleum chlorostachys (sprouts)			Fensham (1994a)[1]
Tall forest	13.2		
Low forest	17.9		
Combretaceae			
Lumnitzera littorea		4.3	Robertson and Duke (1987)
Lumnitzera racemosa		3.0–4.6	Robertson and Duke (1987)
Terminalia ferdinandiana (sprouts)			Fensham (1994a)[1]
Tall forest	7.0		
Low forest	13.0		
Cunoniaceae			
Ceratopetalum apetalum			Lowman (1992a, 1992b)
Sun leaves	9.4–26.9		
Shade leaves	35.3		
Euphorbiaceae			
Excoecaria agallocha		0.3–1.5	Robertson and Duke (1987)
Fagaceae			
Nothofagus moorei	31.0		Lowman (1992a, 1992b)
Lecythidaceae			
Planchonia careya (sprouts)			Fensham (1994a)[1]
Tall forest	15.7		
Low forest	9.1		
Meliaceae			
Toona australis	3.3[1]–6.3		Lowman (1992a, 1992b)
Xylocarpus australasicus		3.0–3.5	Robertson and Duke (1987)
Xylocarpus granatum		6.9–10.0	Robertson and Duke (1987)
Mimosaceae			
Acacia aulacocarpa (sprouts)			Fensham (1994a)[1]
Tall forest	11.9		
Low forest	28.1		
Acacia salicina		9.0	Heatwole and Preker (prev. unpubl.)
Monimiaceae			
Doryphora sassafras			Lowman (1992a, 1992b)
Cool temperate	12.3	12.0	

TABLE 4. Continued.

Taxon and conditions	Folivory (% of total leaf area) L	Folivory (% of total leaf area) D	Reference
Warm temperate			
Sun leaves	17.6	4.5	
Shade leaves	27.8	7.6	
Subtropical			
Sun leaves	13.4	4.4	
Shade leaves	16.3	6.4	
Myrsinaceae			
Aegiceras corniculatum		10.5–17.1	Robertson and Duke (1987)
Myrtaceae (other than eucalypts)			
Melaleuca quinquenervia		3.0–11.1	Heatwole and Preker (pers. obs.)
Osbornia octodonta		6.2	Robertson and Duke (1987)
Nyctaginaceae			
Pisonia grandis		1–14	Heatwole et al. (1981)
Pisonia grandis		1–14	Heatwole et al. (1981)
Pandanaceae			
Pandanus sp.		<2.0	Heatwole et al. (1981)
Plumbaginaceae			
Aegialitis annulata		1.2	Robertson and Duke (1987)
Proteaceae			
Darlingia ferruginea			Hadwen et al. (1998)
Seedlings		6.4	
Mature trees		3.9	
Orites excelsa			Hadwen et al. (1998)
1995			
Seedlings		10.3	
Mature trees		3.6	
1996			
Seedlings		12.5	
Mature trees		2.3	
Stenocarpus salignus			Hadwen et al. (1998)
1995			
Seedlings		14.4	
Mature trees		9.3	
1996			
Seedlings		12.9	
Mature trees		10.7	
Stenocarpus sinuatus			Hadwen et al. (1998)
1995			
Seedlings		11.3	
Mature trees		14.3	
1996			
Seedlings		25.4	
Mature trees		21.2	
Rhizophoraceae			
Bruguiera exaristata		2.9	Robertson and Duke (1987)
Bruguiera gymnorrhiza		1.8–3.7	Robertson and Duke (1987)
Bruguiera parviflora		3.3	Robertson and Duke (1987)
Ceriops tagal var. *australis*		6.8	Robertson and Duke (1987)
Ceriops tagal var. *tagal*		6.3	Robertson and Duke (1987)
Rhizophora apiculata		3.9–5.8	Robertson and Duke (1987)
Rhizophora × *lamarckii*		1.4	Robertson and Duke (1987)
Rhizophora mucronata		2.6	Robertson and Duke (1987)
Rhizophora stylosa		5.1–7.6	Robertson and Duke (1987)
Rhizophora spp. seedlings		3.8–4.2	Robertson and Duke (1987)

TABLE 4. Continued.

	Folivory (% of total leaf area)		
Taxon and conditions	L	D	Reference
Rubiaceae			
Scyphiphora hydrophyllacea		0.7	Robertson and Duke (1987)
Sonneratiaceae			
Sonneratia alba		1.2–10.7	Robertson and Duke (1987)
Sonneratia caseolaris		9.9	Robertson and Duke (1987)
Sonneratia × *gulngai*		7.8	Robertson and Duke (1987)
Sterculiaceae			
Argyrodendron actinophyllum			Hadwen et al. (1998)
1995			
Seedlings		20.4	
Mature trees		14.9	
1996			
Seedlings		11.8	
Mature trees		5.4	
Argyrodendron perlatum			Hadwen et al. (1998)
Seedlings		11.1	
Mature trees		8.9	
Argyrodendron trifoliolatum			Hadwen et al. (1998)
1995			
Seedlings		12.5	
Mature trees		11.8	
1996			
Seedlings		10.7	
Mature trees		12.8	
Heritiera littoralis		29.7–35.0	Robertson and Duke (1987)
Urticaceae			
Dendroenide excelsa	15.5–32.5		Lowman (1992a, 1992b)
EUCALYPTS			
Angophora floribunda	17.0		Lowman and Heatwole (1992)
Angophora floribunda			
Saplings		22.5	Lowman and Heatwole (1987)
Eucalyptus accedens		17	Fox and Morrow (1983)[4]
Eucalyptus amplifolia		16	
Eucalyptus blakelyi		29	
Eucalyptus blakelyi		40	Journet (1981)
Eucalyptus blakelyi		3.6–18.7	Landsberg (1988)
Eucalyptus blakelyi			Lowman and Heatwole (1992)
Pasture trees	16.0		
Woodland trees	7.5		
Saplings		6.8	Lowman and Heatwole (1987)
Eucalyptus botryoides		20	Fox and Morrow (1983)[4]
Eucalyptus bridgesiana			
Undisturbed		7	
Disturbed		15	
Eucalyptus caliginosa			Lowman and Heatwole (1992)
Pasture trees	20.9		
Woodland trees	24.9		
Saplings		66.1	Lowman and Heatwole (1987)
Eucalyptus camaldulensis		10	Lowman and Heatwole (1992)
Eucalyptus campaspe		15	
Eucalyptus cinerea		10	
Eucalyptus confertiflora (sprouts)			Fensham (1994a)[1]
Tall forest	30.3		
Low forest	14.7		
Eucalyptus crebra		9	Fox and Morrow (1983)[4]
Eucalyptus dalrympleana		17	
Eucalyptus dalrympleana (saplings)		32	Burdon and Chilvers (1974b)[2,3]

TABLE 4. Continued.

Taxon and conditions	Folivory (% of total leaf area)		Reference
	L	D	
Eucalyptus dalrympleana (regrowth)		19.1–27.5	Burdon and Chilvers (1974b)
Eucalyptus dalrympleana (seedlings)		7.4–9.4	Williams (1990)
Eucalyptus dalrympleana	19.0		Lowman and Heatwole (1992)
Eucalyptus delagatensis		3–10	Ohmart et al. (1983)[2]
Eucalyptus delagatensis (regrowth)		5.1	Burdon and Chilvers (1974a)
Eucalyptus dives		2–16	Ohmart et al. (1983)[2]
Eucalyptus dives		19.2–20.7	Williams (1990)
Eucalyptus dives (regrowth)		11.2	Burdon and Chilvers (1974a)
Eucalyptus dives			Fox and Morrow (1983)[4]
Upland		20	
Lowland		17	
Eucalyptus drummondi		22	
Eucaliptus fastigiata			
Upland		19	
Lowland		8	
Eucalyptus fibrosa		15	
Eucalyptus foecunda		9	
Eucalyptus globulus (regrowth)		3.07	Wotherspoon (1998)
Eucalyptus globulus		12	Kile (1974)
Eucalyptus grandis			Carne et al. (1974)
Young plantations, mostly of *E. grandis*		Usually 20–80	
Eucalyptus griffithsii		15	Fox and Morrow (1983)[4]
Eucalyptus gullickii		6	
Eucalyptus gummifera			
Undisturbed		10	
Disturbed		5	
Mallee		14	
Eucalyptus incrassata (saplings)	1.22	2.8	Mackay (1991)[5]
Eucalyptus macrorhyncha		16	
Eucalyptus mannifera		10	
Eucalyptus melliodora			Lowman and Heatwole (1992)
Mature trees	10.2		
Saplings		52.5	Lowman and Heatwole (1987)
Eucalyptus microcorys		9	
Eucalyptus miniata (sprouts)	15.4		Fensham (1994a)[1]
Eucalyptus moluccana		18	Fox and Morrow (1983)[4]
Eucalyptus nova-anglica		11.0	Lowman et al. (1987)
Eucalyptus nova-anglica	60.5		Lowman and Heatwole (1992)
Eucalyptus obliqua		22	Kile (1974)
Eucalyptus obliqua			Fox and Morrow (1983)[4]
Upland		15	
Lowland		7	
Eucalyptus obliqua (regrowth)		6.67	Wotherspoon (1998)
Eucalyptus obtusiflora			Fox and Morrow (1983)[4]
Woodland and forests		7	
Mallee		9	
Eucalyptus pauciflora		26	
Eucalyptus pauciflora (new growth)		12.7–20.2	Burdon and Chilvers (1974a)
Eucalyptus pauciflora (saplings)			Burdon and Chilvers (1974b)[2,3]
1750 meters elevation		9	
1650 meters elevation		11	
1480 meters elevation		18	
1220 meters elevation		21	
Eucalyptus pauciflora (seedling)		13.9–20.2	Williams (1990)
Eucalyptus pauciflora		2–18	Ohmart et al. (1983a)
Eucalyptus perriniana		23	Fox and Morrow (1983)[4]
Eucalyptus pilularis		13	
Eucalyptus polyanthemos		31	
Eucalyptus pulchella (regrowth)		2.76	Wotherspoon (1998)

TABLE 4. Continued.

Taxon and conditions	Folivory (% of total leaf area)		Reference
	L	D	
Eucalyptus racemosa		8	Fox and Morrow (1983)[4]
Eucalyptus radiata		9	
Eucalyptus radiata (regrowth)		2.7	Burdon & Chilvers (1974a)
Eucalyptus radiata	14.3		Lowman and Heatwold (1992)
Eucalyptus regnans		22	Kile (1974)
Eucalyptus regnans			Greaves (1966)
Upper canopy			
Trees 3 years old		14.5	
Trees 15 years old		1.1	
Trees 30 years old		0.5	
Middle canopy			
Trees 3 years old		15.0	
Trees 15 years old		2.1	
Trees 30 years old		0.5	
Lower canopy			
Trees 3 years old		11.6	
Trees 15 years old		3.3	
Trees 30 years old		0.4	
Without *Acacia dealbata*		4.3–14.3	
With some *Acacia dealbata*		3.5–13.1	
With many *Acacia dealbata*		2.3–5.5	
Eucalyptus rossii			Fox and Morrow (1983)[4]
Eucalyptus rubida		12	
Eucalyptus saintjohnii		15	
Eucalyptus scelrophylla		23	
Eucalyptus scelrophylla			
Undisturbed		8	
Disturbed		18	
Eucalyptus sideroxyon		8	
Eucalyptus sieberi		10	
Eucalyptus stellulata		44	
Eucalyptus stellulata	35.9		Lowman and Heatwole (1992)
Eucalyptus tereticornis		17	Fox and Morrow (1983)[4]
Eucalyptus tetrodonta (sprouts)	10.9		Fensham (1994a)[1]
Eucalyptus triflora		12	Fox and Morrow (1983)[4]
Eucalyptus viminalis (regrowth)		3.45	Wotherspoon (1998)
Eucalyptus viminalis (regrowth)		3.6	Burdon and Chilvers 1974a)
Eucalyptus viminalis	19.8–52.6		Lowman and Heatwole (1992)
Eucalyptus viminalis			Lowman and Heatwole (1987)[5]
Seedlings		97.1	
Various spp. and localites			Landsberg and Gillieson (1995)
Rich sites	*	11–33	
Poor sites	*	8–24	

* Expressed as rates of herbivory per month in original paper and not comparable to rest of values in table.

[1] Leaf loss other than by herbivory by chewing insects excluded to make comparable with other data in the table.

[2] Values extrapolated from a graph.

[3] Includes some damage by fungi.

[4] Includes coppice regrowth as well as small trees and mature trees.

[5] Control values only; experimental manipulations excluded.

The fact that some samples had many leaves damaged, but still low consumption of leafy material, suggests that at least some grazing herbivores do not continue grazing on an individual leaf, but rather eat only a small amount and then move to another leaf to repeat the process. This could arise either from a particular, perhaps species-specific, behavioral mode of foraging, or more likely from an assessment of the palatability of leaves. In individual trees with strong chemical or physical defenses, or low palatability, such probing by insects might lead to rejection of particular leaves, followed by movement to another leaf or tree to repeat the testing process; each leaf tested would show only minimal damage. A more palatable leaf, or one with less effective defenses, might be subject to sustained grazing after a probing attack. Such leaves would exhibit great damage and lead to a strong correlation between number of leaves damaged and the extent of consumption.

Individual trees, even of the same species at the same locality, may have different palatabilities. Landsberg (1990b) found that the health of trees can influence the content of nitrogen and other nutrients in their leaves, and thus alter their palatability to insects. Conversely, induced amelioration may occur, in which nutrient content of leaves is enhanced by light grazing (see Haukioja et al. 1994).

Grazing, either occurring naturally by insects, or simulated by mechanical clipping of leaves, can induce a tree to increase its production of defensive chemicals either in the short term or on a longer temporal basis, and may serve to reduce herbivory, disperse it over a wider range of foliage, or have more subtle, indirect effects. Agrawal et al. (1999) found that grazing-induced resistance by a host plant not only reduced grazing by herbivores and omnivores directly, but also caused a decrease in herbivore populations through a shift in diet of omnivores toward greater carnivory. Clearly, the history of an individual tree can render it more attractive, or less attractive, to insects. A tree that has been induced to improve its defenses or reduce its palatability might suffer only probing attacks by insects whereas a nearby conspecific with a different individual history might be more susceptible and show a strong correlation between leaf-consumption and proportion of leaves damaged.

Lowman (1985a) found that insectan grazers preferred leaves in shade to those in the sun in some Australian forests. By contrast, Heatwole et al. (1997) found that eucalypt saplings in the open had greater numbers of insects on them than did those under the shade of a canopy and that the former maintained the young appearance of their leaves longer. Young leaves usually are more palatable to insects than older ones because they are more nutritious and have not yet developed their full complement of chemical and physical defenses. Thus, the immediate conditions surrounding individual trees might affect whether they are subject to probing attacks only, or to more sustained grazing.

To further complicate an already complex situation, it has been discovered that conspecific eucalypts, even in close proximity, do not always flush leaves synchronously (Morrow 1977b, 1983, Heatwole et al. 1997) and that some folivores aggregate and do not move to other trees until they have nearly defoliated the one on which they first settled (Carne et al. 1974). Accordingly, individual trees may differ markedly in the numbers and kinds of insects they attract at any one time, and adjacent trees may show quite different temporal changes in insect abundances (Heatwole et al. 1997). One tree may flush during the peak of abundance of a particular grazing insect and be extensively damaged while an adjacent conspecific one without new foliage at that time may suffer little damage. This could impose idiosynchronies in the induction of chemical defenses or nutrient content of leaves in the two trees and might lead to quite different propensities for subsequent attack. Clearly, the susceptibility of a tree to insects is an individual matter that may determine whether sustained, heavy grazing occurs, or merely minor probes. Some trees have high levels of herbivory, others low ones. Morrow (1977b, 1983) suggested that when the phenology of plants is tied to unpredictable environments herbivore emergences may not coincide with leafing, and plants might escape herbivores more often than in more predictable environments.

Longevity of leaves may be important for folivory. For example, Hadwen et al. (1998) suggested that the high productivity of tropical forests is translated into high rates of leaf turnover, ensuring that few leaves have lifespans long enough to accumulate high levels of grazing damage.

The leaves of eucalypt trees remain on the branch for considerable time, in some cases more than four years (Lowman & Heatwole 1992), not merely part of one year as in North American seasonally deciduous trees, and accordingly have been subject to insect attack for longer periods of time. At any one time there are several cohorts of leaves on an individual eucalypt. Some cohorts may have flushed when there was an abundance of insectan grazers and others during times of relative scarcity of insects, leading to differential grazing on different parts of the same branch. Indeed, in the present study, limbs were observed with heavy grazing on the newest leaves, but little damage to any of the older cohorts. On the other hand, other trees showed little damage to relatively new foliage or to the oldest leaves, but extensive damage to leaves of intermediate position on the limb. This probably reflects temporal differences in abundance of grazing insects, the oldest leaves having flushed prior to the emergence of insects that heavily damaged leaves that flushed later; the peak of insect abundance then passed before the flushing of the newest leaves. Perhaps studying differences in extent of damage sequentially along branches might provide a chronological account of the grazing history of particular trees. Theoretically, sampling the oldest leaves (as in the present study) should give the highest estimates of herbivory because such leaves would have sustained nearly all of the grazing that would occur in their lifetime; however, this would be true only if all cohorts were grazed with equal intensity. Given the dynamic interaction of leaves and insects described above, this is seldom likely to occur, and the oldest leaves would give the highest estimates of herbivory only if they were the most heavily grazed cohort. To truly assess the impact of grazing insects in reducing the total photosynthetic machinery of a tree would mean that all cohorts of leaves would need to be sampled appropriately and in relation to the proportion of the total photosynthetic tissue they represent. This problem is not so great for trees that undergo abscission each autumn, because cohorts of leaves with different grazing histories do not occur simultaneously. Thus, Australian eucalypts and North American, seasonally deciduous trees have very different leaf dynamics and therefore comparisons between them of the extent of leaf damage need to address those differences. Even among eucalypts in different situations, and with different grazing histories, comparisons of herbivory lack ecological relevance if account is not made of differences in leaf dynamics and of the temporally changing interactions with insects.

Clearly, following the progressive damage to cohorts of leaves over time, and for a number of trees (Landsberg 1988, Lowman & Heatwole 1992, Fensham 1994a, see review by Lowman 1997) provides a better assessment of herbivory than do discrete samples, but even the former may not be directly comparable with most north-temperate situations.

Baseline Folivory

Folivory by insects in the present study averaged 7.6% (TABLE 3), a result practically identical to the mean value (7.7%) obtained by Morrow and Fox (1989) from 65 herbarium specimens of various eucalypt species collected by early botanists in Australia before widespread European influence. FIGURE 7 summarizes data on folivory in *Eucalyptus* from the literature. The peak category is between 7% and 8%. Thus, despite rather great variability among individual samples, the present study, that of Morrow and Fox (1989), and the collective body of literature reach consensus in setting a baseline of about 7.5% for insect folivory on *Eucalyptus* leaves in Australia.

There are two caveats for the use of this baseline: (1) it refers only to discrete sampling (the method used by the majority of studies to date) and (2) it applies only to healthy trees. Long-term sampling is more accurate and gives higher estimates (Lowman 1995b).

Data from long-term monitoring are fewer than for discrete sampling and a detailed analysis is not possible; however, the mean of all long-term values for eucalypts from the literature (including individual values encompassed by the ranges of means in TABLE 4) is 21.8% (range of 17 sample means = 1.2–60.5%).

Some of our individual trees had high values (up to 26%; see APPENDIX) for healthy eucalypts, but still well below levels of grazing on Australian trees suffering dieback (up to 300%, or three complete defoliations in one year; Lowman & Heatwole 1992).

Comparison of Folivory between Australia and Other Continents

There has been much debate as to whether Australia and other continents differ in the extent of grazing by insects in canopies (see review by Ohmart 1984). One contention is that chronic levels in Australia are higher than elsewhere (Morrow 1977b, 1983, Springett 1978, Fox & Morrow 1983, 1986), and the value oft-quoted is that herbivory in Australia usually lies in the range of 15–20% or 15–50% whereas in other parts of the world (mainly Europe and North America) the values mostly are in the range of 3–10% (Fox & Morrow 1983, Morrow & Fox 1986).

Fox and Macauley (1977) found that the high levels of tannins and phenols in eucalypt leaves did not inhibit feeding or digestion by chrysomelid beetle larvae (*Pauropsis atomaria*) and suggested that such resistance to defensive chemicals among Australian insects might explain high consumption rates of eucalypt foliage. The generality of such immunity to adverse effects of leaf defenses among Australian insects remains to be tested. Fox and Morrow (1989) compared herbarium collections that antedated widespread human disturbance in North America and Australia and found higher levels of herbivory in the latter. They suggested that chronically high folivory has been a long-term phenomenon, not related to human disturbance, and that Australian eucalypts are predisposed to higher herbivory by (1) a high diversity of *Eucalyptus* species coexisting at one site, (2) leaf-flushing occurring over an extended period of

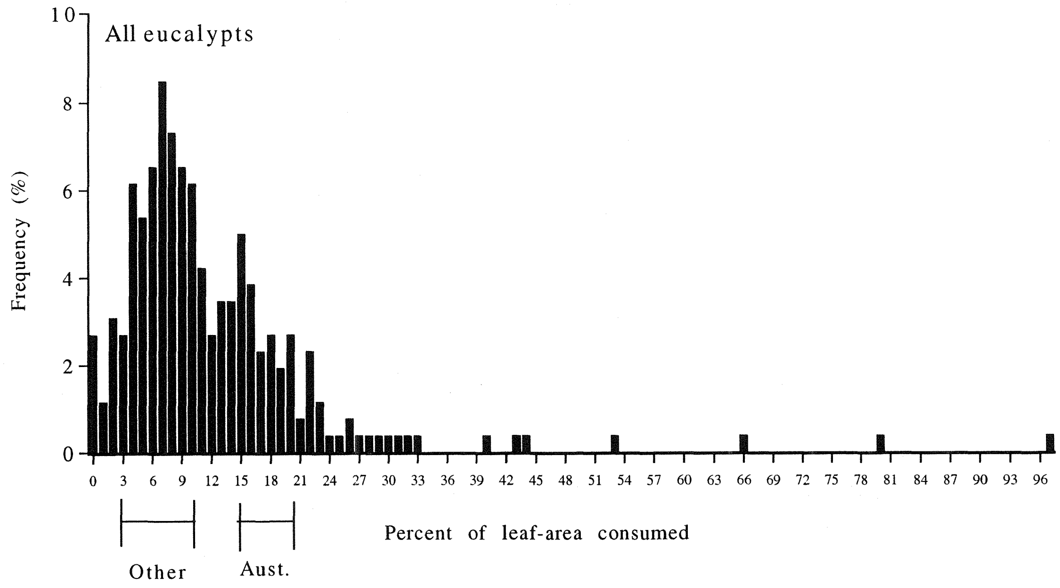

FIGURE 7. Frequency of different levels of folivory (percent of leaf-area consumed) in Australian eucalypts, based on data from the literature (including individual values encompassed by the ranges of means in TABLE 4) and from the present study. $N = 212$. Excluded are data from unhealthy (dieback) trees and values in the literature expressed only as ranges, or in units that could not be converted to the present ones. "Aust." encompasses the range of values previously cited as representing the usual levels of folivory on Australian eucalypts (see text). "Other" indicates the range of values previously reported in the literature as typical of localities elsewhere than Australia (see text).

the year, and (3) a low concentration of nitrogen in eucalypt leaves, thereby making it necessary for insects to eat greater amounts in order to fulfill their nutritional requirements.

The opposing view is that there are no intercontinental differences in folivory (Ohmart et al. 1983a, 1983b; Ohmart 1984, Ohmart & Edwards 1991). Hadwen et al. (1998) noted that higher levels of folivory had been reported from neotropical forests than those they found in Australian tropical forests. Lowman (1997) compared a variety of forests and found that discrete sampling gave estimates of 6.9–7.9% folivory for forests from a range of Australian environmental conditions (tropical, subtropical, montane, dry areas) and that these did not differ greatly from values from African (8.5%) and Central American (7.0–7.9%) forests. Indeed, Peruvian forests had higher folivory (13.7%) than Australian forests. Long-term sampling gave higher estimates overall, but Australian forests sustained lower (15–26%, excluding trees suffering dieback), rather than higher, folivory than did Panamanian forest (30%). Lowman (1985b) concluded that it was impossible, with the information then at hand, to decide whether Australian rain forests are different in herbivory from other forests and her later review (1997) suggested that this is still the case. Majer et al. (1997) also considered the evidence for differences between North American trees and Australian eucalypts in folivory by insects as "far from compelling."

Although our data do not resolve this debate entirely, it is clear that there is broad overlap in levels of herbivory between Australia and other continents and that if intercontinental differences are indeed real, they are neither so consistent nor so great as sometimes stated. For most of the species for which we had multiple samples (see APPENDIX), there were some localities with values of damage within or even lower than the "North American" range of 3–10% and others that were higher; however, only a few of our samples reached the purported "Australian" range of greater than 15%.

A review of the literature revealed a similar pattern. The collective values for all available data on eucalypts peak nearly centrally within the "non-Australian" range of 3–10% (FIGURE 7). Thus, the majority of values obtained on Australian eucalypts in fact conform to expectations based on overseas studies. However,

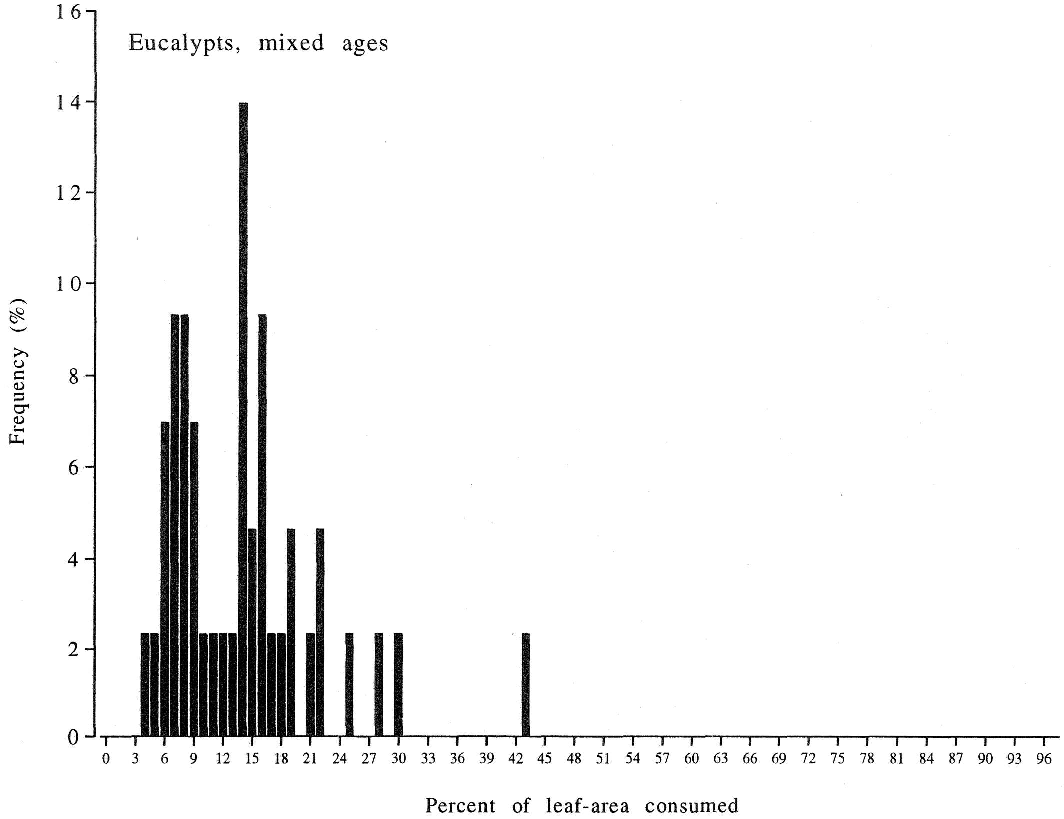

FIGURE 8. Frequency of different levels of folivory (percent of leaf-area consumed) of the subset of those Australian eucalypts from FIGURE 7 that involved mixtures of trees of different ages, but for which data on saplings, regrowth and mature trees could not be separated. $N = 43$.

there is, in addition, a smaller secondary peak centering at 15%, just at the beginning of the purported "Australian" range, beyond which there is a gradual tapering off to a low number of exceptionally high levels (FIGURE 7).

Greaves (1966), among others, demonstrated that young *Eucalyptus* may exhibit markedly higher folivory than conspecific mature trees (see TABLE 4), and it has been suggested (Ohmart et al. 1983, Ohmart 1984) that the reason herbivory in Australia appeared higher than elsewhere was because many of the Australian studies had been restricted to young eucalypts or to regrowth, or dealt with outbreak situations, a conclusion later contested by Fox and Morrow (1986).

The present literature review bears on this controversy. Data were plotted separately for (1) studies involving mixed ages of eucalypts (including regrowth, small trees and mature trees) in which no distinction was made among levels of folivory for the various age categories, and (2) studies of folivory specifically on seedlings, saplings or regrowth. Folivory on eucalypts of mixed ages had two peaks in frequency, one at 7–8% and another at 14–16%; in this case the second peak was the higher one (FIGURE 8). The sample from young trees and regrowth was small, and consequently less reliable; however, it had scattered high values throughout both the "non-Australian" and "Australian" ranges (FIGURE 9). The mixed and young categories collectively accounted for all but two of the seven samples in which mean folivory exceeded 35%. Thus, excluding young trees and regrowth from the samples eliminates most of the higher values and reduces representation in the purported "Australian" range of folivory; the remaining values conform more closely to those reported from other continents. However, the second peak is not entirely eliminated by excluding young trees and regrowth (FIGURE 10) and it may be

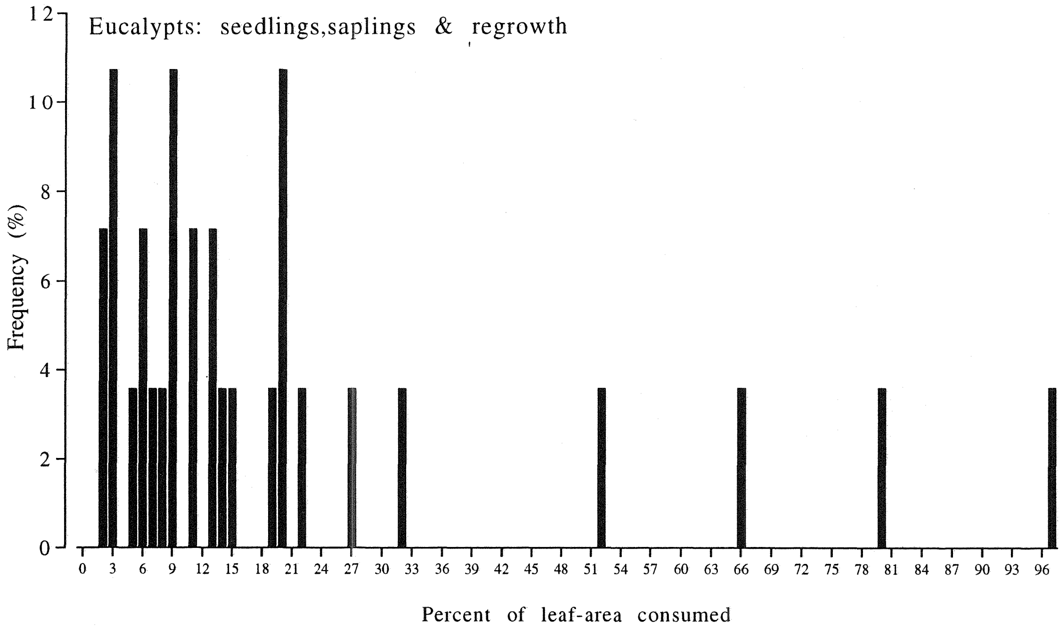

FIGURE 9. Frequency of different levels of folivory (percent of leaf-area consumed) in Australian eucalypt seedlings, saplings or regrowth, based on data from the literature (including individual values encompassed by the ranges of means in TABLE 4). $N = 30$.

that chronic folivory of mature Australian eucalypts extends to a limited degree above the usual levels occurring elsewhere. However, other explanations have not been ruled out, such as the inadvertent inclusion of unhealthy trees with unusually high levels of folivory.

Our results add a further perspective to the debate over intercontinental differences by noting some of the properties of folivory that affect the reliability of data used in making assessments of leaf damage. Of special interest is the distribution of damage among leaves within a sample and among samples (see above). Variability in damage among individual leaves often is great (Lowman 1985a) and probably an inherent attribute of natural systems (Fox & Morrow 1986). Hawden et al. (1998) noted that high variability was ubiquitous in studies of folivory and considered it to be a real property of canopy grazing rather than merely an artifact of insufficient replication.

Compounding the uncertainty about intercontinental differences is the large number of factors, some ecological, others methodological, that affect estimates of levels of folivory (see Introduction). Differences between localities (within or between continents) in one or more of these factors might result in different grazing levels by folivores. To be valid, intercontinental contrasts should compare equivalent climatic zones, patterns of leaf dynamics, extent of seasonality and other variables on the two continents. For example, comparison of seasonally deciduous forest on one continent with evergreen forest on another may reflect patterns of flushing and abscission, rather than geographic differences in herbivory. Landsberg and Cork (1997) pointed out that comparison of levels of damage on leaves from different trees and different environments are only valid if the ages of the leaves are known and taken into consideration. For example, many evergreen species in North America are annual evergreens (average individual leaf-life being one year), whereas most species of eucalypts retain individual leaves for much longer periods (to > four years; Lowman & Heatwole 1992) and some other Australian trees may have life-spans of leaves up to 25 years (Lowman 1995a). Such leaves have a longer time to accumulate damage and may show higher proportions of loss of leaf area, even when the rate of herbivory is the same (or even lower) than in North American trees. Species that flush throughout the year (like some eucalypts) would have leaves of different ages on the tree at any one time, each age group with its own level of accumulated damage (see above).

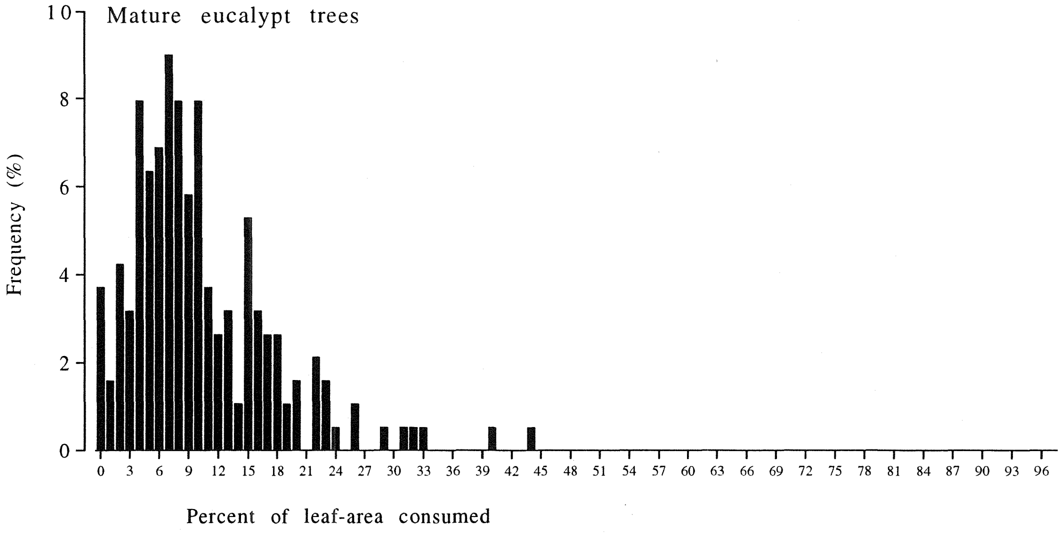

FIGURE 10. Frequency of different levels of folivory (percent of leaf-area consumed) in mature Australian eucalypts, based on data from the literature (including individual values encompassed by the ranges of means in TABLE 4). Excluded are data from unhealthy (dieback) trees and values in the literature expressed only as ranges, or in units that could not be converted to the present ones. $N = 189$.

Leaf damage on such trees would not be directly comparable with values from trees that have nearly simultaneous flushing, resulting in leaves of nearly uniform age. Finally, the extent of leaf damage may vary by 5-fold to 30-fold between different strata or from tree to tree within a given healthy stand of Australian trees (Lowman 1995a) so that broad comparisons with other continents seem tenuous at best, and may be an artifact of differing sampling designs (Lowman 1991, 1997) or of inadvertent inclusion of unhealthy trees with unusually high folivory.

Eucalyptus Versus Other Australian Trees

Fox's and Morrow's (1989) contention that eucalypts have special attributes that predispose them to high chronic levels of folivory (see above section) raises the suggestion that the purported differences in folivory between Australian trees and those of other continents, may not be so much a matter of continental comparisons, but rather one of differences between eucalypts and non-eucalypts. If this is so, then within Australia one would expect eucalypts to have higher chronic folivory than other taxa of trees.

The collective literature (TABLE 4) leaves this as a possibility. The peak in frequency of folivory of mature non-eucalypts is 1–3%, i.e., several percent lower than for eucalypts (compare FIGURES 7, 11). The saplings of non-eucalypt saplings peaked at higher levels of folivory (9–12%) than did the mature trees, and that peak was within the range for young eucalypts (compare FIGURES 9, 11). Thus, there is no present indication of any difference in folivory of young trees between eucalypts and non-eucalypts (samples of both taxa are small), but a suggestion that in mature trees eucalypts may suffer higher herbivory than non-eucalypts. A firm conclusion is premature, however, as many of the low values for herbivory of mature trees came from mangroves; thus, lower herbivory in non-eucalypts may be an artifact of the properties of the mangrove habitat rather than of non-eucalypt Australian trees generally. Against this hypothesis is the finding that mean leaf-area consumed by insects of 23 species of New Guinean mangroves was 6.8% (range 0.24–14.2%) (calculated from Johnstone 1981); massive defoliations of mangroves are known (Whitten & Damanik 1986).

CONCLUSION

Variability in folivory is high in Australian eucalypts, but various sources converge to suggest a baseline of about 7.5% for discrete sampling. Values overlap broadly with those from other continents. It would seem fruitful now to disengage from debate about overly generalized intercontinental differences and move on to

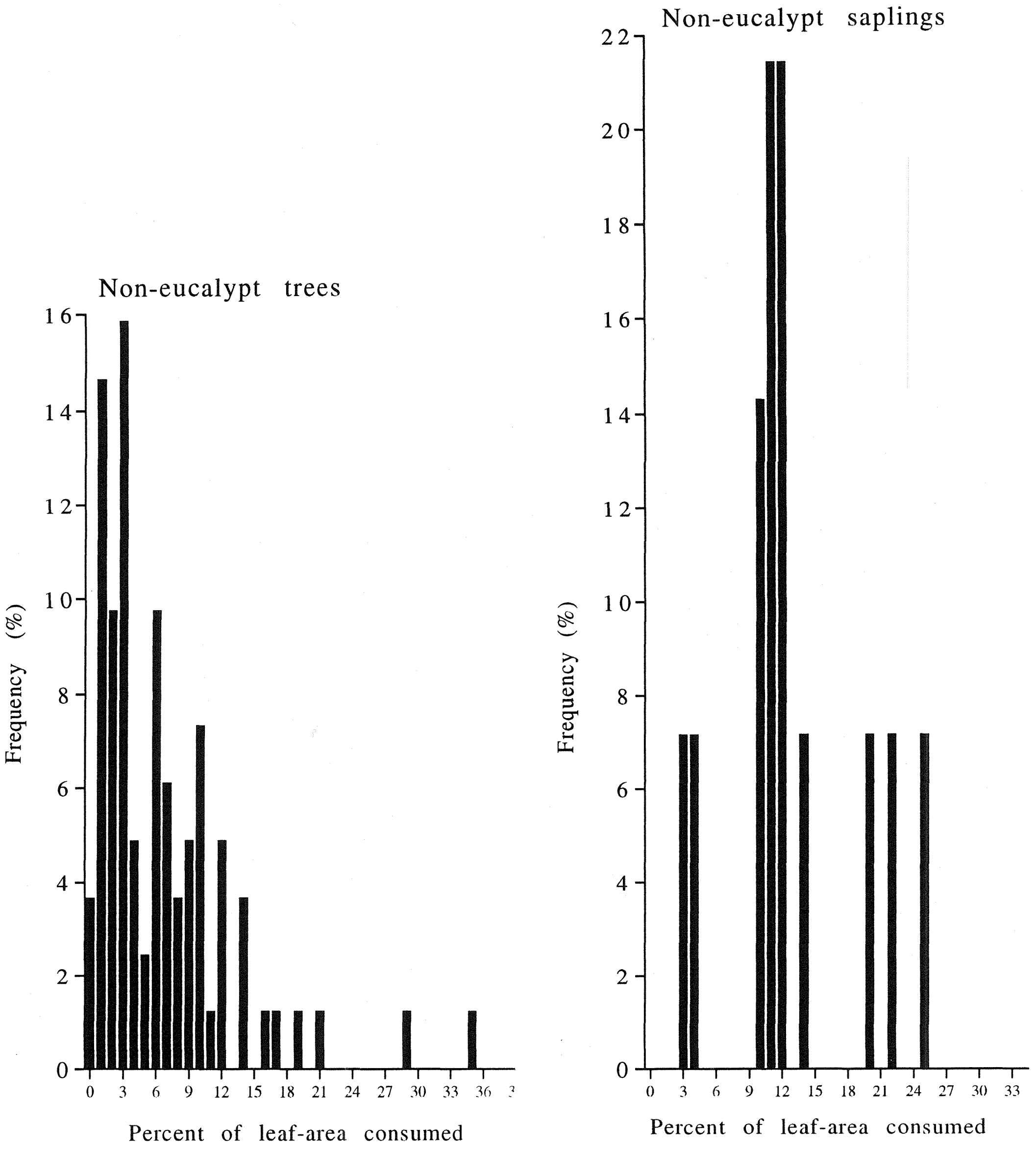

FIGURE 11. Frequency of different levels of folivory (percent of leaf-area consumed) in Australian trees (left; $N = 88$) and saplings (right; $N = 14$) other than eucalypts, based on data from the literature (including individual values encompassed by the ranges of means in TABLE 4).

more direct ecological comparisons. The study by Morrow and Fox (1989) of western North American *Quercus* and Australian *Eucalyptus,* both of which are broadleaved evergreens from similar climates, is a move in that direction. Also, it is likely that more will be gained from comparative process-studies than from further measurements of mean levels of damage to standing crops of leaves. Perhaps the best way to establish valid comparisons among habitats, climatic zones, or continents, is through more precise assessment of rates of herbivory on cohorts of leaves under different environmental conditions and with different patterns of leaf dynamics and flushing phenology. Once the dynamics of herbivory are understood more fully, overall continental differences, if such exist, may become comprehensible.

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APPENDIX. Folivory on Australian Eucalypt leaves.

Species Locality Date	Habitat	*N*	% of leaf-area consumed				% of leaves with damage
			(Mean ± SE)	Range	Median	Mode	
Angophora floribunda							
Sawn rocks, Narrabri, NSW 3 July 1998	Forest	30	7.46 ± 2.303	0–41.0	0	0	40.0
Sawn Rocks, Narrabri, NSW 3 July 1998	Forest	30	16.16 ± 2.955	0–51.3	11.6	0	83.3
Tenterfield, NSW 10 Aug. 1997	Roadside	30	18.47 ± 2.811	0–47.0	16.6	0	86.7
Tenterfield, NSW* 10 Aug. 1997	Roadside	30	7.07 ± 1.667	0–35.2	4.0	0	86.7
Coonabarabran, NSW 14 Aug. 1998	Roadside	30	2.89 ± 1.211	0–29.9	0	0	26.7
Corymbia citriodora							
Between Calliope and Biloela, Qld. 23 July 1997	Forest	28	4.36 ± 1.659	0–46.3	2.7	0	67.9
Eucalyptus albens							
Baan Baa, NSW, 3 July 1998	Roadside	30	5.08 ± 1.499	0–25.2	0.02	0	53.3
Tamworth, NSW 3 July 1998	Roadside	29	26.17 ± 3.600	0–69.7	25.5	29	96.6
Eucalyptus camaldulensis							
Between Gunnedah and Baan Baa, NSW 3 July 1998	Roadside	30	6.09 ± 1.881	0–44.2	1.3	0	73.3
Adelaide, SA 6 Aug. 1998	City Park	30	2.83 ± 1.389	0–33.3	0.1	0	53.3
Mt. Darling Creek, NSW 4 Aug. 1998	Dry stream bed	30	6.47 ± 1.902	0–43.2	1.2	0	66.7
20 km w of Urana, NSW 9 Aug. 1998	Riverbank	30	4.20 ± 1.145	0–20.4	0.1	0	56.7
20 km w of Urana, NSW 9 Aug. 1998	Riverbank	30	11.60 ± 2.131	0–47.6	10.4	0	86.7
Wilcannia, NSW 4 Aug. 1998	Riverbank	30	13.51 ± 2.766	0–46.8	8.4	0	83.3
Eucalyptus cladocalyx							
Riverton, SA 5 Aug. 1998	Roadside	30	4.86 ± 1.254	0–29.8	1.4	0	80.0
Eucalyptus clarksoniana							
Near Calliope, Qld. 23 July 1997	Forest	30	8.00 ± 1.606	0–38.6	4.6	4	93.3
Eucalyptus coolibah							
Rolleston, Qld. 24 July 1997	Woodland	30	7.76 ± 2.232	0–49.3	3.5	0	73.3
Rolleston, Qld.* 24 July 1998	Woodland	25	4.39 ± 1.316	0–30.3	2.1	1	92.0
Eucalyptus dealbata							
"Glacial" Area, Narrabri, NSW 3 July 1998	Woodland	30	5.31 ± 2.228	0–60.7	0	0	46.7

APPENDIX. Continued.

Species Locality Date	Habitat	*N*	% of leaf-area consumed				% of leaves with damage
			(Mean ± SE)	Range	Median	Mode	
Eucalyptus dumosa							
19 km w of Underbool, Vic.							
9 Aug. 1998	Mallee	30	11.85 ± 2.766	0–66.9	6.5	1	96.7
Eucalyptus globosa							
Cobar, NSW							
4 Aug. 1998	Cultivated	30	0.01 ± 0.004	0–0.1	0	0	6.7
Eucalyptus globulus							
Narrabri, NSW							
June 1998	Cultivated	30	0.02 ± 0.011	0–0.3	0	0	10.0
Eucalyptus intermedia							
Miriamville, Qld.							
9 Aug. 1997	Woodland	30	7.32 ± 2.313	0–57.5	1.6	0	60.0
Between Cobar and Wilcannia, NSW							
4 Aug. 1998	Roadside	29	12.69 ± 3.345	0–79.7	7.1	0	89.7
Eucalyptus leucoxylon							
Near Adelaide, SA							
9 Aug. 1998	Woodland	30	7.01 ± 1.431	0–23.0	4.1	0	73.3
Eucalyptus melliodora							
Between Gunnedah and Boggabri, NSW							
3 July 1998	Roadside	30	4.56 ± 1.490	0–30.8	0	0	40.0
Tomingley, NSW							
13 Aug. 1998	Roadside	30	10.64 ± 2.510	0–48.0	1.3	0	76.7
Wagga Wagga, NSW							
9 Aug. 1998	Roadside	19	13.56 ± 2.872	0–36.9	9.5	0	89.5
Eucalyptus microcarpa							
Cowra, NSW							
13 Aug. 1998	Roadside	30	15.52 ± 3.252	0–58.9	7.5	0	90.0
Eucalyptus nova-anglia							
20 km s of Glen Innes, NSW							
10 Aug. 1997	Isolated tree	30	16.38 ± 2.356	0–47.8	13.4	4	96.3
Eucalyptus obliqua							
Near Adelaide, SA							
8 Aug. 1998	Woodland	30	9.71 ± 2.542	0–67.7	5.5	0	90.0
Eucalyptus odorata							
Moorelands, SA							
9 Aug. 1998	Roadside	30	6.18 ± 1.874	0–40.6	1.1	0	66.7
Sherlock, SA							
9 Aug. 1998	Mallee	29	6.98 ± 1.916	0–34.8	0.2	0	51.7
Eucalyptus orgadophila							
Springsure, Qld.							
24 July 1997	Roadside	28	8.51 ± 3.183	0–66.3	3.2	0	60.7
Eucalyptus populnea							
Calliope, Qld.							
23 July 1997	Roadside	30	10.74 ± 1.403	0.7–26.0	9.7	6	100.0
Emerald, Qld.							
24 July 1997	Roadside	28	12.45 ± 2.789	0–52.5	7.3	0	89.3

APPENDIX. Continued.

Species Locality Date	Habitat	*N*	% of leaf-area consumed (Mean ± SE)	Range	Median	Mode	% of leaves with damage
Emerald Qld.*							
24 July 1997	Roadside	30	7.07 ± 1.667	0–35.2	4.6	0	80.0
Warren, NSW							
4 Aug. 1998	Isolated tree	30	7.44 ± 2.174	0–43.7	0.6	0	63.3
Warren, NSW							
4 Aug. 1998	Isolated tree	30	1.89 ± 0.814	0–15.0	0	0	26.7
Eucalyptus radiata							
Applethorpe, Qld.							
10 Aug. 1997	Woodland	30	4.56 ± 1.410	0–31.0	1.0	0	73.3
Eucalyptus sideroxylon							
Narrabri, NSW							
July 1998	Isolated tree	22	2.99 ± 1.381	0–19.1	0	0	31.8
Eucalyptus socialis							
110 km e of Wilcannia, NSW							
4 Aug. 1998	Roadside	29	10.15 ± 1.795	0–33.3	11.1	0	75.9
110 km e of Wilcannia, NSW							
4 Aug. 1998	Roadside	30	4.87 ± 1.662	0–32.7	0	0	66.7
Eucalyptus tessellaris							
Narrabri, NSW							
June 1998	Isolated tree	29	0.41 ± 0.399	0–8.2	0	0	13.8
Eucalyptus torrelliana							
Narrabri, NSW							
June 1998	Cultivated	30	0.13 ± 0.082	0–2.3	0	0	33.3
Eucalyptus viminalis							
Mt. Kaputar, NSW							
2 July 1998	Forest	30	2.65 ± 1.132	0–29.3	0	0	43.3
Narrabri, NSW							
June 1998	Isolated tree	30	1.26 ± 0.580	0–12.2	0	0	20.0
Eucalyptus sp.							
Girard State Forest, NSW							
16 Aug. 1998	Forest	30	8.82 ± 1.73	0–36.9	5.5	0	86.7
Girard State Forest, NSW							
26 Aug. 1998	Isolated tree	30	15.93 ± 3.26	0–64.6	9.6	0	70.0
Muswellbrook, NSW							
26 Aug. 1998	Urban tree	30	23.30 ± 3.53	0–60.1	23.7	0	76.7
Lophostemon suaveolens							
Gin Gin, Qld.							
9 Aug. 1998	Roadside	30	5.56 ± 1.391	0–23.5	1.5	0	66.7

* Recently fallen leaves.