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SPATIAL AND TEMPORAL VARIABILITY IN DEFOLIATION OF AUSTRALIAN EUCALYPTS[1]

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Abstract. Insect defoliation is commonly associated with and assumed to be a cause of mortality in Australian eucalypts, particularly in rural regions where trees suffer from the eucalypt dieback syndrome. To test this, leaf growth and defoliation were measured in the canopies of *Eucalyptus* trees from June 1982 to June 1986, and related to tree health and eucalypt dieback. Over 5000 leaves were monitored, including replicates of branches, canopy heights, individual trees, species, and sites. Three types of sites were selected, representing the most common conditions in the eastern Australian tablelands: woodlands (comprised of healthy trees but with slight signs of dieback), healthy trees in pastures, and dying trees in pastures. Within each site the commonest native tree species were selected for study; species were not always the same between adjacent sites because of interspecific differences in distribution patterns.

Some eucalypt species suffered much greater defoliation than others, and this was related to their observed susceptibility to dieback. *Eucalyptus nova-anglica* (peppermint) and *E. stellulata* lost up to 300% and 274% of leaf surface area, respectively, in one year, and these trees suffered severe dieback. In contrast, *E. caliginosa* and *E. dalrympleana* annually lost as little as 20% and 8%, respectively, and showed little evidence of dieback. Other aspects of leaf growth were quantified for each canopy, including numbers of leaves flushing, amounts of leaf area affected by galls and miners, and leaf longevities. More than half of the leaves monitored senesced from causes other than insect damage. Defoliating insects appeared to have a greater impact on eucalypts in Australia than they do on forest and pasture trees of other continents.

Key words: canopy; defoliation; dieback; Eucalyptus; *herbivory; insects; leaf growth; leaves; tree decline.*

INTRODUCTION

The New England Tableland encompasses 3.3 × 10^6 ha in northeastern New South Wales, Australia, and lies at ≈800–1500 m elevation (Walker 1977, Barker 1980). This region was first settled in the mid-1800s and the land was gradually cleared to establish livestock grazing. In subsequent years the remaining native trees, mainly eucalypts, have undergone periodic mortality, a phenomenon generally referred to as "dieback" because of the characteristic dying of the branches progressively from the tips towards the trunk (Heatwole and Lowman 1986). Beginning in the late 1970s, eucalypt dieback became particularly severe in this region of Australia, prompting scientific attention to address its cause.

A complex of factors has been suggested, including livestock grazing, invasion of non-native grasses, fluctuations in bird populations, frost, salinity, and agricultural practices. Its severity is evident where land use has been most intense (including grazing, aerial fertilizer applications, and establishment of non-native grasses). Insects are believed to be one of the major contributors to the dieback syndrome (Heatwole and Lowman 1986, 1987, Lowman and Heatwole 1987, Landsberg 1988, 1990*a*). For example, insect defoliators such as Christmas beetles (*Anoplognathus* spp.; Scarabaeidae) and others have long been observed to defoliate eucalypt trees periodically (Norton 1886) and were held responsible for the periodic dieback that eucalypts undergo.

The present study was designed to measure insect-related damage to eucalypt trees. We put forward the hypothesis that the extent of defoliation by insects is correlated with a tree's health and subsequent susceptibility to dieback. To test this, damage by insects and senescence of leaves from other causes were measured over several years in individuals of the common species of eucalpyts in both woodlands and pastures on the New England tablelands.

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METHODS

Site and species selection

Preliminary surveys were conducted throughout the New England Tableland to ascertain the typical types of landscapes in terms of species, health, and growth form of trees. Three types were selected for study, with two sites replicated in each type, for a total of six sites. They were:

(a) Healthy trees in pastures, either growing in small clumps or as isolated individuals; they are remnants of previous clearing (Ruby Hills; University of New England [subsequently UNE] Hill);

(b) Dying trees in pastures, growing in similar situations to those above, but showing obvious signs of dieback, such as epicormic shoots, reduced canopy size, dead branches, and degeneration of form (Wood Park; Newholme Farm);

(c) Woodland trees, surrounded by neighbors in a shaded, natural ecosystem with shrubs and a variety of understory plants. This category was the most difficult to find, due to widespread clearing on the tableland. Some trees showed slight signs of dieback (Walcha Woods; Eastwood State Forest).

At each site the most common tree species were selected for long-term monitoring of canopy defoliation. In many pastures very few individuals of some species remained. Due to the local distribution of many eucalypts it was not possible to match all species in every habitat. Consequently, for analyses involving species comparisons, the number of sites was <6. For example, *Eucalyptus blakelyi* and *E. viminalis* were the only species occurring in all three landscape types; they co-occurred at one site in each of two types and at two sites in the remaining type, for a total of four sites.

Regional factors were minimized as much as possible. The study areas were all in the southeastern corner of the New England Tableland on gently rolling topography, well-drained podzolic soils (except for UNE Hill on basaltic soil) in the same climatic zone, and at similar elevations (1040 to 1140 m) (Lea et al. 1977: topographic maps). The only two appropriate woodland sites available were 50 km apart. Each of these was grouped with pasture sites within 5 km. The pasture trees were not outliers in marginal habitats; they were trees left as remnants of former woodlands.

Measurement of insect damage to leaves

For long-term measurement of defoliation, there was replication of leaves with respect to branch, height in the canopy, individual tree, species, site, type of site, and time (months and years). Trees of average size, representing the most common species, were selected at each site. For each tree at least three branches were marked at each of three height intervals: low (0–5 m), medium (>5–8 m), and high (>8 m). Each branch initially contained 6–15 leaves. Leaves on the marked branches were numbered sequentially from the base outwards, and subsequent leaves were numbered as they emerged. Each month the branches were monitored for amount of leaf damage, presence/absence of galls and miners, fruiting and flowering, and other phenological events.

Leaf damage was measured by one of two quantitative methods, (1) tracing areas of leaves onto graph paper and calculating area missing, or (2) using a planimeter (Lambda model 300 or Tamaya Digital 7). Further information on measurement techniques is presented elsewhere (Lowman 1985). Data were accumulated over 4 yr, from June 1982 until June 1986, or for a shorter period if a tree died. Access to canopies was gained by use of a cherry picker and/or technical hardware and climbing ropes (see Lowman 1984*a*). Data were analyzed in a number of fashions. Monthly herbivory data were stored in a mainframe computer, and both monthly and cumulative defoliation per leaf and over the whole canopy were calculated. Analyses of variance were performed on data when possible (but in many cases the design was not balanced between sites due to differences in species composition of the remaining mature trees). Student-Newman-Keuls (SNK) tests were performed to test for homogeneity of variance and $\log(x + 1)$ transformations were applied to the data.

Defoliation level was expressed as percentage of total leaf area missing (LAM). This proved to be the most reliable way of comparing canopies, since absolute leaf sizes may differ considerably among species and individuals. Earlier studies confirmed that proportions of leaf-hole areas remain consistent throughout the life of a leaf (Lowman 1987, Landsberg 1989). Percentages proved useful for three reasons: (1) proportions missing could be easily compared among individuals, sites, and times; (2) proportions missing could be compared between young and old leaves as well as among leaves of different sizes; and (3) proportions are easily transformed into absolute area (in square centimeters) missing, if required. An analysis of herbivory with respect to leaf age and size is in progress (see also Landsberg 1989).

RESULTS

Defoliation levels were compared with respect to species, type of tree (pasture vs. woodland, dieback vs. healthy), site, individuals within species, heights, and time (months, years).

Variability of annual defoliation levels

Eucalypts on the tablelands averaged 35.7% leaf-area losses annually (Table 1). In the eleven species studied, annual average defoliation varied from negligible to severe amounts. For example, *Eucalyptus blakelyi* lost only 7.5% leaf area in woodlands, whereas trees of this species averaged 87.6% defoliation in pastures where trees appeared unhealthy. Conversely, some species had consistently high or low herbivory throughout their distribution. For example, all individuals of *E. nova-anglica* were heavily defoliated, averaging 60.5% in

TABLE 1. Annual herbivory (% loss of leaf area) for *Eucalyptus* trees at three types of sites on the New England Tablelands, New South Wales, Australia.

Species	Pasture trees, with dieback	Pasture trees, healthy	Woodland trees	Species mean
	% of leaf area lost ($\bar{X}$ ± 1 SE)			
Eucalyptus blakelyi	87.6 ± 5.0	16.0	7.5 ± 3.4	49.7
E. bridgesiana	25.1	· · ·	· · ·	25.1
E. caliginosa	· · ·	20.9	24.9 ± 4.4	22.9
E. dalrympleana	· · ·	19.0 ± 6.6	· · ·	19.0
E. melliodora	74.4	· · ·	10.2 ± 0.5	42.3
E. nova-anglica		60.5 ± 9.0	· · ·	60.5
E. stellulata	· · ·	35.9 ± 8.43	· · ·	35.9
E. radiata	· · ·	· · ·	14.3 ± 1.3	14.3
E. viminalis	53.7 ± 5.7	52.6 ± 17.0	19.8 ± 4.4	42.0
E. youmanii	· · ·	· · ·	14.3 ± 3.5	14.3
Angophora floribunda	· · ·	17.0	· · ·	17.0
Grand mean	60.2 ± 13.6	31.7 ± 7.0	15.2 ± 2.6	35.7

pastures where trees were healthy. (All trees died in pastures where trees initially appeared unhealthy.) Average defoliation among species ranged from as low as 14.3% for *E. radiata* and *E. youmanii* to moderate levels between 15 and 25% for *E. dalrympleana, E. bridgesiana,* and *Angophora floribunda* to severe losses of ≥50% for *E. blakelyi* and *E. nova-anglica.*

Differences among sites

Of the three types of sites studied, pastures with dieback suffered greater annual defoliation (60.2%) than either healthy trees in pastures (31.7%) or those in woodlands (15.2%) (Table 1). Two sites of each type were used for comparison within and between sites (Table 2). Unhealthy pasture trees in two regions averaged 59.9% and 98.5% leaf area losses annually, while healthy pasture trees averaged 15.0% and 7.6%; woodland trees averaged the lowest defoliation (10.6% and 9.0%); defoliation corresponded to visual ranking of tree health at each site (Table 2).

In a two-factor ANOVA assessing defoliation of *E. viminalis* and *E. blakelyi* (the most widely co-occurring species pair; see *Methods*) at the four sites they were found together, herbivory was statistically different among sites ($F_{3,58} = 11.2$; $P < .01$), whereas species differences were not significant ($F_{1,58} = 0.41$; NS; no significant interactions). This suggests that site—with unique land-use history, stocking rates, and tree density—was more important than the taxonomic identity of trees. For the above two species, woodland trees and healthy pasture trees have statistically lower defoliation than dieback trees in pastures (13.4% = 17.8% < 60.7%; SNK ranking).

The monthly and cumulative levels of defoliation illustrate different patterns of herbivory among different sites (Fig. 1). Cumulative amounts do not represent total defoliation for trees since branches subsequently grew new leaves after complete defoliation, but they show the amount of leaf area lost to the trees at a site during the study.

TABLE 2. Herbivory of *Eucalyptus* trees at different sites of the New England Tablelands (northeastern New South Wales, Australia).

Site*	Visual ranking†	Percentage leaf area consumed					
		Long-term sampling‡					Discrete sampling‡ ($\bar{X}$ ± SE)
		1982	1983	1984	1985	$\bar{X}$	
Pastures with dying trees							
Wood Park	3	68.2	128.7	NS	NS	98.5	30.6 ± 1.3
Newholme	3	30.3	89.5	NS	NS	59.9	33.9 ± 1.4
Pastures with healthy trees							
UNE Hill	2	21.7	20.0	NS	NS	20.8	15.0 ± 1.2
Ruby Hills	2	NS	49.1	25.8	43.9	39.6	7.6 ± 0.7
Woodlands							
Walcha Woods	1	NS	19.1	11.9	13.0	14.7	10.6 ± 1.2
Eastwood Forest	1	13.0	19.9	19.9	10.2	15.8	9.0 ± 0.6

* For additional site information, see *Methods: Site and species selection.*

† Prior to measurements, the sites were visually ranked for evidence of dieback: 1 = healthy trees, no sign of stress; 2 = foliage beginning to die from the tips of the branches toward the trunk; 3 = many branches dead, but the trunk and base of major branches with new epicormic growth; 4 = most of epicormic foliage dead; 5 = whole tree dead. Sketches of trees in each of these stages are pictured in Heatwole and Lowman (1986).

‡ $N > 500$ leaves for all sites. See *Methods: Measurement of insect damage to leaves* for explanation of discrete and long-term sampling. NS = not sampled that year.

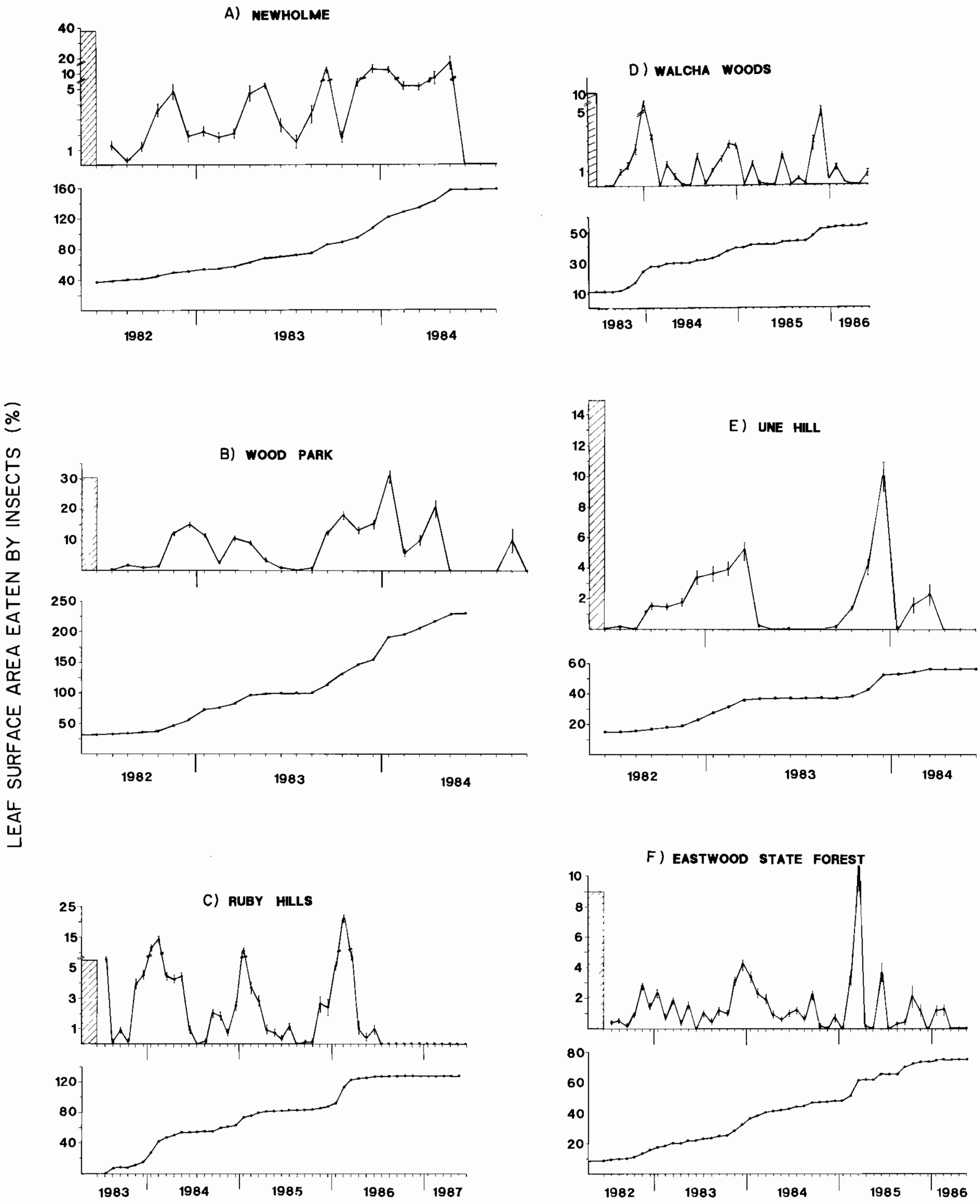

FIG. 1. Annual and cumulative herbivory at Newholme and Wood Park (parts A and B, pastures with trees exhibiting signs of dieback); Ruby Hills and University of New England (UNE) Hill (C and E, pastures with healthy trees); and Walcha Woods and Eastwood State Forest (D and F, woodlands). For annual herbivory, points represent the proportions of leaf surface area eaten by insects during the course of one month ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study. For cumulative herbivory, points indicate the amount of damage incremented throughout the study. In cases where insects defoliated several flushes, cumulative herbivory was >100%.

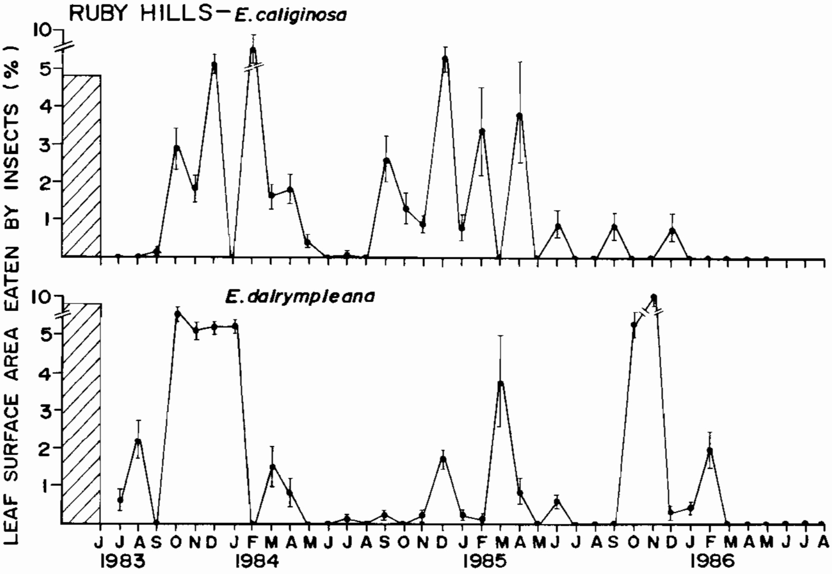

Fig. 2. Herbivory of species in pastures with trees that exhibited relative resistance to herbivory (*Eucalyptus caliginosa* and *E. dalrympleana*). Points represent proportion of leaf surface area eaten by insects during the course of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study. Letters on the horizontal axis refer to months.

In the woodland sites, monthly removal of leaf area ranged from 0 to 10%, but averaged 1–2%, a moderate amount (Fig. 1: C and D). The woodland tree canopies were monitored over a 5-yr period. This was a longer time than for canopies of dying pasture trees for two reasons; the leaves in the shaded portions of woodland trees lived longer (up to 3 yr) than leaves in the sun, and the branches in the upper portions of woodland trees grew vigorously, thereby requiring more time to follow all branches through their entire lifespans (1982–1986). Cumulatively, woodland canopies lost 50–75% leaf surface area, but this was offset by subsequent vigorous growth in new branches.

Healthy pasture-trees ranged from 0 to 23% monthly defoliation, although leaves averaged 2–4% per month (Fig. 1: C and E). This was double the defoliation in woodlands. Monthly fluctuations were more pronounced in trees of pastures than those of woodlands, with peaks of 15–23% occurring during outbreaks of beetles during summer months. Cumulative herbivory reached levels of 50–120% for different trees; the larger amounts were common in peppermints that lost several flushes annually to beetle infestations and subsequently grew new leaves during the same season. Despite such relatively high losses, these healthy pasture-trees underwent vigorous regrowth and showed few signs of dieback at the completion of the study.

The dying pasture-trees had the highest levels of defoliation, averaging monthly losses in leaf area of 5–10% (Fig. 1: A and B). During the study, all trees at Newholme died and all trees at Wood Park either died or showed severe signs of dieback. Consequently, cumulative herbivory was well over 100% at Newholme, and ≥200% at Wood Park (where the last few leaf flushes were eaten entirely by defoliators and the branches simply died, leaving only epicormic shoots remaining on the trees).

All sites showed similar seasonality of herbivory, with peaks in leaf-area losses during summer months (December, January, February). Most defoliation occurred just after leaf flush, before leaves had matured and developed a hard cuticle. The levels of damage varied among sites. They were highest in the dying pasture-trees, and lowest in the woodland trees.

Differences among individual species

Some species appeared relatively resistant to dieback (e.g., *E. caliginosa*), whereas others appeared very susceptible (e.g., *E. nova-anglica*). Both susceptible and resistant species were compared for differences in herbivory, within healthy and dieback sites.

Both susceptible and resistant eucalypt species were growing in the healthy pasture sites, and the monthly herbivory patterns of four species at Ruby Hills (healthy pastures) are illustrated (Figs. 2 and 3). Both *E. caliginosa* and *E. dalrympleana* showed no apparent signs of dieback, and their respective levels of leaf area losses were low (20.9 and 19%; Table 1). Monthly fluctuations in insect attack ranged from 0 to 10%, with negligible amounts during winter and peaks during summer. In almost all cases, leaves senesced after a lifespan of 2–3 yr, without being entirely eaten by insects (cockatoos also removed leaves from *E. dalrympleana* on rare occasions). In contrast, many leaves of both *E. nova-anglica* and *E. stellulata* were eaten entirely (Fig. 3), resulting in monthly herbivory ranging from 0 during

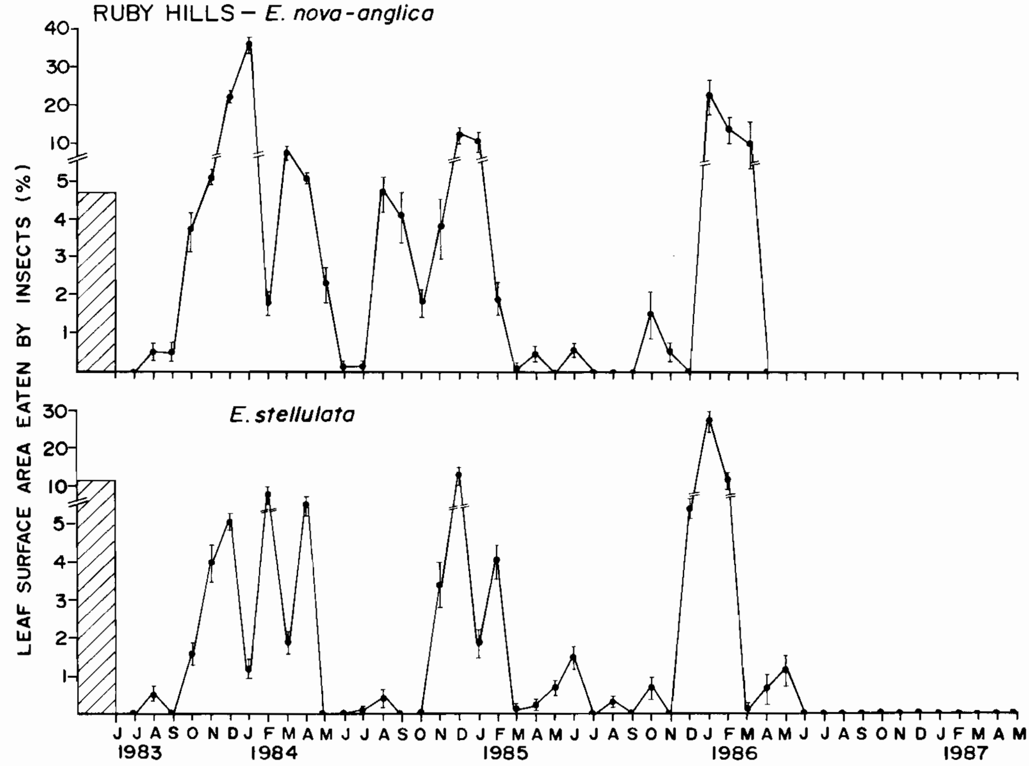

FIG. 3. Herbivory of species in pastures with trees that exhibited susceptibility to herbivory (*Eucalyptus nova-anglica* and *E. stellulata*). Points represent proportion of leaf surface area eaten by insects during the course of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study. Letters on the horizontal axis refer to months.

winter to almost 40% during beetle outbreaks in summer. In many instances herbivory levels showed a peak and trough pattern, whereby new leaves were eaten during one month followed by low herbivory during the next month despite the fact that other, new leaves were flushing. Because of the high mortality of leaves caused by herbivores, the mean longevity of leaves was <1 yr. These trees showed visible signs of dieback (epicormic shoots, dying patches in the crown, dead branches), but they recovered every season. Peppermints (*E. nova-anglica*) recovered despite the loss of several leaf flushes.

Two species, *E. blakelyi* and *E. viminalis,* occurred in all three types of sites (see *Methods*) and were useful for comparison of species among sites (Fig. 4). Once again, the patterns of herbivory were more characteristic of sites than of species; lowest defoliation and longest-lived leaves were at the woodland site, highest defoliation and subsequent reflushing most prominent at the pasture site with dying trees, and intermediate patterns at the pasture site with healthy trees. *E. blakelyi* averaged almost 10% monthly defoliation at the dying pasture site, but only 1% leaf-area losses at the woodland site, and 1–2% losses at the healthy pasture site. In all three sites, both species were more heavily defoliated in summer than in winter, although woodland trees had more (albeit low) herbivory during colder months than did pasture trees. Standard errors were usually greater during winter, because herbivory by sawflies was concentrated on intermittent branches rather than being homogeneous throughout the canopy (Fig. 4).

Herbivory among different canopy heights

Leaves in the upper canopy had shorter lifespans and higher defoliation than did those below (Fig. 5), especially in pastures where beetles tended to feed selectively on higher branches (Fig. 5B). The woodland trees showed greater differences in leaf longevity with height (leaves on shaded lower branches living longer than the more exposed sun leaves) (Fig. 5A). In both pasture and woodlands, however, herbivory fluctuated from month to month, with less defoliation during colder months, and peaks that correlated with insect activities in the warmer ones. When there was high defoliation, it occurred throughout the tree, albeit slightly later in the lower branches that tended to leaf out several days after the upper ones.

Monthly herbivory levels of individual species are illustrated (Fig. 6). Woodland trees had relatively long-lived leaves in the lower canopy as compared to the upper canopy (Fig. 6: A and B), although the low-level

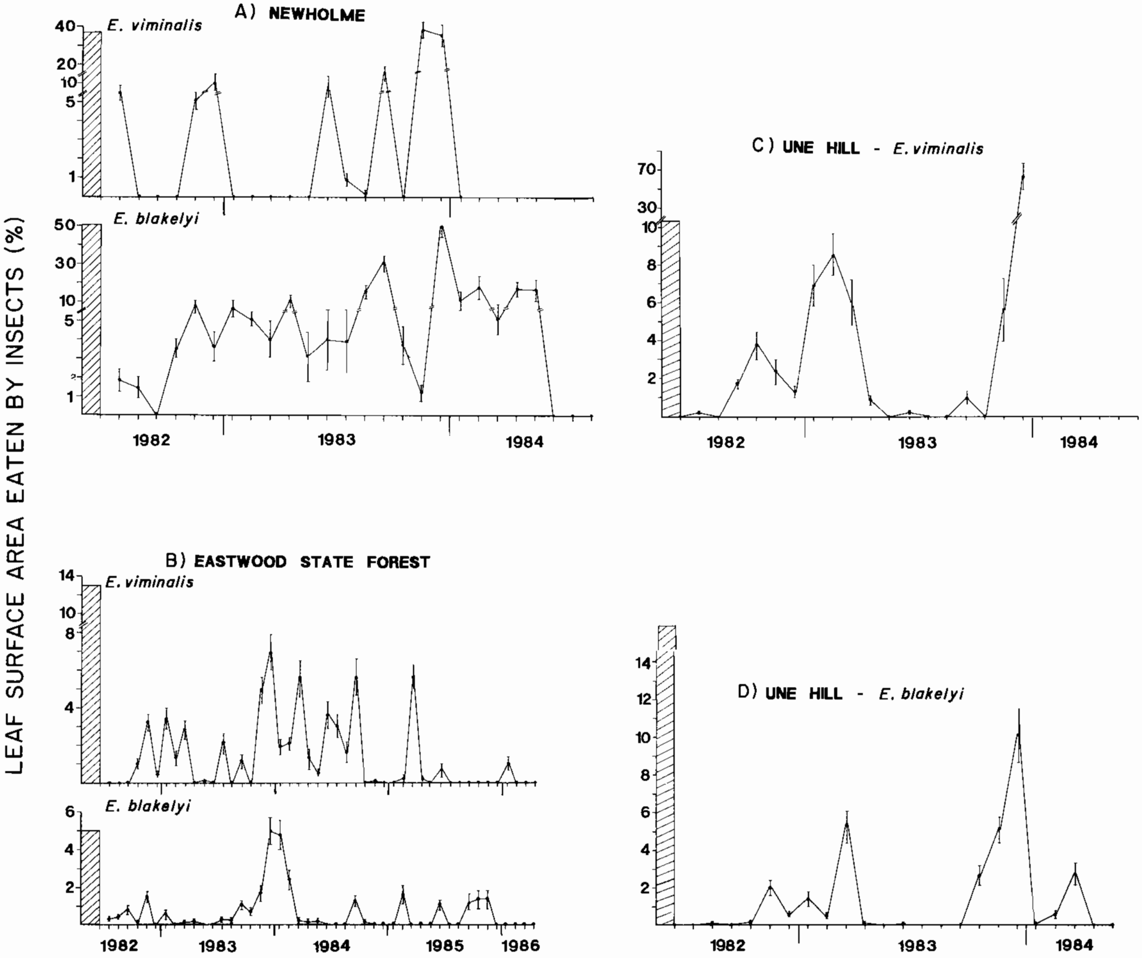

FIG. 4. Herbivory of two species that grew in all three types of sites: *Eucalyptus viminalis* and *E. blakelyi* in pastures with dying trees (Newholme); in woodland (Eastwood forest), and in pastures with healthy trees (UNE Hill). Points represent proportion of leaf surface area eaten by insects throughout the span of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study.

leaves suffered negligible defoliation during their last year. Leaves at all three levels suffered sporadic defoliation throughout most of their lifespan, with peaks in damage occurring during summer months regardless of leaf age. Both *E. viminalis* and *E. caliginosa* had moderately low levels of herbivory throughout their entire canopies in the woodland.

In contrast, *E. viminalis* with dieback in a pasture suffered much higher levels of herbivory throughout all three canopy heights, with no apparent differences among heights (Fig. 6C). The mid-canopy leaves persisted longest. Healthy pasture trees suffered intermediate levels of damage, with the upper canopy sustaining the most defoliation but also re-flushing most actively (Fig. 6 right). *E. nova-anglica* had intermittent peaks of heavy defoliation corresponding to insect outbreaks, whereas the more resistant *E. caliginosa* had lower (but intermittent) herbivory. In the lower canopy of *E. nova-anglica,* herbivores ate the leaves completely, and branches failed to flush again ("low" in Fig. 6E), whereas in all other healthy pasture-trees the leaves senesced without undergoing complete defoliation.

Differences among canopies of adjacent trees of the same species

Levels of insect attack among three individuals of one species growing in close proximity were compared at the healthy pasture site, Ruby Hills (Fig. 7). *E. nova-anglica,* a susceptible species, showed remarkably different patterns of insect attack, despite the fact that all three trees were heavily defoliated (Fig. 7 upper). Trees 1 and 2 lost their final flush to senescence, while tree 3 lost its last leaves as a result of defoliation (note that the graph in Fig. 7A, tree 3, shows a right-hand peak of 70%). The branches of tree 1 died before the 1985 spring (November) flush that occurred in trees 2 and 3, although this flush was followed by extensive defoliation in those two trees. All three trees, however,

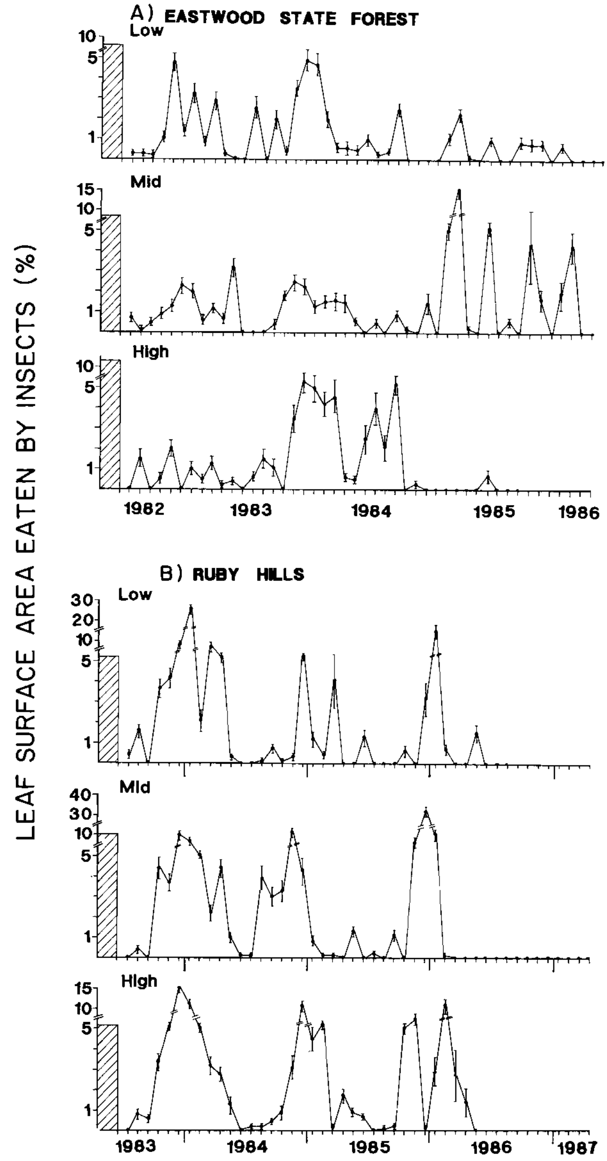

FIG. 5. Herbivory among three canopy heights (Low: 0–5 m, Mid: >5–8 m, High: >8 m) for woodlands (Eastwood Forest) and pastures with healthy trees (Ruby Hills). Note: Pastures with unhealthy trees did not usually have enough canopy left to enable studies spanning three heights. Points represent proportion of leaf surface area eaten by insects throughout the span of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study.

had sharp peaks in insect damage during both spring and summer, whenever new leaves flushed.

In contrast, *E. dalrympleana,* a species less susceptible to defoliation than peppermint, had remarkably different patterns of herbivory (Fig. 7B). Trees 1 and 3 had low peaks of defoliation of new flushes during spring and summer, damage being negligible during colder months. Tree 2, however, had relatively high defoliation during the first summer (November, December 1983) when most leaves were damaged; the crown never fully recovered, leading to eventual death of all marked branches. Trees 1 and 3 underwent seasonal fluctuations in herbivory, but almost all leaves eventually died from senescence during autumn and winter.

Differences among branches within a canopy

Within individual trees, the branch-to-branch variability in defoliation was high. For *E. nova-anglica* (Fig. 8 A, B, and C), four branches at different heights on one individual were defoliated and killed by cockatoos. A combination of natural senescence and insect defoliators (especially Christmas beetles and sawfly larvae) resulted in mortality of other branches. In no canopy were the patterns of defoliation among all branches similar. Rather, although peaks generally occurred during the spring and summer months, different branches suffered different pulses of attack. All peppermint branches suffered 20–30% defoliation during peak months of insect attack during summer, much higher than for other species. In contrast, damage levels on an individual of *E. dalrympleana* averaged 2–3%/mo (with a peak of 17%) (Fig. 8D). Most of the damage, albeit moderate, occurred during spring (September–November), with little or no damage throughout the remaining months. Some branches (e.g., Fig. 8D: branch 2 low, 8 high) suffered no defoliation throughout the study, whereas others (e.g., Fig. 8D: branch 6) were considerably damaged and subsequently flushed more often. The new foliage from these flushes suffered heavy defoliation. Most leaves senesced naturally, rather than being killed directly by insect defoliation.

Variability of herbivory with time

Herbivory fluctuated between months, with most insect damage occurring during spring and summer, and negligible defoliation during autumn and winter. Despite these generalities, exceptions occurred. For example, sawfly larvae occasionally defoliated portions of a canopy during March (e.g., Fig. 8), and January or February often had low herbivory if insects had destroyed the first flush of the season and were awaiting

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FIG. 6. Herbivory of the predominant species at each of the three different types of sites: woodland (*Eucalyptus viminalis* and *E. caliginosa* at Eastwood Forest); pastures with healthy trees (*E. nova-anglica* and *E. caliginosa* at Ruby Hills), and pastures with dying trees (*E. viminalis* at Wood Park). Points represent proportion of leaf surface area eaten by insects during the course of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study.

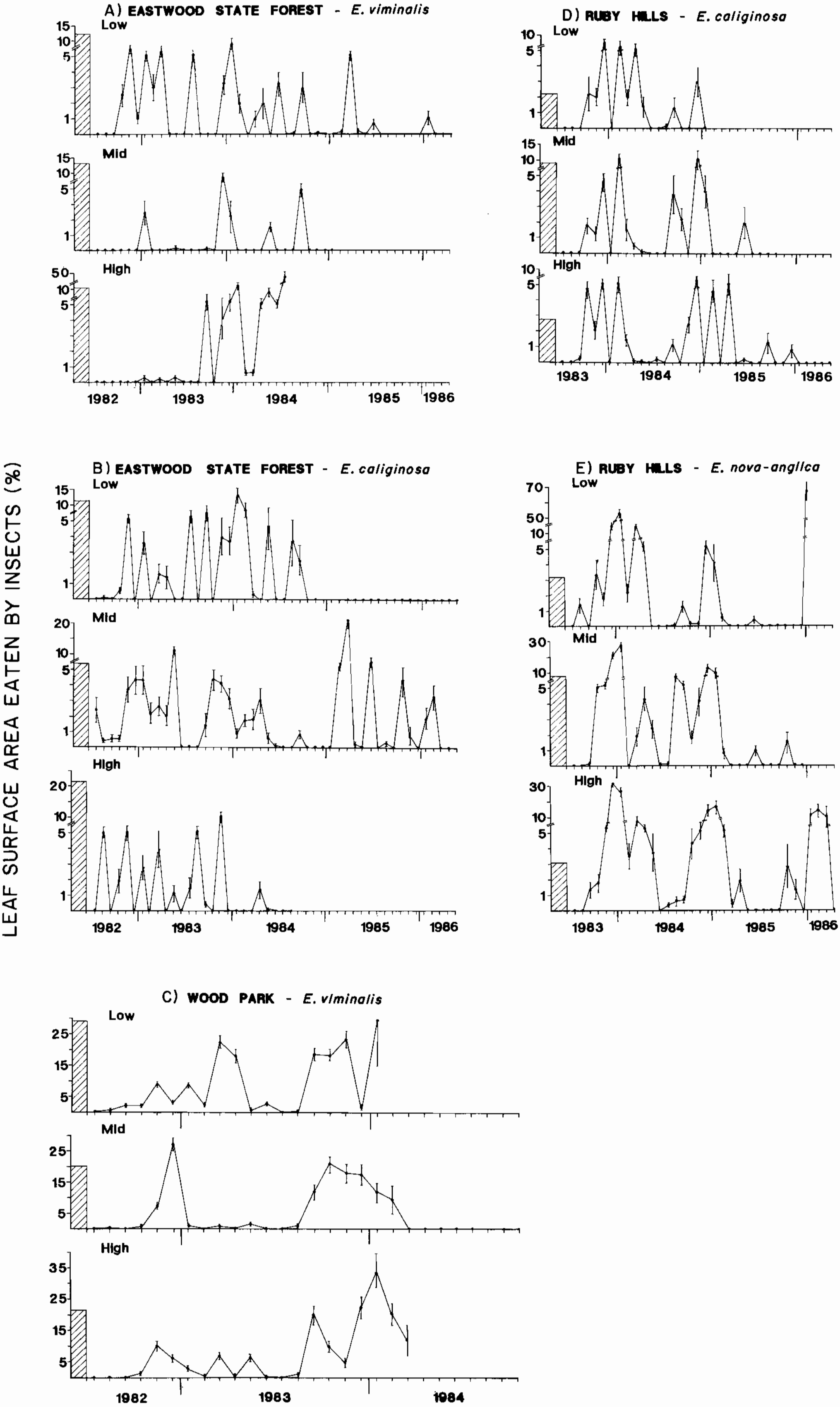

A) EASTWOOD STATE FOREST - E. viminalis
Low
Mid
High
15
10
5
1
50
1982
1983
1984
1985
1986
D) RUBY HILLS - E. caliginosa
Low
Mid
High
B) EASTWOOD STATE FOREST - E. caliginosa
20
E) RUBY HILLS - E. nova-anglica
70
30
C) WOOD PARK - E. viminalis
25
35
LEAF SURFACE AREA EATEN BY INSECTS (%)

TABLE 3. Summary of herbivory and other events affecting the survival of canopy leaves in *Eucalyptus* trees of the New England Region, New South Wales, Australia.

Site and species	% with browning*	% with galls	% with flowers	% Leaves totally eaten	% Leaves abscised	% Leaves turned color
Pastures with dying trees						
Wood Park— *Eucalyptus viminalis*	3.7	4.5	0.7	35.0	65.0	12.2
E. blakelyi	11.1	0	0.7	42.3	57.7	0.7
Site mean	6.9	2.5	0.7	38.1	61.9	7.2
Newholme— *E. viminalis*	0	0	0	32.8	67.2	12.5
E. blakelyi	21.3	0.7	0	52.7	47.3	7.3
E. bridgesiana	18.9	1.0	0	38.3	61.7	10.4
E. melliodora	15.5	0	0	30.2	69.8	11.6
E. nova-anglica	0	0	0	14.9	85.1	14.9
Site mean	14.3	0.5	0	36.3	63.7	10.8
Pastures with healthy trees						
UNE‡ Hill— *E. viminalis*	11.7	1.3	0	14.3	85.7	9.1
Angophora floribunda	24.9	1.5	0	16.4	83.6	7.5
E. blakelyi	21.9	0	0	8.6	91.4	5.3
Site mean	20	1.0	0	13.4	86.6	7.3
Ruby Hills— *E. nova-anglica*	12.2	1.6	4.5	33.8	66.2	6.4
E. dalyrmpleana	32.9	1.4	12.8	14.4	85.6	4.3
E. stellulata	42.9	3.6	6.8	12.4	87.5	6.7
E. caliginosa	35.3	0	0.8	15.0	85.0	8.0
Site mean	29.4	2.1	7.0	20.5	79.5	6.0
Woodlands						
Eastwood— *E. viminalis*	15.3	1.8	5.8	13.8	86.2	2.5
E. blakelyi	29.3	2.0	5.7	9.1	90.9	6.7
E. melliodora	22.4	1.0	6.6	5.6	94.4	25.5
E. caliginosa	19.2	1.7	0.7	17.0	83.0	8.1
Site mean	21.0	1.6	4.6	11.5	88.5	5.0
Walcha Woods						
E. youmanii	61.7	1.7	0	8.9	91.1	18.9
E. radiata	69.0	3.0	1.0	9.0	91.0	21.0
Site mean	66.0	2.5	0.7	9.0	91.0	20.3
Overall totals or means	25.3	1.8	3.6	20.5	79.5	7.9

* Brown blotches due to leaf mining or fungal infection.
† This column shows site totals (not site means).
‡ University of New England.

the growth of a second. Herbivory between seasons was statistically different, with summer undergoing significantly more defoliation than the other three seasons ($F_{3,243} = 8.05$, $P > .001$).

Herbivory averaged 22.6%, 46.4%, 17.4%, and 24.4% over the 4 yr, respectively (1982–1983 through 1985–1986). Among years, herbivory was also significantly different, with 1983–1984 having the highest levels of damage ($F_{3,43} = 2.69$, $P > .05$). The first season (1982–1983) represented the end of a drought, when presumably insect numbers and also leaves had not recovered in numbers; 1983–1984 was a good season with vigorous leaf growth and subsequent defoliation; 1984–1985 was a season of recovery from the heavy herbivory of the previous year; and by 1986 many of the trees sampled had died, especially if their canopies had exhibited dieback at the commencement of the study.

Other leaf-growth dynamics

Events (other than herbivory) in the life of a leaf were tabulated for all species at all sites (Table 3). Fungal pathogens were evident on 25% of all leaves, and were highest at Walcha Wood with 66% of leaves exhibiting brown regions of infection. Galls were not common in any site, with only 1.8% of the leaves developing galls throughout their life-spans. Few trees underwent flowering and fruiting during the course of the study. Since eucalypts only flower every 3–5 yr, it is assumed that this study occurred between flowering seasons. Alternatively, it may mean that the dry conditions of the early 1980s inhibited flowering.

Of all leaves that were monitored, almost 80% senesced, whereas only 20% were totally eaten by herbivores (with only 5 leaves of >5000 left intact at the time of data analyses). This shows that herbivory was not the major direct cause of leaf disappearance in most eucalypts, although it may indirectly cause leaf abscission in some cases. However, more leaves were totally eaten in the most unhealthy trees. Over 30% of the leaves at the pasture sites with dying trees (Wood Park and Newholme) were totally eaten, as compared to <12% in the woodland sites (Eastwood and Walcha

Table 3. Continued.

Number of new leaves that grew†	Total number of leaves†	% new leaves	Leaves left†
159	403	39.5	0
129	305	42.3	0
288	708	40.7	0
29	64	45.3	0
66	150	44.0	0
45	201	22.4	0
34	129	26.4	0
40	87	46.0	0
214	631	33.9	0
42	154	27.3	0
76	201	37.8	0
82	151	54.3	0
200	506	39.5	0
369	639	57.7	0
254	423	60.0	0
415	643	64.5	0
77	133	57.9	0
1115	1838	60.7	0
140	326	42.9	0
80	297	26.9	0
178	392	45.4	0
201	407	49.4	0
599	1422	42.0	0
61	180	33.9	0
66	338	20.0	5
127	518	24.5	5
2543	5623	45.2	

Woods). Intermediate numbers of leaves were lost in their entirety to herbivores at the pasture sites with healthy trees: 20.5% at Ruby Hills and 13.4% at UNE Hill. In some instances leaves changed to red or yellow before falling, but this did not correspond to insect attack.

Of 5623 marked leaves, 2543 flushed during the study, and these were monitored throughout their entire lifespans. Only five of the initially marked leaves remained on the last day of fieldwork, and these were shaded leaves in woodland trees.

Discussion

Damage to leaves by insects is not uniform in *Eucalyptus* canopies. The present study has shown that it varies widely over time, among different heights in the tree, and among different individuals and sites. Some species (e.g., *E. caliginosa*) are more resistant than others (e.g., *E. nova-anglica*). Although more than half of the leaves senesced or died from causes other than direct grazing in the present study, some trees were

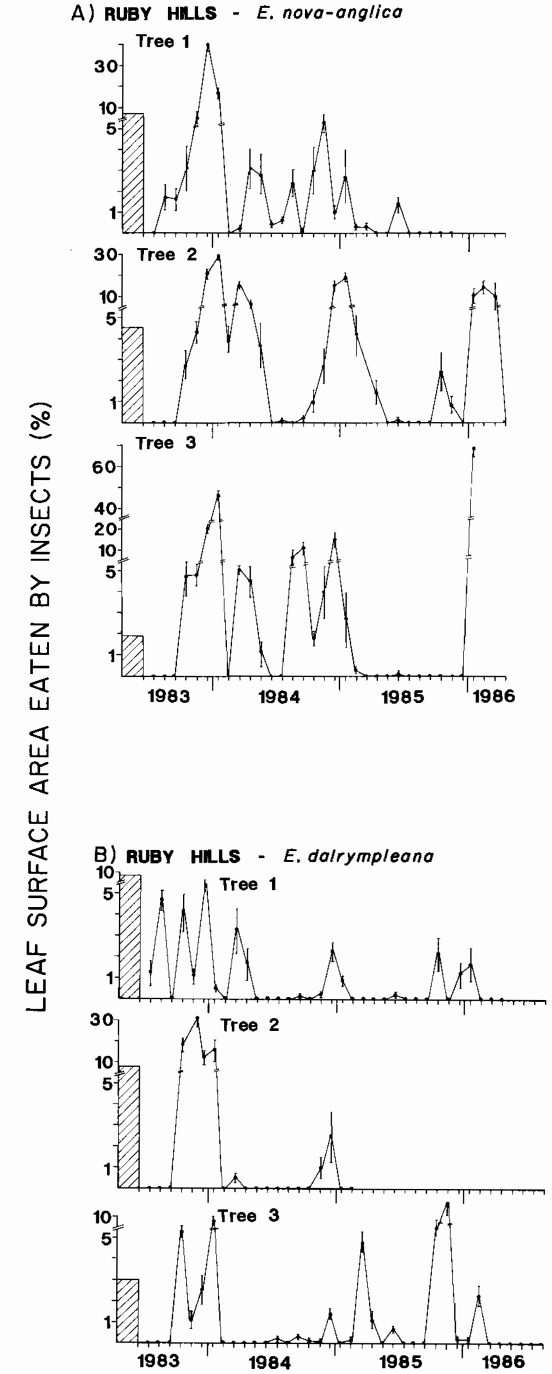
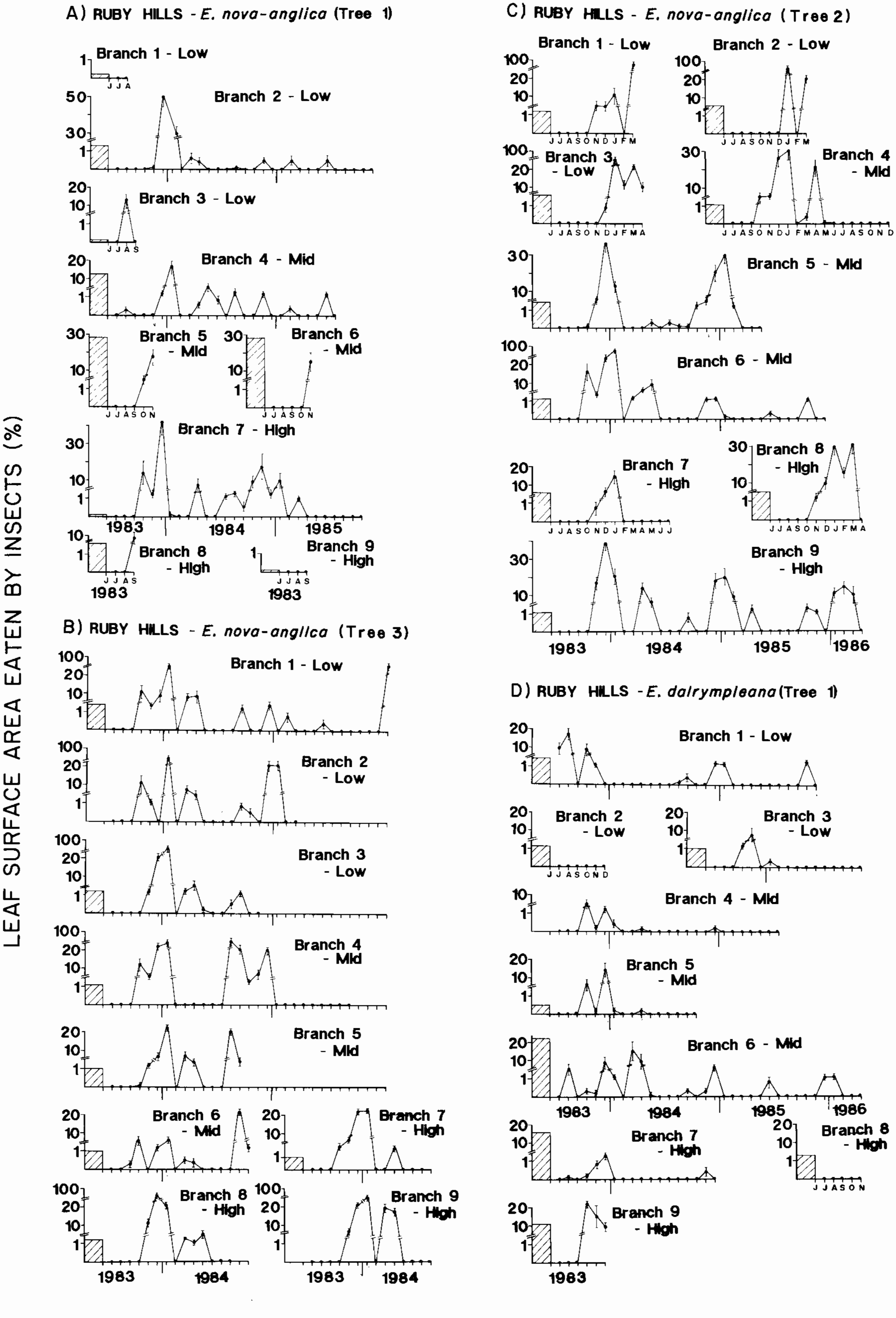


Fig. 7. Herbivory of individual trees at one pasture site with healthy trees (Ruby Hills): *Eucalyptus nova-anglica*, a species susceptible to herbivory; and *E. dalrympleana*, a species resistant to herbivory. Points represent proportion of leaf surface area eaten by insects during the course of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study.


LEAF SURFACE AREA EATEN BY INSECTS (%)
A) RUBY HILLS - E. nova-anglica (Tree 1)
Branch 1 - Low
Branch 2 - Low
Branch 3 - Low
Branch 4 - Mid
Branch 5 - Mid
Branch 6 - Mid
Branch 7 - High
Branch 8 - High
Branch 9 - High
1983
1984
1985
B) RUBY HILLS - E. nova-anglica (Tree 3)
Branch 1 - Low
Branch 2 - Low
Branch 3 - Low
Branch 4 - Mid
Branch 5 - Mid
Branch 6 - Mid
Branch 7 - High
Branch 8 - High
Branch 9 - High
1983
1984
C) RUBY HILLS - E. nova-anglica (Tree 2)
Branch 1 - Low
Branch 2 - Low
Branch 3 - Low
Branch 4 - Mid
Branch 5 - Mid
Branch 6 - Mid
Branch 7 - High
Branch 8 - High
Branch 9 - High
1983
1984
1985
1986
D) RUBY HILLS - E. dalrympleana (Tree 1)
Branch 1 - Low
Branch 2 - Low
Branch 3 - Low
Branch 4 - Mid
Branch 5 - Mid
Branch 6 - Mid
Branch 7 - High
Branch 8 - High
Branch 9 - High
1983
1984
1985
1986
J J A S O N D J F M A M J J A S O N D
100
30
20
10
1

completely defoliated by insects several times per year. Unlike deciduous forests where herbivory is highly seasonal, eucalypt defoliation is year-round; there are peaks during spring and summer, but also significant damage during autumn and winter. High rates of herbivory have been documented for Australian vegetation, including sclerophyll forests (Fox and Morrow 1986), rain forests (Lowman 1984*a,* 1987), and plants on coral islands (Lowman 1984*b*); insect consumption has ranged up to 40–50% of leaf surface area. By contrast, Ohmart et al. (1983) and Ohmart (1984) reported lower values and Robertson and Duke (1987) found generally low damage to Australian mangrove foliage. Most studies on other continents have found lower herbivory levels than those reported for Australia (reviewed by Lowman 1986). This raises one question of interpretation: do Australian trees suffer greater defoliation, or are the methods employed by scientists on different continents extremely variable? Some of the eucalypts in the present study conform to the higher defoliation levels, and, in cases of dieback trees, have even greater levels than those found in most of the studies cited above. Trees left isolated in pastures appear particularly susceptible.

The present study indicates that trees suffering from New England Tableland dieback have a higher rate of herbivory than healthy trees. Similar correlations in the past (e.g., Landsberg 1988) led to the belief that insect grazing was a contributing cause of dieback. This raises another question of interpretation: does heavy damage to foliage by insects make trees more susceptible to dieback, or does incipient dieback make trees more susceptible to insect attack, through weakening their defensive mechanism or altering the quality of their foliage? A third alternative is that both are related to some third factor or set of factors. These alternatives are not mutually exclusive, and a variety of synergisms is possible.

There is some evidence that dieback does predispose eucalypts to heavier insect attack. Landsberg (1990*a*) found that the dietary quality of leaves from dieback trees (*E. blakelyi*) was generally superior to that of those from healthy trees, and accordingly these leaves suffered heavier insect grazing. Defoliation (and simulated grazing by mechanical clipping) can result in enhancement of the dietary quality of leaves (Landsberg 1990*b*), leading to self-perpetuating chronic herbivory. This effect may be at least a partial explanation for the present finding that trees suffering dieback had higher herbivory rates. In experimental studies on seedlings and grafted plants of *E. blakelyi,* Landsberg (1990*c*) found, contrary to previous ideas, that trees stressed by nutrient deficiencies, drought, water-logging, or salinity had foliage of lower dietary quality than that of unstressed trees. (Excess phosphorus was an exception and Landsberg's seedlings were relatively insensitive to it.) Thus, most of these stresses do not seem to predispose trees to insect attack, but rather to have a reverse synergistic effect. Clearly, the relationships among factors affecting herbivory on eucalypts are complex.

Some of the scarab beetles in the New England Tableland region feed on grass roots as larvae and on tree foliage as adults. Beetle larvae have also been observed feeding on tree roots of eucalypts, perhaps leading to tree mortality (Lowman et al. 1987). High numbers of scarab beetle larvae (biomass up to 179 g per 100 m of furrow in a pasture) have been counted (Roberts et al. 1982), most of which emerge later as adults to feed upon the eucalypts. Thus, as land is cleared for pasture the amount of larval habitat increases and that of adults decreases. Consequently there are proportionally more adult beetles to feed upon the declining trees. Given the fecundity of beetles, even a rather small adult population can produce large numbers of larvae. These can be sustained by the increased area of pastures, and, within the vicissitudes of weather and other variables affecting insect populations in other ways, can lead to increasing pressure on the dwindling food resources of adults. Such changes may contribute to the heavier defoliation that occurs in trees left in pastures.

Diebacks are worldwide and have various origins and etiologies (Mueller-Dombois 1986, 1987), but most are not so strongly linked with defoliation as on the New England Plateau of Australia. While herbivory in New England is higher in trees showing signs of dieback than in healthy ones, further investigation is required to establish whether or not this link is a causal one.

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FIG. 8. Herbivory of individual branches over three canopy heights within four individual trees at one pasture site with healthy trees (Ruby Hills). Points represent proportion of leaf surface area eaten by insects during the course of each month, expressed as a percentage of total leaf area ($\bar{X} \pm 1$ SE); hatched bars on the left-hand side indicate average herbivory measured at the commencement of study.

Eucalyptus nova-anglica tree 1 (part A): Cockatoos were responsible for the damage to branch 1 low, branch 3 low, branches 5 and 6 mid, and branches 8 and 9 high. Christmas beetles (Scarabaeidae) caused the highest peak on branch 2 low and on branch 7 high. Chrysomelids caused the first peak on branch 7 high.

E. nova-anglica tree 2 (part C): Christmas beetles were responsible for the highest peak on branch 2 low, and sawfly larvae for the final damage to branches 1 and 2 low.

All other damage on these trees and on *E. nova-anglica* tree 3 (part B) and *E. dalrympleana* tree 1 (part D) was by unknown insects.

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LITERATURE CITED

Barker, T. 1980. Armidale, a cathedral city of education and the arts. Cassell Australia, North Ryde, Australia.

Fox, L. R., and P. A. Morrow. 1986. On comparing herbivore damage in Australian and north temperate systems. Australian Journal of Ecology **11**:387–394.

Heatwole, H., and M. Lowman. 1986. Dieback, death of an Australian landscape. Reed, Sydney, Australia.

Heatwole, H., and M. Lowman. 1987. Dieback: death of an Australian landscape. Pages 42-49 *in* R. Love, editor. If atoms could talk; search and serendipity in Australian science. Greenhouse, Richmond, New South Wales, Australia.

Landsberg, J. 1988. Dieback of rural eucalypts: tree phenology and damage caused by leaf feeding insects. Australian Journal of Ecology **13**:251–267.

———. 1989. A comparison of methods for assessing defoliation, tested on eucalypt trees. Australian Journal of Ecology **14**:423–441.

———. 1990*a*. Dieback of rural eucalypts: does insect herbivory relate to dietary quality of tree foliage? Australian Journal of Ecology **15**:73–87.

———. 1990*b*. Dieback of rural eucalypts: response of foliar dietary quality and herbivory to defoliation. Australian Journal of Ecology **15**:89–96.

———. 1990*c*. Dieback of rural eucalypts: the effect of stress on the nutritional quality of foliage. Australian Journal of Ecology **15**:97–107.

Lea, D. A. M., J. J. J. Pigram, and L. Greenwood. 1977. An atlas of New England. Two volumes. Department of Geography, University of New England, Armidale, New South Wales, Australia.

Lowman, M. D. 1984*a*. An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? Biotropica **16**:264–268.

———. 1984*b*. Grazing of *Utethesia pulchelloides* larvae on its host plant, *Argusia argentea,* on coral cays of the Great Barrier Reef. Biotropica **16**:14–18.

———. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest species. Australian Journal of Ecology **10**:7–24.

———. 1986. Insect herbivory in Australian rainforests—is it higher than in the Neotropics? Proceedings of the Ecological Society of Australia **14**:109–120.

———. 1987. Relationships between leaf growth and holes caused by herbivores. Australian Journal of Ecology **12**: 189–191.

Lowman, M. D., and H. Heatwole. 1987. The impact of defoliating insects on the growth of eucalypt saplings. Australian Journal of Ecology **12**:175–181.

Lowman, M. D., A. D. Burgess, and W. D. Higgins. 1987. The biomass of New England peppermint (*Eucalyptus nova-anglica*) in relation to insect damage associated with rural dieback. Australian Journal of Ecology **12**:361–372.

Mueller-Dombois, D. 1986. Perspectives for an etiology of stand-level dieback. Annual Review of Ecology and Systematics **17**:221–243.

———. 1987. Natural dieback in forests. BioScience **37**: 575–583.

Norton, A. 1886. On the decadence of Australian forests. Proceedings of the Royal Society of Queensland **3**:15–22.

Ohmart, C. P. 1984. Is insect defoliation in eucalypt forests greater than that in other temperate forests? Australian Journal of Ecology **9**:413–418.

Ohmart, C. P., L. G. Stewart, and J. R. Thomas. 1983. Phytophagous insect communities in the canopies of three *Eucalyptus* forest types in southeastern Australia. Australian Journal of Ecology **8**:395–403.

Roberts, R. J., A. J. Campbell, M. R. Porter, and N. L. Sawtell. 1982. The distribution and abundance of pasture scarabs in relation to Eucalyptus trees. Pages 207–214 *in* K. E. Lee, editor. Proceedings of the 3rd Australasian Conference on Grassland Invertebrate Ecology, Adelaide, 30 November–4 December 1981. South Australia Government Printer, Adelaide, South Australia, Australia.

Robertson, A. I., and N. C. Duke. 1987. Insect herbivory on mangrove leaves in North Queensland. Australian Journal of Ecology **12**:1–9.

Walker, G. T. 1977. Relief. Pages 11–16 *in* D. A. M. Lea, J. J. J. Pigram, and L. Greenwood, editors. An Atlas of New England. Volume 2. The Commentaries. Department of Geography, University of New England, Armidale, New South Wales, Australia.