

The biomass of New England peppermint (*Eucalyptus nova-anglica*) in relation to insect damage associated with rural dieback

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Abstract

Two adjacent mature trees of New England peppermint (*Eucalyptus nova-anglica*) were harvested with the aid of a cherry picker to determine their biomass distribution and insect damage. One suffered from obvious symptoms of rural dieback and the other was healthy. Weights of foliage and wood were measured, and insect damage for all leaves and branches was quantified. For each tree 25% of the roots were extracted from the soil using a bulldozer and manual methods; they were then weighed and damage by insects estimated. The healthy tree lost more leaf surface area to insects (11% or 1.1 kg vs 9.2% or 0.3 kg); but the dieback tree had four times more wood affected by boring insects (19% cf. 5%); and only 20% root biomass remaining (92 kg cf. 488 kg). The accuracy of sampling techniques needed to measure defoliation and the consequences of insect damage to dieback of rural eucalypts are discussed.

Introduction

The distribution of dry matter in mature trees is not widely known due to the obvious logistic difficulties of harvesting and weighing both above- and below-ground parts. Most estimates in the literature have two major drawbacks. First, the biomass is usually extrapolated from subsamples and formation of a logarithmically transformed linear regression related to tree size; these results are adequate for estimating stand biomass, but are not accurate for estimating individual trees (Ovington *et al.*

1968; Satoo 1968, 1970; Madgwick & Satoo 1975). Second, biomass measurements represent only the plant parts present and do not account for the portions consumed by insects or other herbivores.

Most ecological analyses of tree biomass and productivity have involved northern temperate species (e.g. Whittaker & Woodwell 1971). Very few quantitative measurements of entire eucalypts have been made (but see Westman & Rogers 1977), although there have been analyses of canopies (Pook 1984) or other isolated parts.

One of the major problems faced in assessing the current eucalypt dieback syndrome has been the lack of basic comparative information on healthy eucalypts. Root damage cannot be identified without knowledge of the biomass of roots of healthy trees to serve as a standard, and it is difficult to evaluate whether or not poor condition of trees is related to heavy grazing if normal levels of herbivory are unknown. Furthermore, if insect damage has not been measured quantitatively, one cannot correct for the portions missing.

Insect damage has been implicated widely as a major cause of dieback affecting eucalypts in Australia (Norton 1886; Old *et al.* 1980; Mackay *et al.* 1984). In particular, some herbivorous beetles, especially chrysomelids and the scarab *Anoplognathus hirsuta*, have been observed defoliating the canopies of trees in plague proportions in the New England tablelands of New South Wales, where there has been extensive dieback during the last few decades (Nadolny 1984). Severe defoliation during outbreaks lowers the amount of canopy leaf area remaining for photosynthesis and probably has indirect effects on other metabolic processes of the trees relating to tree growth and survival (Morrow & La Marche 1978). Despite the implications that insect pests are a factor in dieback, very little quantitative information is available on their impact on native vegetation

(but see Fox & Morrow 1983; Ohmart 1984) and it is uncertain to what extent they may be responsible for tree mortality.

As part of a long-term research project on the herbivory of eucalypts, the present field study addressed two major questions:

(1) How is the total biomass of a mature eucalypt distributed spatially and allocated to components of roots, stems and foliage?

(2) What are the differences in biomass between healthy and dieback eucalypts, and how do their levels of insect damage — both above- and below-ground — compare?

Methods

Two mature trees of *Eucalyptus nova-anglica* Deane and Maiden were selected in open pasture on 'Ruby Hills' property near Walcha, NSW, during January 1985. The trees were growing about 500 m apart on relatively flat, well drained terrain in paddocks dominated by *Phalaris tuberosa*, *Demeter fescue* and white clover. They were similar in stature: 11 m height, 90–100 cm girth, single-stemmed, and open-grown (Table 1). The one obvious difference was that one tree appeared healthy with a well developed canopy, and the other (subsequently called the 'dieback tree') exhibited signs of rural dieback such as epicormic shoots, dead branches and reduced canopy. Both trees were approximately 50–75 years of age (B. Burgess pers. comm.).

TABLE 1. Comparisons between a healthy and a dieback-affected individual of New England peppermint (*Eucalyptus nova-anglica*)

	Healthy	Dying
Height (m)	11.5	11.5
Circumference (cm at breast height)	100	95
No. of m ³ of leafy canopy	161	90
Leaf biomass	9.1	3.0
Wood biomass	989.1	644.8
Weight of stump	113.1	64.0
Weight of roots	487.7	92.2
Total weight	998.2	647.8

All weights are expressed in kilograms of dry weight.

Above-ground biomass

The entire above-ground portions of each tree were divided into cubic metre sections. The sections ran vertically from 0 to 11 m height, and horizontally in labelled quadrats that were delineated by direction: N, S, E or W (Fig. 1). A horizontal grid was laid out on the ground using stakes and flagging tape; vertical 1 m intervals were marked up the tree trunk, also with flagging tape. Harvesting, facilitated by the use of a mobile cherry picker, commenced from the top of each tree downwards and from the edges of the canopy inwards.

Branches and leaves were clipped and bagged from each cubic metre and were weighed and sorted immediately. Branch material was sorted into three size classes: small (0–1 cm

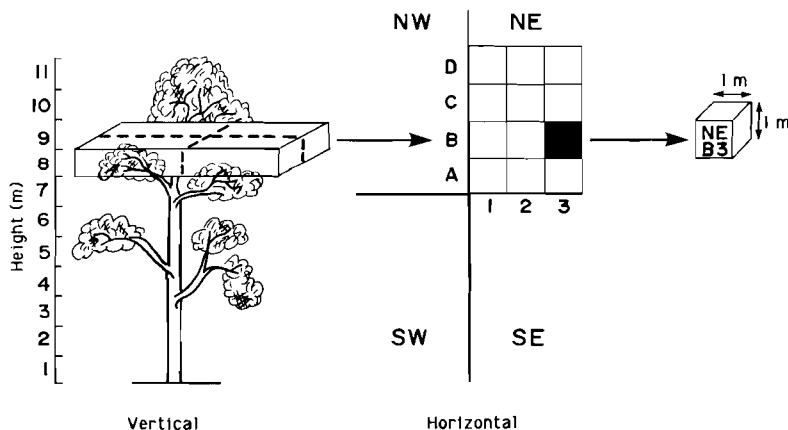


FIG. 1. Diagrammatic illustration of the grid constructed to section the two New England peppermint trees into cubic metres for harvesting, weighing, and measuring insect damage.

diameter), medium (1–5 cm diameter), and large (> 5 cm diameter). Fresh weights of wood (including bark) were recorded for all branch size classes in each cubic metre, and also for the main trunk by 1 m sections. The stump section, defined as the trunk portion that extended from ground level to approximately 50 cm below (where major roots extended out from the central trunk), was also weighed.

All branches were examined for signs of insect damage, both externally by visual examination and internally by cutting the branches at intervals of 5–10 cm to examine cross-sections for tunnels of boring insects, termite activity or kino veins. Proportions of insect-damaged branches were estimated by weight, and dead wood was also weighed separately within each harvested cubic metre.

Leaves from each cubic metre were sorted into four types: young and entire; young and partially eaten; old and entire; and old and partially eaten. (Young leaves were defined as the current December–January flush, and old leaves as any previous flushes.) Once sorted, leaves were weighed and then frozen in plastic bags. Over the next 6 months, total leaf areas and areas grazed by insects were measured using Leaf Area meters and the technique of taping over holes (Lowman 1982). This method underestimates real amounts of leaf area eaten, however, because it fails to account for those leaves eaten entirely (Lowman 1984); but it is not possible to avoid this in destructive sampling.

Fresh weights of all wood and leaves were measured in the field. Over 100 subsamples (representing all heights, aspects and size classes of wood and leaves) were oven-dried for 1 week at 65°C to calculate fresh:dry weight ratios. Leaf data were analysed using the ELF statistical package. (ELF is the econometrics and linear modelling program written for Apple II microcomputers by the Winchendon Group in Alexandria, Virginia.)

Below-ground biomass

A circular area of ground extending 5 m beyond the circumference of tree canopy was excavated by a bulldozer under each tree. (No roots were observed to extend beyond this distance.) The soil conditions and root distribution appeared homogeneous, so a 90° section of ground area

radiating out from each tree stump was excavated more thoroughly and the biomass of roots within it quadrupled to estimate the total root biomass of each tree. Trenches were dug by a bulldozer along the edges and midway through the excavated quarter-section; subsequent manual digging and sieving exposed the smaller roots; and finally, pressurized water hoses were used to remove soil particles from the main tap root. Roots were sorted into size classes (as for branches) and weighed. It is assumed that some fine roots (< 1 mm) were lost during extraction; although functionally important, they would contribute only a small proportion of total root dry weight.

Roots were examined visually for external insect damage, and tunnels filled with faecal material were 'followed' through the soil by careful digging to estimate entire consumption of smaller roots. Roots were also cut at regular intervals to examine them for evidence of internal boring by insects.

Results

Total biomass

The healthy eucalypt weighed 998 kg (all figures expressed in dry weights), compared with 648 kg for the dieback tree (Tables 1, 2). All major biomass components of the dieback tree (leaf, trunk and branches, stump, and roots) weighed less than those of the healthy tree, except for dead wood (Fig. 2, see also Appendix). The root system, leaves, above-ground wood, and stump weights were only 20, 33, 66 and 50% of those of the healthy tree, respectively. The weights of leaves, dead wood and live wood weights varied markedly both vertically and horizontally in their distribution on the trees (Fig. 3a–f).

Leaf biomass

Leaf biomass was three times greater in the healthy tree than in the dieback tree (9.1 vs 3.0 kg; Fig. 2). The healthy canopy occupied 161 m³, while that of the dieback tree occupied only 90 m³, a smaller canopy in both expanse and in leaf material (Fig. 3a, b). From averages of dry weights of leaves, it was estimated that the healthy and dieback canopies contained

TABLE 2. Comparisons of insect damage between healthy and dieback-affected individuals of *Eucalyptus nova-anglica*

Factor		Healthy tree (s.d.)	Dieback tree (s.d.)	Significance [†]
(A) LEAF AREA LOSSES				
Among sides of trees	NE	12.0 (7.0)	8.2 (7.3)	$F_{3,83} = 2.89, P < 0.05$ (within dieback canopy)
	SE	8.9 (4.9)	8.0 (4.5)	
	NW	11.7 (7.4)	15.1 (10.8)	$F_{3,210} = 1.75$ NS (within healthy canopy)
	SW	11.1 (6.2)	12.9 (7.2)	
Among heights of trees	1 m	n.a.	n.a.	$F_{6,76} = 4.09, P < 0.01$ (within dieback canopy)
	2 m	n.a.	n.a.	
	3 m	12.3 (10.0)	n.a.	
	4 m	11.1 (8.3)	26.7 (26.7)	
	5 m	11.1 (8.3)	19.1 (9.1)	$F_{7,147} = 0.60, NS$ (within healthy canopy)
	6 m	13.1 (7.3)	11.0 (11.6)	
	7 m	9.9 (5.7)	7.5 (4.8)	
	8 m	10.5 (5.1)	9.3 (5.6)	
	9 m	11.7 (6.6)	7.5 (3.7)	
	10 m	11.1 (5.4)	7.1 (5.6)	
	11 m	*	*	
Between ages of leaves	young	16.0 (5.9)	9.7 (6.5)	$F_{1,85} = 0.42, NS$ (within dieback canopy)
	old	6.6 (3.8)	8.7 (8.0)	$F_{1,212} = 200.163, P < 0.001$ (within healthy canopy)
Total tree		11.3 (6.9)	9.2 (7.3)	$F_{1,244} = 5.30, P < 0.05$ (between two trees) [‡]
(B) OTHER ASSESSMENTS				
Entire leaves (%)		75	50	
Dead branches (%)		6	31	
Wood (m ³) with borers (%)		5	19	

*Leaves not analysed. [†]Comparisons 'within' a tree refer to analyses among different cubic metres of either the healthy or dieback tree. [‡]Variance between two trees was homogeneous.

149 000 and 83 000 leaves, respectively, photosynthetic areas equivalent to 67.3 and 44.8 m². (The total leaf area would have been at least 76 and 49 m², respectively, had insect damage not occurred.)

The healthy tree had leaves distributed from 2 m up to 11 m and over a horizontal span of 9 m (Fig. 3a). In contrast, the dieback tree had canopy only between 4 and 11 m, with a maximum diameter of 7 m (Fig. 3b). The healthy tree had up to 362 g of leaves per m³ and a broad, umbrella-shaped canopy. In the uppermost canopy, the dieback tree had a vigorous cluster of epicormic shoots and these had as much as 473 g of leaves per m³ (Fig. 3, 11 m). The dieback tree had over a third of its canopy at 11 m, having lost the bulk of its lower canopy.

Wood biomass

The healthy tree had 989 kg of wood, whereas the dieback tree had 645 kg (Fig. 2). Similarly, wood occupied only 119 m³ of space in the dieback canopy compared with 196 m³ in the healthy tree (Fig. 3c-f). Dead wood above ground comprised 23 kg (distributed over 42 m³) in the healthy tree and 48 kg (73 m³) in the dieback tree. The healthy tree also had a greater biomass in stump (113 kg cf. 64 kg) and root (488 cf. 92 kg) components. In total, the healthy tree had 1.5 times more wood biomass than the dieback tree.

Insect damage

Our discrete measurements showed an average

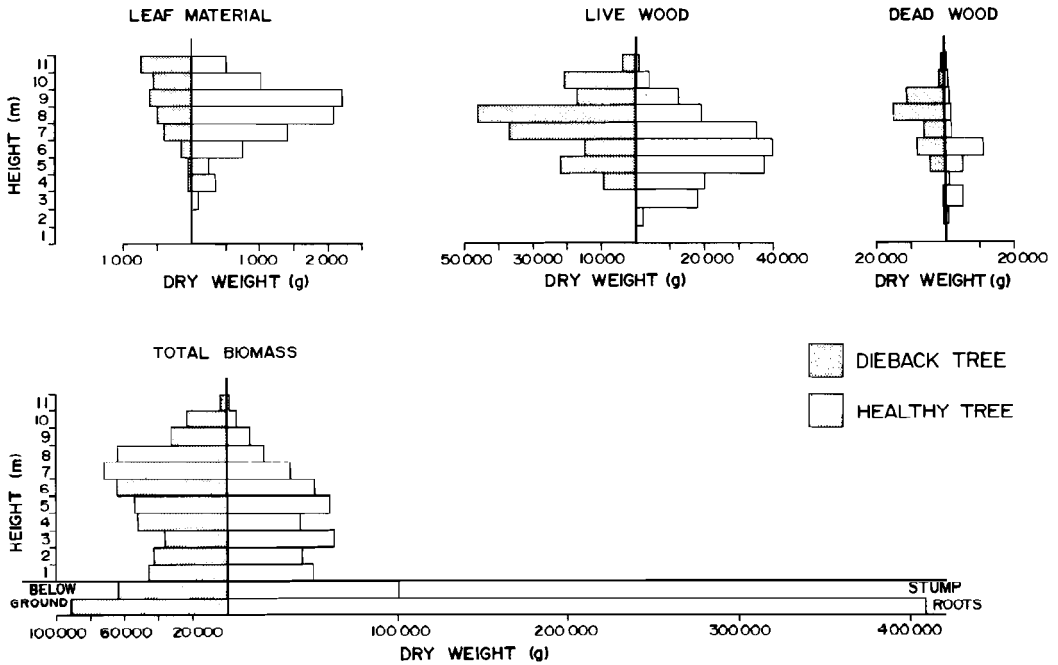


FIG. 2. Comparison of the vertical distributions of biomass components (leaf, live wood, dead wood and total) for the healthy and dieback trees.

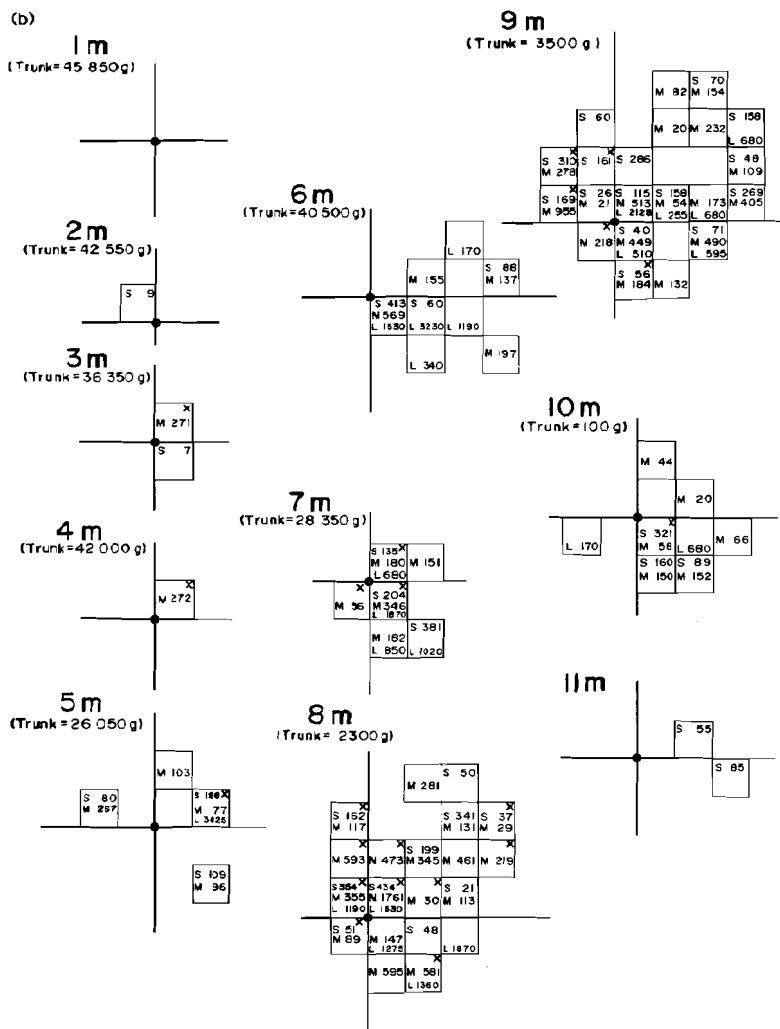
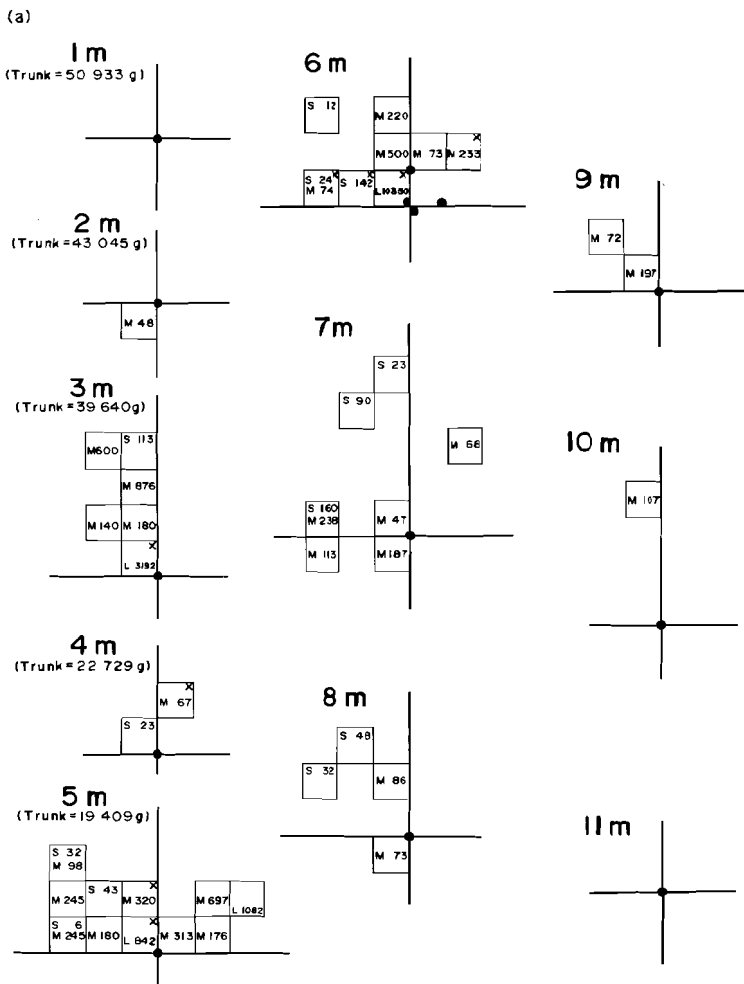
loss of 9.2% (s.d. = 6.9) surface areas per leaf in the dieback tree compared with 11.3% (s.d. = 6.9) in the healthy tree, a significant difference ($F_{1,244} = 5.30$, $P < 0.05$; Table 2). These are conservative estimates, however, since leaves that were consumed completely were not accounted for (see Discussion). Leaf damage varied with height, leaf age and aspect in both canopies (Table 2). In the healthy tree, leaf damage was homogeneous throughout the canopy, except that young leaves had significantly more herbivory than old leaves. In the dieback tree, however, leaves showed statistically higher losses of area on the western sections and lower regions of canopy, but similar losses in both young and old leaves.

The wood components of the dieback tree had greater insect infestation than did the healthy tree. Borers and termites occupied 19% of the branches of the dieback tree, but only 5% of those of the healthy trees. Once again, these are conservative figures since the branches and roots consumed entirely by insects could not be detected. Most wood damage appeared as tunnels through the sapwood, with relatively little damage to cambial sections. A greater number

of both species and individuals of Coleoptera were found associated with the roots of the dieback tree than with those of the healthy tree, including larvae and adults of Christmas beetles (*Anoplognathus* spp.), golden stag beetles (*Lamprima aurata*), pasture scarabs (*Sericesthis* spp.), redheaded whitegrub (*Dasygnathus dejeani*) and dung beetles (Scarabaeinae). It was difficult to determine from frass tunnels, however, whether insects had consumed healthy roots or rather had consumed roots already damaged by another source of tree stress.

Potential biomass

If insect attack had not occurred, biomass of both trees would have been higher. It is impossible to estimate all missing biomass, since the amount of leaves and wood that were removed *entirely* from the trees by insects is not known from the destructive sampling techniques utilized here. Corrections for the partially eaten biomass were calculated, however, and provide a closer estimate of each



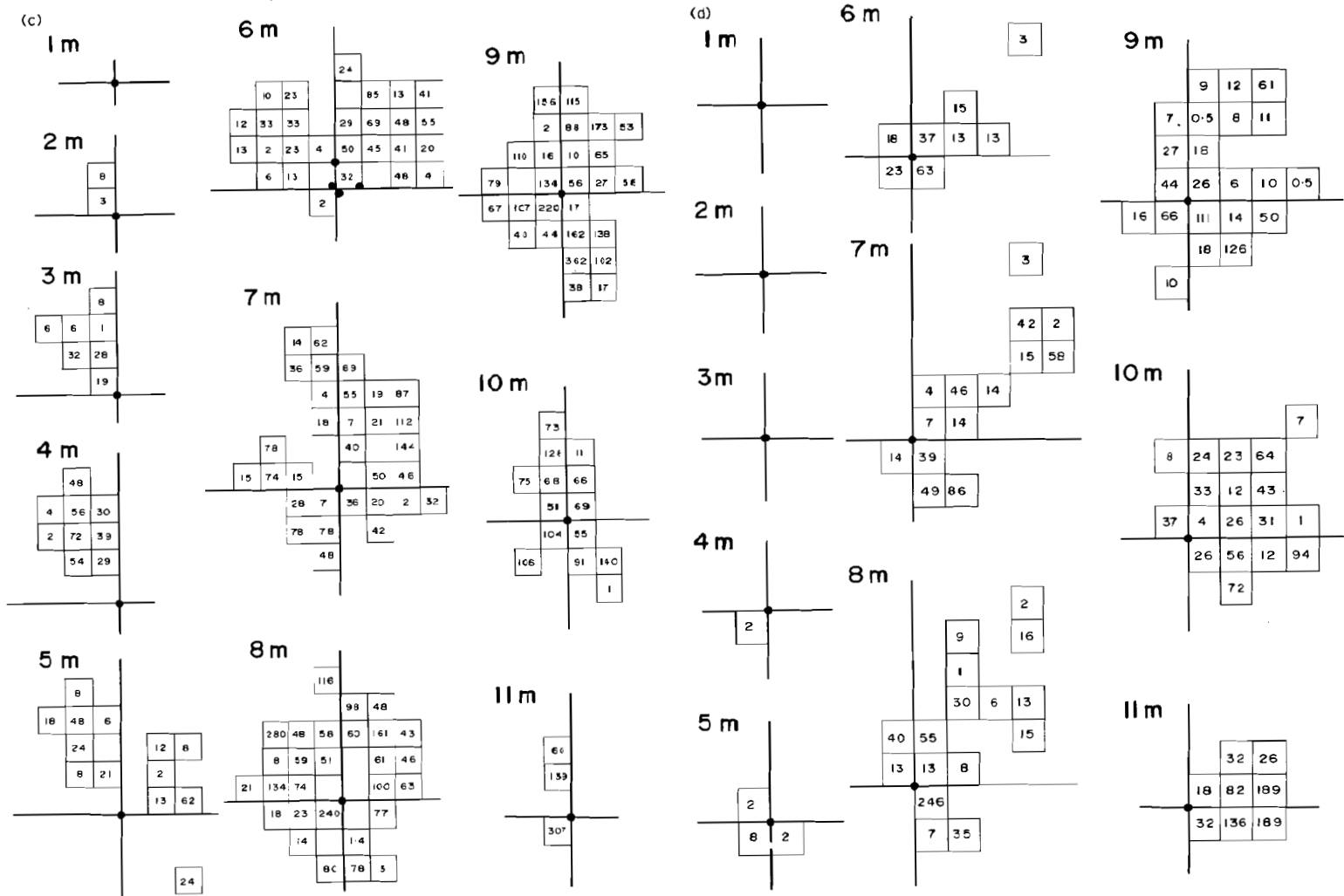
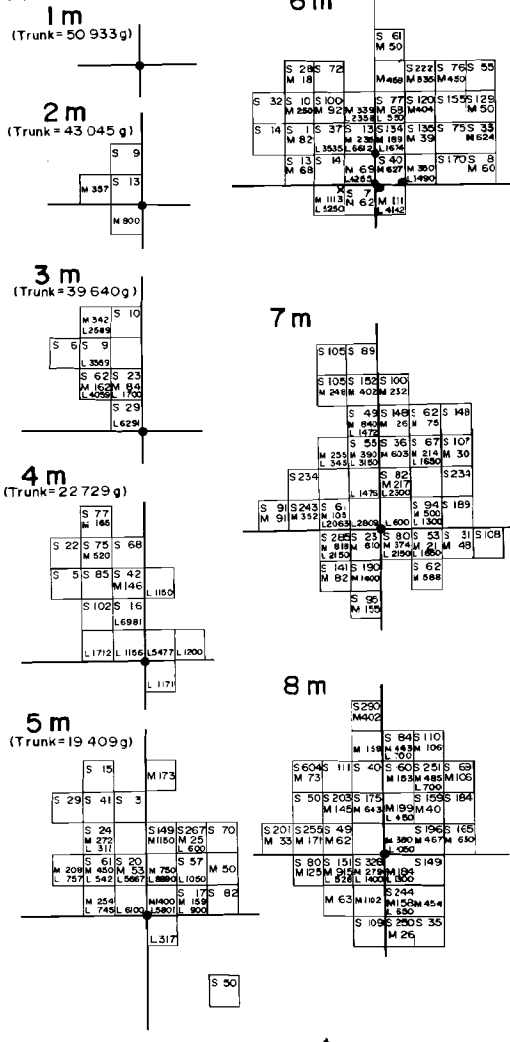


FIG. 3. Vertical and horizontal distributions of dry weights for dead wood, leaf material and live wood on a healthy (a, c, e) and a dieback (b, d, f) New England peppermint tree near Walcha, NSW. Weights expressed as $g\ m^{-3}$. Black circles indicate position of main trunks. Wood weights are further divided into size classes of S (small), M (medium) and L (large); see text for explanation. 'X' indicates the presence of borers or termites within a cubic metre section.

FIG. 3 continued.

(e)



(f)

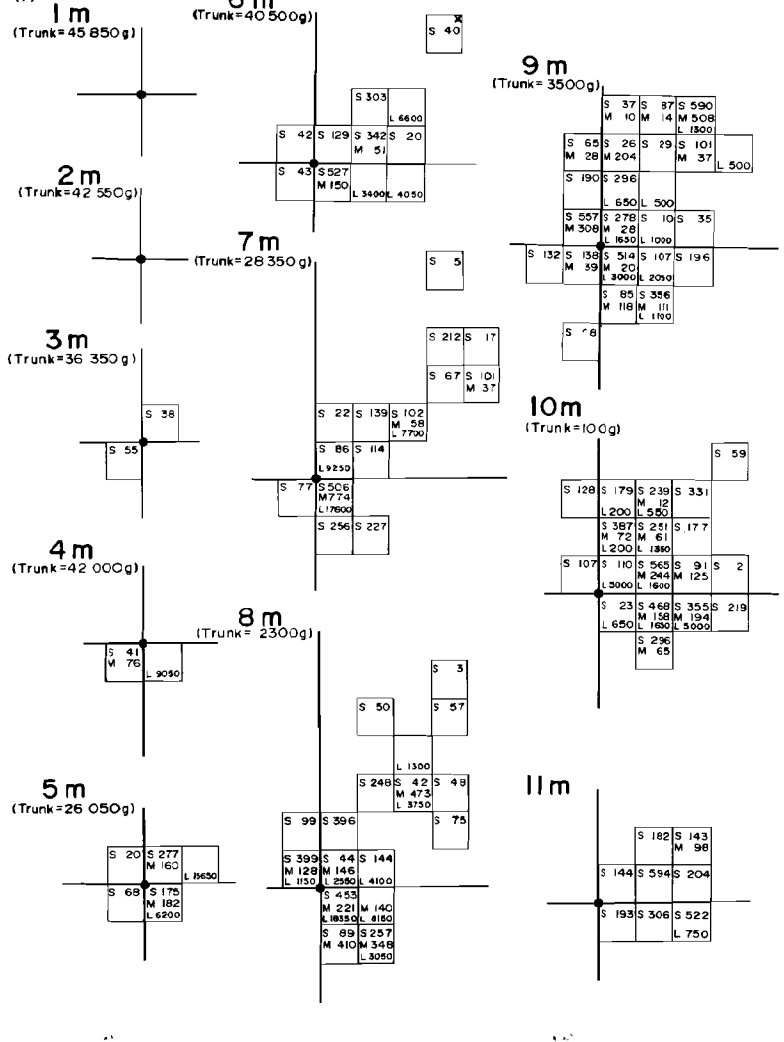


TABLE 3. 'Potential biomass' of New England peppermint trees with corrections for insect damage

	Original (kg)	Healthy Missing* (%)	Corrected (kg)	Original (kg)	Dieback Missing* (%)	Corrected (kg)
Leaf	9.1	11.3	10.2	3.0	9.2	3.3
Wood	989.1	5	1041.2	644.8	19	796.0
Total biomass			1051.4			799.3

*Missing amounts were determined only by directly observed damage: by leaf surface area eaten or by proportions of damaged branches in the case of wood. No attempt was made to estimate missing root area. In all cases, additional biomass losses in the dieback tree most likely occurred through loss of growth vigour.

tree's original biomass (Table 3). The difference of 249.1 kg between the potential biomass for these two similar-sized trees suggests that on the dying tree many leaves, roots and branches had either senesced or had been eaten entirely by insects, both during the year of this study and in previous years, so that it had produced less new biomass. The number of leaves consumed entirely by insects in dieback peppermint trees has been measured in other studies and is extremely high (M. D. Lowman & H. Heatwole unpubl. data), and proportionately higher than in healthy eucalypts. Branches and roots of dieback peppermints probably had a similar fate, leading to the loss of stature characteristic of the dieback syndrome.

Discussion

The logistic organization required to harvest accurately and to weigh an entire adult tree is large. The fact that only two trees were harvested is an obvious limitation of this study, posing obvious questions: how comparable were the two trees initially and how representative were they of all New England peppermints? To minimize potential errors arising from extrapolating these results to other peppermints, the selection of the trees was given great consideration. Many pairs of trees were examined as candidates over a wide range of conditions and sizes. The two peppermints selected appeared to represent typical New England peppermints, and also grew in conditions devoid of any obvious complicating factors (e.g. no adjacent trees, no unique soil or water conditions, no slope, no unique land use history in this particular paddock, etc.). Nonetheless, since only two trees were sampled, the conclusions from this study must be regarded as

tentative. The biomass of our healthy tree was similar to results obtained for other healthy eucalypts of similar stature (e.g. Westman & Rogers 1977).

The differences between the healthy and the dieback tree were striking, the healthy tree having a greater number of leaves, root biomass, photosynthetic area, and above-ground biomass. The huge differences in root biomass suggest that dieback trees suffer extensive root loss during their decline; whether this is a direct result of insect larval attack or a consequence of canopy decline is not yet known. And whether root damage occurred throughout the root system or merely to the portion harvested is not known. The similar loss of above-ground wood biomass was consistent for all canopy regions of the dieback tree. Past studies (e.g. Landsberg & Wylie 1983; Mackay *et al.* 1984; Nadolny 1984) have observed that dieback eucalypts suffer greater herbivory than healthy trees, and long-term measurements (using different methods from this study) are confirming this (M. D. Lowman & H. Heatwole unpubl. data).

The levels of herbivory obtained in this study do not appear to follow these predictions but there are three possible explanations. First, this method of sampling measures only uneaten or partially eaten leaves and so is less accurate than observations that also monitor losses of entire leaves (Lowman 1984). If the dieback tree suffered greater removal of entire leaves by insects than the healthy tree, then its grazing levels would have been greatly underestimated. The harvested trees were growing within 0.5 km of three peppermint trees used for more extensive monitoring of insect grazing (M. D. Lowman & H. Heatwole unpubl. data). Eventually, these 'long-term measurements' will

indicate the extent to which total leaf consumption may have been underestimated in the present destructive sampling (termed 'discrete measurements'; see Lowman 1982, 1984). Second, the 1984–85 summer season was dry, with relatively low numbers of Christmas beetles compared with other years. Up until January (the time of harvest), Christmas beetles had not yet been observed feeding in large numbers as in previous years. And further, if the leaf flush of the healthy tree was slightly ahead of the dieback tree, then other herbivores may have fed on the healthy but not yet on the dieback tree. Third (but least likely), dieback trees may not suffer higher herbivory than healthy trees, suggesting a need to re-evaluate the causes of rural dieback. Perhaps factors other than defoliation — such as root damage — may correlate more directly with tree decline. A healthy tree offers a greater supply of leaf tissue for herbivores, although the toxins and nutrients contained in leaf tissue of healthy and dieback eucalypts will determine their palatability; these comparisons are underway for New England eucalypts (M. D. Lowman & J. Schultz unpubl. data). Losses of leaf tissue between the two trees, at the time of harvest and as measured by our methods, appear similar (Table 2). This apparent statistical difference is somewhat misleading, since ANOVA invariably become significant with increased sample size (Marascuilo 1971); and in this case, the entire population of canopy leaves comprised the sample size.

Whereas the high levels of insect grazing in eucalypts suffering rural dieback have long been observed (Norton 1886) and more recently quantified (M. D. Lowman & H. Heatwole unpubl. data), the marked difference in root biomass between healthy and dieback trees has never been measured before. If both the roots and the leaves are severely and repeatedly attacked, the stress placed upon the tree by insects is much greater than that caused by defoliation alone. The eucalypt dieback syndrome in New England is complex, with many factors potentially stressing the trees, including seasonally extreme temperature, land clearing and subsequent exposure, insect defoliators, livestock, applications of fertilizers, fungal pathogens and the introduction of non-native grasses (Heatwole & Lowman 1986). The consumption of tree roots by insect larvae may

represent a new source of potential stress and mortality of the trees.

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