

Leaf, tree and soil properties in a *Eucalyptus saligna* forest exhibiting canopy decline

Christine Stone^A and Jack A. Simpson^B

^ANew South Wales Department of Primary Industries Science and Research, PO Box 100, Beecroft, NSW 2119, AUSTRALIA.

^B15 Sprent Street, Narrabundah, ACT, 2604, AUSTRALIA. ^ACorresponding author email: christines@sf.nsw.gov.au

Abstract: The extent of eucalypt decline in moist coastal forests of south-eastern Australia is increasing with resultant losses in biodiversity and productivity. This survey aimed to identify factors associated with the decline of *Eucalyptus saligna* (Sydney Blue Gum) in Cumberland State Forest, a moist sclerophyll forest within urban Sydney. *Eucalyptus saligna* was the dominant overstorey species in six 20 m radius plots, which differed in floristic composition, structure and crown condition. One plot was colonised by bell miners (*Manorina melanophrys*). A range of leaf, tree and plot scale parameters were assessed including insect damage and free amino acid content, visual crown condition, floristics and soil chemistry. The plot permanently colonised by bell miners also had *Eucalyptus saligna* trees in the poorest condition. Both the weed *Lantana camara* and the soil pathogen *Phytophthora cinnamomi* were present in some of the plots but neither was strongly consistent with the severity of crown decline. There were, however, significant correlations among the foliar traits of insect damage, free amino acid content and relative chlorophyll content. Free amino acid content differed significantly between leaf age cohorts. Plots differed notably in topsoil organic matter and soil nitrogen, but the plot with the poorest visual crown condition score had intermediate mean values for both soil properties within the ranges presented by the six plots. Overall, crown condition score was weakly negatively correlated with topsoil organic carbon and total nitrogen content. The unhealthiest plot also had the highest density of shrubby understorey. Site factors that could influence both the quantity and quality of foliage (e.g. free amino acid content) in eucalypt crowns, and hence the population dynamics of herbivorous insects and bell miners, are discussed in relation to *Eucalyptus saligna* crown decline.

Cunninghamia (2006) 9(4): 507–520

Introduction

Stand decline has been observed in Australian native forests and woodlands for many decades (e.g. Edgar et al. 1976; Landsberg & Wylie 1988). Awareness of the extent of eucalypt canopy decline in Australian native forests has increased considerably over recent years (e.g. Stone 1999, Old 2000, Jurskis 2005). Past studies have attempted to identify the causal agents or processes associated with eucalypt decline in native forests but with mixed success (Podger et al. 1980, Old 2000). Numerous factors, both biological and environmental, have been related to dieback but on their own usually do not account for all the observed variation associated with a particular decline syndrome. For example, both West (1979) and Podger (1981) presented strong circumstantial evidence of drought being a principal causal factor for stand death in Tasmanian eucalypt forests referred to as ‘regrowth dieback’. However, drought-affected trees in these forests were predisposed to defoliation by paropsine beetles and to root rot caused by *Armillaria* spp. (Kile 1974, 1980). In another series of Tasmanian studies (e.g. Ellis 1985; Ellis & Pennington 1989) the severity of the eucalypt dieback in high altitude *Eucalyptus delegatensis* forests was proposed to be related to the development of successional rainforest in the absence of fire.

There is currently debate about the causal factors of another form of eucalypt decline ‘Bellminer associated dieback’ (Wardell-Johnson et al. 2005). Eucalypt stands colonised by bell miners (*Manorina melanophrys*) often exhibit symptoms of crown decline (e.g. Clarke & Schedvin 1999; Jurskis & Turner 2002; Stone 2005). Bell miners are insectivorous, territorial birds that live in large colonies covering an area of several hectares (Clarke & Fitz-Gerald 1994). This eucalypt decline occurs most commonly in moist coastal forests, extending from southern Victoria to southern Queensland. While the actual extent of this dieback is unknown, numerous observations and regional surveys indicate that it is spreading (e.g. Stone et al. 1995; Jurskis 2005; Wardell-Johnson et al. 2005). Many thousands of hectares in the Northern Rivers and Upper North Coast regions of NSW have been identified as being affected by Bell miner associated dieback resulting in significant losses in biodiversity and productivity (Bell miner Associated Dieback Working Group, unpublished data, NSW Department of Environment). Colonisation by bell miners correlates with high densities of leaf damaging psyllids in eucalypt tree crowns (Loyn et al. 1983; Stone 1996; Clarke & Schedvin 1999). If bell miners are removed from a site, it is invaded by other insectivorous birds, and psyllid numbers decline, often resulting in tree crown recovery (Loyn et al. 1983). A reduction in psyllid numbers, however, does not

always lead to recovery of stand health (Clarke & Schedvin 1999). Eucalypts constantly replacing damaged leaf tissue deplete their reserves, are weakened and become more susceptible to secondary insect pests such as stem borers and fungal pathogens (e.g. Old et al. 1990). A stand of eucalypts colonised by bell miners for approximately 20 years did not recover upon their removal (Clarke & Schedvin 1999).

Jurskis and Turner (2002) have proposed a generic model of eucalypt dieback that includes stands colonised by bell miners. A central theme of their model is that recent changes in land management practices, particularly the exclusion of low intensity fire in forests and woodlands, has favoured the development of dense mesic understoreys. This results in increased rates of litter fall which changes the soil conditions and inhibits tree roots and mycorrhizae. They cite a series of studies that support their claim that these factors are likely to promote unhealthy roots, nitrification, insect damage to leaves and eucalypt dieback. Stone (1999), studying crown decline of *Eucalyptus saligna* colonised by bell miners, proposed that success and persistence of a bell miner colony may be related to site factors including the maintenance of high insect numbers in tree crowns as a food source, a dense understorey providing nesting sites, available drinking water, and a defensible territory. Processes that maintain these site factors therefore contribute directly to the success of the bell miner colonies, and hence the risk of persistent crown defoliation by larger populations of herbivorous insects.

Discussions on eucalypt forest decline have elements in common, but often lack consensus in the identification of factors that initiate the decline process. There may be several reasons for this apparent lack of consensus. Most studies on eucalypt decline (or dieback) have only considered some of the possible associated factors. This precludes quantitative syntheses such as meta-analyses of published studies, and limits reviews to narrative summaries (Bennett & Adams 2004). The majority of published studies have not been established as replicated field experiments with manipulated treatments that can be analysed to establish cause-effect relationships (Schreuder & Thomas 1991). Also native eucalypt forests span a large number of vegetation types (e.g. Forestry Commission of NSW 1989), varying considerably in species composition and structure and are inherently complex multi-tropic ecosystems that function across a range of temporal, spatial and organisational scales. Most published studies have not attempted to examine issues of physical and functional scale and how they inter-relate (e.g. leaf, crown, stand, landscape scales). The complex, yet finely balanced nature of native forests, and the differing approaches of investigation have contributed to a diversity of opinions and lack of consistent statistical evidence.

This study was a preliminary survey of some factors that have been implicated in Bell miner associated dieback, with the results to be used to design future studies in identifying cause and effect relationships across a range of scales. Six 20 m radius plots in a small moist sclerophyll forest were selected

(Fig. 1) with the criteria that the dominant overstorey species was *Eucalyptus saligna*, but otherwise they differed in terms of floristic composition, structure and crown condition (Figs. 2A – F, Table 1). Only one of the six plots was colonised by bell miners. Although this survey lacked appropriate replication to enable statistical comparisons between plots colonised by bell miners and non-colonised plots, it was possible to address the following questions: i) Is there an association between crown condition and plot vegetation?; ii) Does the incidence of the fungal pathogens *Armillaria luteobubalina* and *Phytophthora cinnamomi* differ between plots?; iii) Is there an association between crown condition and soil chemical properties?; iv) Does the suite of foliar insects on *Eucalyptus saligna* foliage differ between plots? and v) What correlations exist among a range of physical and chemical leaf traits measured from *Eucalyptus saligna* foliage sampled from each plot?

Methods

Study area and plot assessment

The study site was Cumberland State Forest (S.F.) (33°47'S, 150°58'E), Sydney, New South Wales (Fig. 1). The site consists of 39 ha of intensively managed regrowth forest

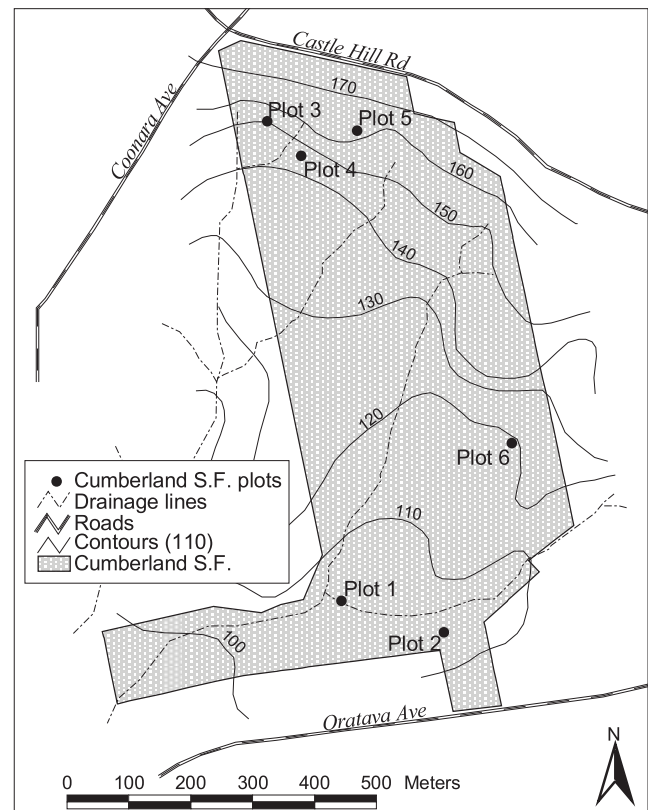


Fig. 1 Location of the six plots in Cumberland State Forest, Sydney.

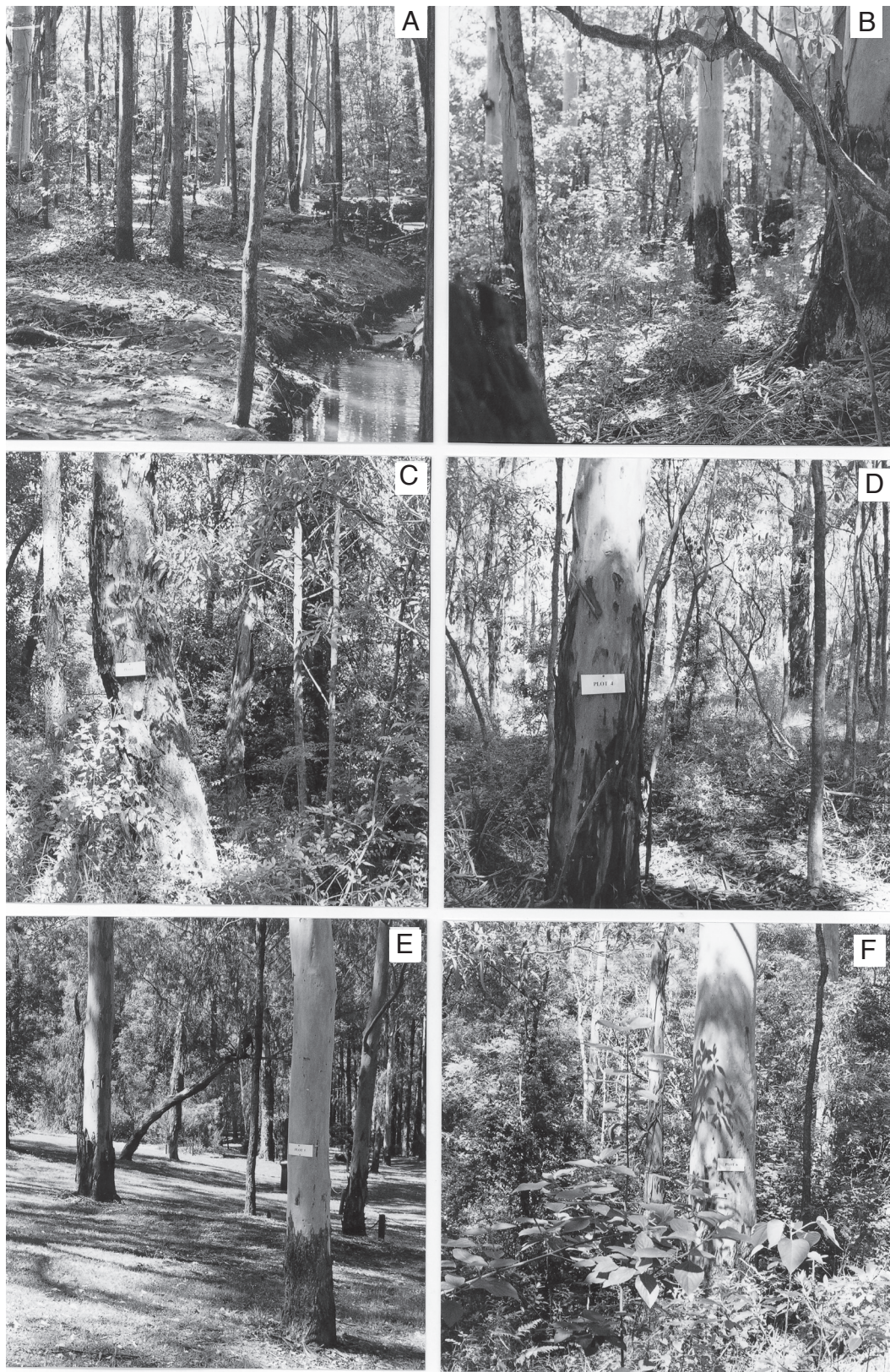


Fig. 2. Photographs illustrating the type of understorey present in each of the six plots in Cumberland State Forest: (A) plot 1, the creek plot; (B) plot 2, the mid slope plot; (C) plot 3, the bell miner plot; (D) plot 4, plot adjacent to the bell miner colony; (E) plot 5, the picnic area plot; (F) plot 6, the bird counts plot.

surrounded by suburban development and is used principally for recreation. In the early 1900s part of Cumberland S.F. was cleared for fruit tree orchards, but in the 1930s areas were allowed to regenerate or were replanted with eucalypts. Cumberland S.F. receives an average annual rainfall of approximately 1100 mm and moderate daily temperatures (January mean max. 29°C, min. 16°C; July mean max. 16°C, min. 5°C) (Forestry Commission of NSW 1984). Monthly rainfall records from 1970 to 2003 for Cumberland S.F. were used to calculate White's Moisture Stress Index (White 1986). Standard normal deviates of their long-term means (33 years) were calculated for the periods November to February and May to August.

Six plots, approximately 20 m radius in size were located in mixed-age, moist stands within Cumberland S.F. In the northern half of Cumberland S.F. the geology is Wianamatta group Ashfield Shale. Soils derived from this Shale are deep, red, podsollic soils of clay loam texture with heavy clay layers in the B horizons (Forestry Commission of NSW 1984). Plots 3, 4, 5 and 6 (Fig. 1) were located on this soil. The soils in the southern half are derived from a combination of Hawkesbury Sandstone and Ashfield Shale parent materials, the latter washed down from higher shale areas. They are yellow podsollic soils with a sandy loam texture still retaining reasonable structure (Forestry Commission of NSW 1984). Plots 1 and 2 were located on this soil (Fig. 1). The six plots were selected so as to represent a range of floristic composition and structures present in the forest (Figs. 2A–F). A common factor for all the plots was the presence of mature trees of *Eucalyptus saligna*. Other tree species present in the overstorey included *Eucalyptus pilularis*, *Eucalyptus paniculata* and non-eucalypt species such as *Pittosporum undulatum* and *Glochidion ferdinandi*. The understorey varied considerably because of manual weed control and control burning, and ranged from grass (*Microlaena stipoides*) that was regularly mowed, to dense mesic shrubs that included the exotic weeds *Lantana camara* and *Ligustrum* spp. (Table 1). The structure of the plots was further characterised by stem density (stems per ha) and mean stem diameter per plot. Small sections of the forest had been treated with hazard reduction burns in 1991, 1993 or 1994. Plots 3 and 6 were burnt in 1993 and plot 1 in 1994. Remnant earthworks very close to plot 3 were from a road built in 1987 and subsequently abandoned.

Bell miner colonies have been recorded in Cumberland S.F. for approximately 30 years and movements between locations within the forest have been observed. Some formerly densely populated areas, now no longer support bell miners. More recently bell miners have tended to remain in proximity to a large dam on the northwestern boundary of the forest (Ian Johnson, member of the Cumberland Bird Observers Club). Some of the remnant Sydney blue gum forest in the surrounding suburbs also supports bell miner colonies but these habitats are declining due to clearance for housing.

Structure and crown measurements

Within each of the six plots, five similar-sized, mature *Eucalyptus saligna* trees were randomly selected and labeled for assessment and foliage sampling. At the time of foliage assessment (May 2002), tree heights, diameters (over bark at breast height) and diameter increments (20 months after the initial measurement) were measured. Plot 3 was the only plot permanently colonised by bell miners. A further five *Eucalyptus saligna* trees per plot were selected in the two plots situated close to plot 3 (neither of which were colonised permanently by bell miners) and differing from one another in understorey composition (Figs. 1, 2D & 2E; Table 1). The remaining 3 plots (plot 1, plot 2 & plot 6) were located at least 500 m south of the northern cluster of 3 plots (Fig. 1). The crown condition of each of the five labelled *Eucalyptus saligna* per plot was assessed using the visual crown scoring system for eucalypts (in Stone et al. 2003–Appendix 2). To provide a relative comparison of bell miner numbers between plots, four ten-minute bird counts were undertaken at the centre of each plot during Spring 2001; Autumn 2002 and Spring 2003 using the 10 m concentric circle technique (Shields 1990). Data were only accepted to the 30 m radius circle.

Pathogen sampling

Four soil samples per tree per plot were tested for the soil-borne fungal pathogen *Phytophthora cinnamomi*. The presence of *Phytophthora cinnamomi* was determined in the laboratory by baiting water suspensions of each soil sample with highly susceptible lupin seedlings (Chee & Newhook 1965). Searches for basidiomes of *Armillaria luteobubalina*, which is known to occur in Cumberland S.F. (J. Simpson, unpublished data) were made of each plot in autumn and winter in 2002 and 2003. Stumps and the butts of any dead trees in each plot were examined for the characteristic mycelial fans of *Armillaria luteobubalina*.

Soil sampling

Topsoil samples were also obtained from each plot. After brushing away the surface litter a hand-held auger was used to obtain four volumetric samples, 15 cm deep and located 2 m from the base of each labelled *E. saligna*, at the cardinal points. The samples from near each tree were then bulked and mixed well, before a 500 gm sub-sample was placed, within 30 minutes and numbered of sampling, into a drying oven for 48 hours at 40°C. After air drying, the thirty soil samples were sent to the Victorian State Chemistry Laboratory for chemical analysis using standard procedures (T. Ives, Victorian Dept of Natural Resources & Environment, Werribee, *pers. comm.*; Rayment & Higginson 1992). The chemical properties assayed are listed in Table 4.

Table 1. Native and exotic plant species recorded in the six plots in Cumberland State Forest

	Ground covers	Shrubs	Trees	Exotics
Plot 1	<i>Adiantum aethiopicum</i> <i>Blechnum cartilagineum</i> <i>Calochlaena dubia</i> <i>Clematis aristata</i> <i>Eustrephus latifolius</i> <i>Hypolepis muelleri</i> <i>Lomandra mutiflora</i> <i>Microlaena stipoides</i> <i>Pandorea pandorana</i>	<i>Acmena</i> sp. <i>Clerodendrum tomentosum</i> <i>Cordyline stricta</i> <i>Lomandra</i> sp. <i>Morinda jasminoides</i> <i>Pittosporum revolutum</i> <i>Platycerium bifurcatum</i>	<i>Brachychiton</i> sp. <i>Eucalyptus saligna</i> <i>Eucalyptus pilularis</i> <i>Ficus coronata</i> <i>Glochidion ferdinandi</i> <i>Pittosporum undulatum</i> <i>Syncarpia glomulifera</i>	<i>Ligustrum lucidum</i> <i>Ligustrum sinense</i> <i>Rubus fruticosus</i> (exotics = 5% abundance)
Plot 2	<i>Adiantum aethiopicum</i> <i>Blechnum cartilagineum</i> <i>Clematis aristata</i> <i>Dianella</i> sp. <i>Dichondra repens</i> <i>Morinda jasminoides</i> <i>Oplismenus aemulus</i> <i>Pandorea pandorana</i>	<i>Pittosporum revolutum</i> <i>Pittosporum undulatum</i> <i>Polyscias sambucifolia</i>	<i>Eucalyptus saligna</i> <i>Eucalyptus pilularis</i> <i>Ficus coronata</i> <i>Glochidion ferdinandi</i> <i>Pittosporum undulatum</i>	<i>Ligustrum lucidum</i> <i>Ligustrum sinense</i> <i>Ochna serrulata</i> <i>Olea europaea</i> <i>Protasparagus aethiopicus</i> <i>Tradescantia albiflora</i> (exotics = 25% abundance)
Plot 3	<i>Cayratia clematidea</i> <i>Cissus</i> sp. <i>Dianella</i> sp. <i>Entolasia stricta</i> <i>Lomandra</i> sp. <i>Microlaena stipoides</i> <i>Morinda jasminoides</i> <i>Plectranthus parviflorus</i>	<i>Clerodendrum tomentosum</i> <i>Leucopogon juniperinus</i> <i>Omalanthus populifolius</i> <i>Ozothamnus diosmifolius</i> <i>Pittosporum revolutum</i> <i>Trema aspera</i>	<i>Acacia parramattensis</i> <i>Brachychiton</i> sp. <i>Eucalyptus paniculata</i> <i>Eucalyptus saligna</i> <i>Glochidion ferdinandi</i> <i>Pittosporum undulatum</i>	<i>Asparagus asparagoides</i> <i>Lantana camara</i> <i>Ligustrum lucidum</i> <i>Ligustrum sinense</i> <i>Rubus fruticosus</i> <i>Solanum mauritianum</i> (exotics = 40% abundance)
Plot 4	<i>Adiantum aethiopicum</i> <i>Clematis aristata</i> <i>Echinopogon ovatus</i> <i>Eustrephus latifolius</i> <i>Lomandra longifolia</i> <i>Pandorea pandorana</i> <i>Pteridium esculentum</i>	<i>Pittosporum revolutum</i>	<i>Eucalyptus pilularis</i> <i>Eucalyptus punctata</i> <i>Eucalyptus saligna</i> <i>Pittosporum undulatum</i>	<i>Asparagus asparagoides</i> <i>Ehrharta erecta</i> <i>Lantana camara</i> <i>Nephtolepis cordifolia</i> <i>Protoasparagus aethiopicus</i> <i>Rubus fruticosus</i> <i>Solanum mauritianum</i> (exotics = 15% abundance)
Plot 5	<i>Microlena stipoides</i>	<i>Acmena smithii</i>	<i>Acacia</i> sp. <i>Eucalyptus pilularis</i> <i>Eucalyptus saligna</i>	<i>Cynodon dactylon</i> <i>Ehrharta erecta</i> <i>Pennisetum clandestinum</i> (exotics = 80% abundance)
Plot 6	<i>Adiantum aethiopicum</i> <i>Clematis glycinoides</i> <i>Commelina cyanea</i> <i>Dichondra repens</i> <i>Hypolepis muelleri</i> <i>Lomandra longifolia</i> <i>Pteridium esculentum</i>	<i>Breynia oblongifolia</i> <i>Omalanthus populifolius</i> <i>Pittosporum revolutum</i>	<i>Alphitonia excelsa</i> <i>Angophora costata</i> <i>Eucalyptus pilularis</i> <i>Eucalyptus saligna</i> <i>Pittosporum undulatum</i>	<i>Araujia sericifolia</i> <i>Asparagus asparagoides</i> <i>Lantana camara</i> <i>Ligustrum sinense</i> <i>Ochna serrulata</i> <i>Protoasparagus aethiopicus</i> <i>Rubus fruticosus</i> <i>Sonchus oleraceus</i> (exotics = 25% abundance)

Leaf assessments

In May 2002, two upper crown branches were randomly selected from each tree and brought down with a pole-mounted slingshot (Big Shot: Jameson Corporation, Clover, South Carolina, USA). The labelled branches were taken immediately to a laboratory within Cumberland S.F. for leaf assessment. Three distinct leaf age cohorts, described as young, mature and old, were identified. The dominant leaf age cohort was the mature leaf age class, being fully expanded and initiated in the current season. The assessments of leaves from this leaf age cohort were used for comparisons of all the morphological, damage and physiological leaf traits except for free amino acid content in which the young leaf age cohort was also assayed. All measurements were based on a random sample of 20 mature leaves per branch ($n = 200$ per plot). A total of 556 young leaves were assayed for free amino acid content.

Initially, a measure of photosynthetic capacity was obtained by measurements of F_v/F_m , the ratio of variable fluorescence to maximum chlorophyll fluorescence, using a portable chlorophyll fluorometer (Fluorescence Induction Monitor 1500: ADC BioScientific Ltd, UK). One leaf clip was applied randomly on the leaves for 15-min dark adaptation while still attached to the branches that were standing upright in buckets of water. A SPAD chlorophyll meter (model 502, Minolta Co., Ltd, Tokyo, Japan) was used to obtain a unitless relative measure of chlorophyll concentration (an index from 0 to 1.0) from the same leaves used for the F_v/F_m measurements (Stone et al. 2005). These leaves were cut from the branches and the amount of leaf tissue with damage attributed to fungi visually estimated for each leaf according to the following sigmoid scale classification: 0; 1–5; 6–10; 11–20; 21–50;

51–90; 91–95 and 96–100% (e.g. Horsfall & Barratt 1945) and then ranked from 0 to 7 corresponding to the estimated percentage classification. For example, an estimate of 10 to 20 percentage leaf tissue damaged would receive a score of 3. Any damage that was attributed to feeding by the psyllid *Glycaspis baileyi* was scored separately usually the same scoring method as for fungal damage. This species was the most abundant damage-causing agent present on the foliage sampled. The 20 leaves per branch were then photocopied and the images used to measure total leaf length; the ratio of maximum potential length along the midrib to maximum breadth and percentage leaf area missing because of insect herbivory, with a hand-held digital planimeter (Planinx7: Tamaya Technics Inc., Tokyo, Japan).

After being photocopied, the leaves of the young and mature age cohorts (Plots 3, 4, 5 and 6 only) were used for analysis of free hexose and total free amino acids content. A 10 mm diameter disc of tissue was obtained with a leaf punch from each leaf, avoiding the leaf midvein. The small leaf discs from each branch were placed into cryogenic vials, snap frozen in liquid nitrogen before transferal to a -80°C freezer. The material was ground in liquid nitrogen and extracted with 80% ethanol in a mortar and pestle. The extract was boiled for 30 minutes at 80°C before being centrifuged for five minutes. The supernatants were collected and the pellet re-extracted twice more. A sample of pooled supernatants was used to determine free amino acid concentration using the ninhydrin method of Moore & Stein (1948) using arginine to calibrate the test. Free hexoses were analysed as a measure of total soluble sugars using the anthrone method of Fales (1951). Glucose was used to calibrate the test. The ratio of free hexose to amino acid concentration was then calculated.

Table 2. Mean plot variables and tree-scale traits (mean \pm standard deviation) from five mature *Eucalyptus saligna* per plot in sites in Cumberland State Forest presenting a range of crown dieback symptoms.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Plot variables						
Stem per ha [†]	2399	1807	4339	1977	169	3675
Mean stem diameter (cm) [†]	13.3 \pm 2.2	12.6 \pm 2.9	4.6 \pm 0.9	8.8 \pm 2.0	30.8 \pm 10.1	5.9 \pm 0.9
Presence of <i>Phytophthora cinnamomi</i> at base of tree [‡]	0.4 \pm 0.5	0.4 \pm 0.9	2.2 \pm 1.3	2.2 \pm 0.8	0.0 \pm 0.0	1.2 \pm 0.8
Tree traits from the five mature <i>Eucalyptus saligna</i>						
Height (m)	37.9 \pm 7.6	36.2 \pm 2.2	28.6 \pm 4.7	31.6 \pm 3.7	34.4 \pm 4.3	30.5 \pm 2.5
Diameter over bark at breast height (cm)	57.3 \pm 12.5	55.9 \pm 11.5	53.3 \pm 6.9	54.1 \pm 10.1	62.6 \pm 18.5	49.4 \pm 8.4
Diameter increment over 20 months, (cm)	1.7 \pm 0.2	1.7 \pm 0.7	-0.20 \pm 0.9	0.9 \pm 0.5	1.4 \pm 0.8	0.5 \pm 0.3
Tree Crown Condition Score*	13.9 \pm 0.9	12.9 \pm 1.1	7.5 \pm 1.4	12.3 \pm 0.5	14.6 \pm 0.5	11.4 \pm 1.3

[†] All stems diameters over 2.0 cm at DOBBH were measured irrespective of plant species

[‡] Maximum detection score = 5.0; four soil samples per tree per plot, five trees per plot

* Crown condition was visually assessed using the crown scoring system for eucalypts presented in Stone *et al.* (2003, Appendix 2). Higher values indicate healthier crowns

Correlations among the soil, tree and leaf variables were examined by computing either Pearson's correlation coefficients (r) or Spearman rank correlation coefficients (r_s) depending on the normality of each attribute using the Corr Procedure in SAS System for Windows (SAS Institute Inc. 1987).

Results

Moisture content of the topsoil was not measured but during the first five months of 2002, Cumberland S.F received 550 mm of rainfall which is half the mean annual rainfall. White's Moisture Stress Index (MSI) calculated for the years 2001 and 2002 gave values of -1.67 and -1.87 respectively. High positive values of this index indicate a season of stressful weather; relatively large negative values signify an absence of stressful weather (White 1986). The most stressful year prior to this was 1997 with a value of $+2.01$; MSI values gradually declined over the next 5 years.

Structure and crown measurements

Stands dominated by *Eucalyptus saligna* exhibit a range of floristic structure and condition (Fig. 2A–F, Tables 1 and 2). Plot 1 with the tallest *Eucalyptus saligna* trees and healthy crowns (Table 2) was in a site subjected to a hazard reduction burn 20 years previously, and that can become briefly inundated during high rainfall events. Compared to the other plots, it possessed a relatively dense overstorey but there was little ground cover or lower midstorey present (Fig. 2A). In Plot 2, located 200 metres east of plot 1 at slightly higher elevation, the *Eucalyptus saligna* crowns were of moderate condition, but the stems were gaining increment at a similar rate as trees in plot 1 (Table 2). The density of overstorey trees was lower than plot 1 and a more pronounced midstorey existed (Fig. 2B). Bell miners were not recorded in any of the three southern plots (plots 1, 2 and 6, Table 3).

The *Eucalyptus saligna* trees in plot 3, the only plot permanently colonized by bell miners, were in the poorest condition (Table 2) and several dead trees of *Eucalyptus saligna* and *Eucalyptus paniculata* were observed in the plot. The high stem density was due to a dense mid-storey dominated by exotics including lantana (Table 1, Fig. 2C)

and the plot included an area that had been subjected to a low intensity fire in 1993. In Plot 4, approximately 100 m downslope from Plot 3, the *Eucalyptus saligna* crowns were of moderate condition but no dead trees were present (Table 2). The midstorey was less mesic than the understorey in plot 3 (Table 1) and of lower density, due in part to the selective, manual removal of *Pittosporum revolutum*. Bell miners were observed to fly occasionally into plot 4 from the adjacent area, that included plot 3, but during the 3 years of bird counts, had not been observed to nest in plot 4 (Table 3). Plot 5, the third plot comprising the northern cluster of plots, differed significantly from the others in several ways. A midstorey was non-existent and groundcover was dominated by exotic grasses (Fig. 1E). There was a relatively low density of mature *Eucalyptus saligna* and all five crowns were assessed as very healthy (Table 2). Occasionally a few bell miners would fly over from the area of plot 3 and then return (Table 3). Plot 6 was located on the south-western side of Cumberland S. F. It was similar to Plot 3 in having a relatively dense midstorey (Fig. 1F) and the area had been burnt in 1993. The *Eucalyptus saligna* crowns were of moderate condition (Table 2). No bell miners were observed in the stand during the 3 year bird count survey.

Pathogens

Phytophthora cinnamomi was detected in some soil samples from all plots, except plot 5 (Table 2). All the isolates were A2 mating type. Trace levels of *Phytophthora cinnamomi* were detected in plots 1 and 2, while plots 3 and 4 had the highest detected levels (Table 2). No evidence of infection of trees or stumps by *Armillaria luteobubalina* was found in any of the plots.

Comparison of soil variables between plots

The topsoil samples from each plot was moderately acidic and did not differ noticeably with respect to pH (water), electrical conductivity, and total soluble salts (Table 4). Plot 5, the only plot without a midstorey component (Fig. 1E), had notably less organic matter and oxidisable organic matter in the topsoil than the other five plots. The mean percent of total nitrogen (w/w) ranged from 0.17 in plot 1 to 0.35 in plot 6. The plots differed noticeably in the carbon/nitrogen

Table 3. Bell miner bird counts in Cumberland State Forest. Birds counts from 0.28 ha circular plots, converted to average bird counts per ha. Range in brackets.

Bell miner counts	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Spring 2001	0	0	82 (106 – 71)	13 (0 – 21)	N.A .	0
Autumn 2002	0	0	88 (124 – 74)	21 (0 – 32)	4 (0 – 7)	0
Spring 2003	0	0	94 (134 – 74)	11 (0 – 18)	2 (0 – 4)	0

Table 4. Selected soil chemical properties (means \pm standard deviation) of the topsoil (0-15 cm) from near the base of five mature *Eucalyptus saligna* in six plots presenting a range of crown symptoms in Cumberland State Forest.

Soil properties	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
pH (water)	5.68 \pm 0.19	5.02 \pm 0.23	5.54 \pm 0.28	5.46 \pm 0.26	5.84 \pm 0.11	5.38 \pm 0.14
Electrical conductivity (dS/m)	0.064 \pm 0.004	0.062 \pm 0.004	0.067 \pm 0.015	0.074 \pm 0.005	0.072 \pm 0.005	0.080 \pm 0.007
Total soluble salts (%w/w)	0.02 \pm 0.0	0.02 \pm 0.0	0.024 \pm 0.005	0.024 \pm 0.005	0.022 \pm 0.004	0.028 \pm 0.004
Organic matter (%w/w)	8.20 \pm 0.78	12.42 \pm 2.85	7.80 \pm 1.91	3.94 \pm 3.40	1.52 \pm 0.35	3.62 \pm 3.51
Oxidisable organic carbon (% w/w)	4.32 \pm 0.18	6.50 \pm 1.40	4.10 \pm 1.01	2.06 \pm 1.79	0.78 \pm 0.19	1.89 \pm 1.84
Total nitrogen (% w/w)	0.17 \pm 0.03	0.25 \pm 0.04	0.26 \pm 0.06	0.24 \pm 0.03	0.24 \pm 0.05	0.35 \pm 0.02
Carbon/Nitrogen ratio	26.4 \pm 4.5	25.7 \pm 2.5	15.7 \pm 1.2	8.4 \pm 7.2	3.5 \pm 1.2	5.7 \pm 6.2
Exchangeable calcium (meq/100g)	2.94 \pm 1.51	2.16 \pm 0.86	2.48 \pm 1.21	3.00 \pm 0.72	5.74 \pm 0.59	3.14 \pm 0.53
Exchangeable magnesium (meq/100g)	3.40 \pm 0.75	1.94 \pm 0.44	3.32 \pm 0.86	3.16 \pm 0.3	3.68 \pm 0.694	3.56 \pm 0.49
Exchangeable sodium (meq/100g)	0.26 \pm 0.04	0.16 \pm 0.02	0.28 \pm 0.07	0.33 \pm 0.06	0.26 \pm 0.05	0.43 \pm 0.05
Exchangeable potassium (meq/100g)	0.42 \pm 0.07	0.39 \pm 0.03	0.62 \pm 0.23	0.55 \pm 0.06	0.72 \pm 0.15	0.53 \pm 0.07
Sum of the 4 cations (meq/100gm)	7.08 \pm 2.17	4.68 \pm 1.31	6.76 \pm 2.14	7.08 \pm 0.93	10.36 \pm 2.12	7.70 \pm 1.12
Calcium/Magnesium ratio (meq/100gm)	0.86 \pm 0.35	1.12 \pm 0.19	0.78 \pm 0.25	0.98 \pm 0.19	1.58 \pm 0.19	0.92 \pm 0.08

Table 5. Mean leaf-scale traits (mean \pm standard deviation) measured from foliage of five mature *Eucalyptus saligna* per plot in Cumberland State Forest presenting a range of crown dieback symptoms.

$n = 200$ for variables measured from six plots and $n = 40$ for variables measured from four plots. All leaves of similar age being mature and initiated in the current growing season.

Fungal damage score and *Glycaspsis* damage score: 0% leaf area affected = 0; 1-5% = 1, 6-10% = 2, 10-20% = 3, 20-50% = 4, 50-90% = 5; 91-95% = 6, 96 - 100% = 7

Leaf traits	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Morphological variables						
Total length (mm)	159.3 \pm 1.6	121.8 \pm 2.1	110.7 \pm 2.4	117.0 \pm 2.0	131.9 \pm 2.4	143.5 \pm 2.6
Ratio of max. leaf length to max. leaf breadth	5.7 \pm 0.1	3.4 \pm 0.1	3.2 \pm 0.08	3.4 \pm 0.07	4.4 \pm 0.08	4.3 \pm 0.08
Total potential leaf area (cm ²)	29.9 \pm 0.58	31.5 \pm 0.75	28.6 \pm 0.77	30.2 \pm 0.75	27.8 \pm 0.71	36.7 \pm 2.10
Damage variables						
Percentage leaf area missing due to insect herbivory	0.9 \pm 2.1	3.2 \pm 5.4	2.2 \pm 5.1	5.0 \pm 7.5	2.7 \pm 4.9	2.4 \pm 3.9
Fungal damage score	0.21 \pm 4.3	0.34 \pm 0.59	0.15 \pm 0.48	0.29 \pm 0.59	0.28 \pm 0.42	0.32 \pm 0.56
<i>Glycaspsis</i> damage score	0.0	0.0	2.3 \pm 0.8	0.0	0.0	0.0
Physiological variables						
Relative measure of chlorophyll content (SPAD) values)	46.3 \pm 4.1	44.4 \pm 3.5	41.1 \pm 4.8	46.4 \pm 5.3	47.0 \pm 3.3	48.3 \pm 3.8
Ratio of variable to maximum chlorophyll fluorescence (Fv/Fm)	0.83 \pm 0.01	0.83 \pm 0.01	0.81 \pm 0.03	0.83 \pm 0.02	0.84 \pm 0.01	0.84 \pm 0.01
Free Hexose (mg Hexose g Leaf Dry Weight ⁻¹)			7.5 \pm 4.8	9.4 \pm 5.0	8.3 \pm 3.3	9.7 \pm 2.2
Free amino acids (mg amino acids g LDW ⁻¹)			57.9 \pm 31.5	38.0 \pm 27.1	20.4 \pm 13.2	12.0 \pm 4.7

(C/N) ratio of the topsoil (Table 4). Plots 1 and 2 had much higher C/N ratios than plots 4, 5 and 6. Plot 3, the plot with the visually unhealthiest *Eucalyptus saligna* crowns had a mean C/N of 15.7 which is in the mid range of values (3.48 to 26.4). Crown condition scores were weakly negatively correlated with both higher topsoil organic C content (%w/w) ($r_s = -0.37$, $P = 0.034$, $n = 30$) and total N ($r_s = -0.34$, $P = 0.064$, $n = 30$) and not correlated to the C/N ratio.

The soil samples from the six plots did not differ notably in cations; calcium, magnesium, sodium, and potassium, except that plot 5 had more exchangeable calcium than the other plots. Correlations based on rank scores, were significant between tree crown condition score and the topsoil sampled at the base of each tree for pH ($r_s = 0.55$, $P = 0.002$, $n = 30$), calcium content (meq/100g) ($r_s = 0.392$, $P = 0.032$, $n = 30$); and the calcium/magnesium ratio ($r_s = 0.51$, $P = 0.004$, $n = 30$), however, examination of the individual scatterplots revealed high variation associated with these trends.

Comparison of leaf-scale traits

Mature leaves from plots 5 and 1 were the most lanceolate in shape with larger leaf length to breadth ratios, while the leaves from unhealthy trees in plot 3 were the broadest in shape (Table 5). All leaves sampled had relatively low levels of tissue damage from fungal infections or insect herbivory. Damage by species of *Mycosphaerella* and their anamorphs, and other Ascomycota were negligible (Table 5). Leaves from plot 1 had virtually no insect damage while leaves from plot 4 had, on average, approximately 5% leaf area missing (Table 5). The exception was the impact of the sap-sucking psyllid, *Glycaspis baileyi*, on leaves of *Eucalyptus saligna* trees in plot 3. The twenty mature leaves per branch assessed had approximately 10% leaf tissue damaged from *Glycaspis* feeding. Leaves from plot 3 also had the lowest relative chlorophyll content (SPAD units) and values of the chlorophyll fluorescence parameter F_v/F_m (Table 5). Not surprisingly, both relative chlorophyll content and chlorophyll fluorescence were significantly correlated with *Glycaspis* score ($r = -0.742$ and -0.740 , $P < 0.001$). These two photosynthetic leaf traits were also significantly correlated with leaf shape (length / breadth ratio) ($r = 0.508$ and 0.467 , $P < 0.01$). When all leaves infested with *Glycaspis* were removed from the data set, a similar relationship remained but was weaker ($r = 0.35$ and 0.29 , $P > 0.05$).

The foliar content of soluble sugars, as measured by free hexoses, did not differ much between plots 3, 4, 5 and 6 though there were large differences in free amino acid content among these plots (Table 5). Leaves from plot 3 had the highest mean content of free amino acids while leaves from plot 6 had the lowest (Table 5). Both free amino acid content and the ratio of free hexose to free amino acids were significantly correlated to relative chlorophyll content ($r = -0.810$ and 0.755 respectively, $P < 0.001$). These two chemical leaf variables were also significantly correlated with *Glycaspis* score ($r_s = 0.650$ and -0.660 respectively,

$P < 0.001$). When leaves infested with *Glycaspis* were removed from the data set, this relationship was still significant ($r_s = -0.682$ and 0.582 , $P < 0.01$). This trend appears to exist across all leaves sampled and not just leaves affected by *Glycaspis* feeding. The presence of *Glycaspis* seems to strengthen the relationship between increasing free amino acid content with decreasing chlorophyll content (SPAD units). There was also a significant negative correlation between leaf shape (leaf length and leaf length to breadth ratio) and free amino acid content. Leaves lanceolate in shape had less free amino acid content than shorter and or rounder leaves (while for chlorophyll content the reverse was true). This trend is maintained in the absence of *Glycaspis* but is statistically weaker. The mean free amino acid content of all leaves sampled and classed as young leaves was higher (40.7 ± 12.9 mg amino acids g LDW⁻¹) (mean \pm standard deviation) than the mean free amino acid content of the mature leaves sampled (31.7 ± 25.8 mg amino acids g LDW⁻¹).

Discussion

The bell miner plot (plot 3) had *Eucalyptus saligna* crowns in the poorest condition and negative stem diameter increments for some trees indicated that they were dying. Plot 3 also had a dense mesic understorey dominated by exotic species including lantana, though lantana was also present in plots 4 and 6, but not to the same extent as in plot 3, because of manual weed removal. Although plot 5 was near plot 3, and occasionally frequented by the bell miners, the *Eucalyptus saligna* trees in this plot were healthy, but as this site was maintained as a picnic site a midstorey did not exist. Using data from a survey of eucalypt crown dieback in north-eastern NSW, Stone et al. (1995) concluded that although lantana was commonly correlated with the presence of bell miners there was not a linear trend, and bell miners appeared to prefer a dense shrubby understorey for nesting sites, irrespective of plant species composition (Stone 2005). Lantana prefers warm, moist sites with partial shade or patchy sunlight (Swarbrick et al. 1998), and under these conditions can dominate the understorey and suppress regeneration of native plant species. While lantana may not be a primary causal factor initiating dieback of *Eucalyptus saligna*, it can persist in the presence of this crown syndrome.

Pathogens

The soil-borne pathogen *Phytophthora cinnamomi* was isolated from all plots except plot 5. Hundreds of native plant species are known to be susceptible *Phytophthora cinnamomi* (Shearer & Smith 2000), and within *Eucalyptus*, species of *Monocalyptus* tend to be the most susceptible, though *Eucalyptus saligna* is generally regarded as relatively resistant (Tippett et al. 1985; Gerrettson-Cornell 1973). Nevertheless, the susceptibility of unhealthy *Eucalyptus saligna* to infection from *Phytophthora cinnamomi* is likely to be greater than that of healthy trees (Gerrettson-Cornell

1973). Several studies have demonstrated a strong relationship between the distribution of *Phytophthora cinnamomi* and soil moisture (e.g. McDougall et al. 2002) with the fungus being difficult to isolate during dry conditions. The site distribution of *Phytophthora cinnamomi* is therefore influenced by factors such as drainage, as well as the presence of susceptible hosts (e.g. Marks et al. 1975). *Armillaria luteobubalina* was not detected in any of the plots.

Soil factors

A comparison of the chemical properties of the topsoil of the Hawkesbury Sandstone (plots 1 and 2) with Ashfield Shale soils (plots 3, 4, 5 and 6) did not reveal noticeable differences, except perhaps the slightly lower mean calcium content for the plots on sandstone. Other factors that could contribute to the observed variation in organic carbon and nitrogen content of the topsoil in Cumberland S.F. include nutrient run-off from neighbouring urban properties and roads, soil disturbance through regular but patchy weed management, and changes in the composition of the understorey (e.g. Granger et al. 1994). Hazard reduction burns in plots 1, 3 and 6 were done approximately 8 years before plot assessment but the residual effects from these low intensity burns are assumed to be minimal.

In general, crown condition scores were weakly negatively correlated with topsoil organic C content and total N. The *Eucalyptus saligna* trees in plot 1 (the creek plot) were relatively healthy (high crown condition scores), even though the plot was occasionally inundated after heavy rain. Nor did these trees appear to be limited by the lowest mean total N content recorded from the six plots. The only plot without a distinct midstorey, plot 5, also had healthy *Eucalyptus saligna* trees; it also had the lowest organic matter and percent carbon in the topsoil among the six plots.

Numerous published studies have demonstrated that concentration of ammonium nitrogen in the topsoil can be promoted by fire (e.g. Polglase et al. 1986; Weston & Attiwill 1990; Neave & Raison 1999) but this effect is only temporary due to rapid immobilisation of ammonium (and nitrate) by soil microfauna over several months (e.g. Adams & Attiwill 1986; Weston & Attiwill 1990). It is this period after a fire that allows for the rapid establishment of ammonium assimilating eucalypt species, providing other site factors, including adequate soil moisture, sunlight and viable seed, are non-limiting (e.g. King 1985; Nicholson 1999). Frequent low-intensity fires could result in replacing a mesic understorey with fire-tolerant species producing litter of higher C/N ratios (e.g. Guinto 2001) and reduced soil moisture (e.g. York 1999). These soil conditions might promote the ammonifying heterotrophic component of the soil microflora, and thereby provide a competitive advantage to eucalypt species that assimilate ammonium nitrogen over nitrophilic species, but these assumptions require further examination.

Leaf scale relationships

Tissue damage on individual mature leaves was relatively low (cf. Stone 1996) except on leaves from *Eucalyptus saligna* in the plot colonised by the bell miners (plot 3). These leaves were heavily infested with the lerp-forming psyllid *Glycaspis baileyi*. *Glycaspis* species are phloem feeders and initiate their feeding sites on developing leaf flush which are photosynthetic sinks (Woodburn & Lewis 1973). The reddish – purple discolouration associated with *Glycaspis baileyi* feeding is due to localised accumulation of anthocyanins that has been linked to photoinhibition (Close et al. 2003) arising from impairment of the photosynthetic apparatus in tissue damaged by psyllid feeding. This relationship was supported in this study by the significant linear correlations between the damage score for *Glycaspis* and relative chlorophyll content (SPAD units) and photosynthetic efficiency (F_v/F_m) measured from the mature foliage. The broader shape of the mature leaves from plot 3, compared to the other plots, is indicative of replacement foliage, which for some eucalypt species, has been shown to have chemical and physical characteristics more in common with immature leaves than mature foliage (e.g. Landsberg 1990).

Phloem feeders obtain their nitrogen nutrition from free amino acids, amides and small polypeptides (Brodbeck & Strong 1987). Assays of total nitrogen do not indicate the nutritional quantity for phloem feeders because total nitrogen also includes compounds, such as insoluble proteins and nitrogen-based secondary compounds of little nutritional value to these insects (Mattson 1980). The mature leaves sampled from plot 3 had higher mean concentrations of free amino acids than similar aged foliage from plots 4, 5 and 6. The observed negative correlation between foliar chlorophyll content and free amino acids appeared to be strengthened by *Glycaspis* feeding.

In addition to localised cellular damage associated with insect feeding (e.g. Taylor 1997), other processes have been identified as influencing the soluble nitrogen content of leaves in tree crowns including: leaf age; environmental stresses, and soil nutrition (e.g. Stewart & Larher 1980; Brodbeck & Strong 1987; Adams & Atkinson 1991; Adams et al. 1995; Marsh & Adams 1995). This study demonstrated that, on average, younger leaves had a higher free amino acid content than mature leaves. Other studies have also shown younger eucalypt foliage to have a higher free amino acid content and lower chlorophyll content than mature leaves (Journet & Cochrane 1978; Adams et al. 1995; Taylor 1997; Choinski et al. 2003; Stone et al. 2005). Younger eucalypt foliage also has lower specific leaf weight (dry wt per unit area) compared to mature foliage, and hence is more palatable to insect leaf chewers, such as chrysomelid larvae (e.g. Ohmart 1991; Steinbauer 2001; Lawrence et al. 2003).

Most eucalypt species have seasonal patterns of new leaf production, but many are also opportunistic, responding

quickly to improved conditions, for example, a rainfall event. A flush of new foliage (epicormic growth) can also be initiated after rapid defoliation from an outbreak of insects (e.g. cup moths *Doratifera* spp.). Epicormic refoliation is also a common response after crown damage from drought, fire or frost (e.g. Gill 1997). *Glycaspis baileyi* is a multivoltine insect having six or seven generations per year (Moore 1961), and has the capacity to respond quickly to altered crown phenology such as a foliar flushing event. White (1971) observed that female *Glycaspis brimblecombei* females usually, but not always, lay their eggs on soft young leaves that are still expanding.

Increased leaf production can also be induced by increased irradiation penetration of the canopy, through windthrow, selective logging or edge effects from roads or rural clearings. Leuning *et al.* (1991) observed that foliar nitrogen is distributed within *Eucalyptus grandis* crowns according to the prevailing light environment. This is because eucalypt foliage receiving high irradiation has greater photosynthetic capacity and hence higher nitrogen content than shaded leaves (Leuning *et al.* 1991; Sands 1996). Medhurst (2000) and Pinkard *et al.* (1998) demonstrated that thinning of *Eucalyptus nitens* plantations improved irradiation penetration to the lower leaves of tree crowns, and this in turn, resulted in the initiation of more leaves over a greater area of the crown (i.e. increased tree leaf area).

Numerous studies have also reported the positive response by herbivorous insects to the sun-lit portions of tree crowns. White (1970), for example, reported that although eggs of the psyllid *Cardiaspina densitexta* were laid on the lower shaded side of individual leaves of *Eucalyptus fasciculosa*, greater numbers of eggs were laid on the northern side of tree crowns compared to the southern side. Populations of the aphid, *Essigella californica*, were found to be significantly higher on the upper crowns of trees growing on north-facing sunny aspects in comparison of other aspects (Appleton *et al.* 2003). Therefore eucalypt tree crowns responding to increased penetration of sun light into the canopy would possess a greater proportion of expanding foliage favourable to psyllids, as well as many leaf chewing insects (Ohmart 1991) compared to more shaded crowns. Medhurst (2000) demonstrated that the enhanced photosynthesis in the mid and lower sections of the *Eucalyptus nitens* crowns disappeared after canopy closure.

Stressful environmental processes have been shown to also influence the physiological function of leaves. Numerous definitions of plant stress have been proposed (e.g. Jones & Jones. 1989). Waring (1991) examined plant stress in terms of damaging processes or agents causing a reduction in photosynthetic CO₂ assimilation. While one indicator of reduced photosynthesis is the reduction in foliar production (e.g. Whitehead & Beadle 2004), another is the mobilisation of soluble nutrients including free amino acids (Brodbeck &

Strong 1987). In our study, the White's Moisture Stress Index values indicated that the trees in Cumberland S.F. were not under soil moisture stress at the time of plot assessment in 2002, but would have suffered moisture stress in 1997 (stress index = +2.01).

Conclusions

The data from this survey supports the findings of others (e.g. Loyn *et al.* 1983; Stone 1996; Clarke & Schedvin 1999) of a strong association between the presence of bell miners, leaf damage from sap-sucking insects, and eucalypt crown decline. Conditions that contribute to the success of bell miner colonies also directly or indirectly contribute to this form of crown decline. This study has also demonstrated a correlation between psyllid population levels and foliage condition, including the phenology and nutritional status of the leaves. Clarke and Schedvin (1999) reported that bell miners were capable of re-establishing a small colony before psyllid numbers had risen to high levels, and that after bell miners had gained control of the site again, psyllid numbers rose substantially. Nevertheless, it is assumed that newly-founded colonies would benefit if the tree crowns had the initial capacity to carry high populations of herbivorous insects. Site factors that might improve both the quantity and quality of available foliage, to which populations of herbivorous insects would respond, have been discussed. Controlled experimental field studies are now required to confirm and quantify the influence of these factors on the initiation and maintenance of bell miner associated dieback. Further studies are also needed on the effects of *Phytophthora cinnamomi* on growth and vigour of mature *Eucalyptus saligna* trees in the presence or absence of bell miner colonies.

Acknowledgements

We thank Grahame Price and Darren Waterson (NSW DPI Science & Research), and Amelia Jones (Forests NSW) for their technical assistance. The plot bird counts were done by Matthew Stanton (NSW DPI Science & Research) and leaf analysis for free hexose and amino acid concentrations undertaken by Matthew Searson (University of Western Sydney). Their contribution to this study is appreciated. John Raison (CSIRO FFP), Lorraine Spohr (NSW DPI Science & Research) and Ross Florence provided comments that improved this manuscript. The chemical soil analysis was done at the Victorian State Chemistry Laboratory, Dept. of Natural Resources & Environment, Werribee. Financial support for the soil and foliar analyses was provided by the Cumberland S.F. management unit and Baulkham Hills Shire Council is gratefully acknowledged.

References

- Adams, M.A. & Atkinson, P.I. (1991) Nitrogen supply and insect herbivory in eucalypts: the role of nitrogen assimilation and transport processes. In: *Productivity in perspective. Proceedings Third Australian Forest Soils and Nutrition Conference* (ed. P.J. Ryan). pp. 67–75. (Forestry Commission of NSW: Sydney)
- Adams, M.A. & Attiwill, P.M. (1986) Nutrient cycling and nitrogen mineralization in eucalypt forests of south-eastern Australia. II Indices of nitrogen mineralization. *Plant Soil* 92: 341–362.
- Adams, M.A., Attiwill, P.M. & Wang, L.M. (1995) Effects of phosphorous supply on growth and nitrogenous fractions in xylem sap and foliage of *Eucalyptus regnans* (F.Muell.), *E. nitens* (Maiden) and *E. globulus* (Labill.) seedlings: implications for herbivory. *Trees* 9: 324–331.
- Appleton, C., Gresham, B.A. & Zydenbos, S.M. (2003) Monitoring *Essigella californica* populations in Bay of Plenty forests. *New Zealand Plant Protection* 56: 45–50.
- Bennett, L.T. & Adams, M.A. (2004) Assessment of ecological effects due to forest harvesting: approaches and statistics issues. *Journal of Applied Ecology* 41: 585–598.
- Brodbeck, B. & Strong, D. (1987) Amino acid nutrition of herbivorous insects and stress to host plants. In: *Insect outbreaks* (eds. P. Barbosa & J.C. Schultz). pp. 347–363. (Academic Press Inc.: San Diego)
- Chee, K.H. & Newhook, F.J. (1965) Improved methods for use in studies on *Phytophthora cinnamomi* Rands and other *Phytophthora* species. *New Zealand Journal of Agricultural Research* 8: 88–95.
- Choinski, J.S., Ralph, P. & Eamus, D. (2003) Changes in photosynthesis during leaf expansion in *Corymbia gummifera*. *Australian Journal of Botany* 51: 111–118.
- Clarke, M.F. & Fitz-Gerald, G.F. (1994) Spatial organisation of the co-operatively breeding bell miner *Manorina melanophrys*. *Emu* 94: 96–105.
- Clarke, F.C. & Schedvin, N. (1999) Removal of bell miners *Manorina melanophrys* from *Eucalyptus radiata* forest and its effect on avian diversity, psyllids and tree health. *Biological Conservation* 88: 111–120.
- Close, D., McArthur, C., Paterson, S., Fitzgerald, H., Walsh, A. & Kincade, T. (2003) Photoinhibition: A link between effects of the environment on eucalypt leaf chemistry and herbivory. *Ecology* 84: 2952–2966.
- Edgar, J.G., Kile, G.A. & Almond, C.A. (1976) Tree decline and mortality in selectively logged eucalypt forests in central Victoria. *Australian Forestry* 39: 288–303.
- Ellis, R.C. (1985) The relationships among eucalypt forest, grassland and rainforest in a highland area in north-eastern Tasmania. *Australian Journal of Ecology* 10: 297–314.
- Ellis, R.C. & Pennington, P.I. (1989) Nitrification in soils of secondary vegetational successions from *Eucalyptus* forest and grassland to cool temperate rainforest in Tasmania. *Plant Soil* 115: 59–73.
- Fales, F.W. (1951) The assimilation and degradation of carbohydrates by yeast cells. *Journal of Biological Chemistry* 193: 113–121.
- Forestry Commission of New South Wales (1984) *Management Plan for Cumberland Management Area*. (Forestry Commission of NSW: Sydney).
- Forestry Commission of New South Wales (1989) *Forest Types in New South Wales. Research Note No. 17*. (Forestry Commission of NSW: Sydney).
- Gerretson-Cornell, L. (1973) The recovery of *Phytophthora cinnamomi* Rands from Ourimbah State Forest (Wyong, Newcastle District, New South Wales, Australia) and its pathogenicity to eucalypt seedlings under controlled conditions. *Phyton* 31: 111–116.
- Gill, A.M. (1997) Eucalypts and fires: interdependent or independent? In: *Eucalypt ecology: individuals to ecosystems* (eds. J.E. Williams & J.C.Z. Woinarski). pp. 151–167. (Cambridge University Press: Cambridge).
- Granger, L., Kasel, S. & Adams, M.A. (1994) Tree decline in southeastern Australia: Nitrate reductase activity and indications of unbalanced nutrition in *Eucalyptus ovata* (Labill.) and *E. camphora* (R.T. Baker) communities at Yellingo, Victoria. *Oecologia* 98: 221–228.
- Guinto, D.F., Xu, Z., House, A.P.N. & Saffigna, P.G. (2001) Soil chemical properties and forest floor nutrients under repeated prescribed-burning in eucalypt forests of south-east Queensland, Australia. *New Zealand Journal of Forest Science* 31: 170–187.
- Horsfall, J.G. & Barratt, R.W. (1945) An improved grading system for measuring plant diseases. *Phytopathology* 35: 655.
- Jones, H.G. & Jones, M.B. (1989) Introduction: Some terminology and common mechanisms. In: *Plants under stress* (eds. H.G. Jones, T.J. Flowers & M.B. Jones). pp. 1–10. (University Press: Cambridge).
- Journet, A.R.P. & Cochrane, P.M. (1978) Free amino acids in leaf tissue of *Eucalyptus blakelyi*. *Phytochemistry* 17: 1789–1790.
- Jurskis, V. (2005) Eucalypt decline in Australia, and a general concept of tree decline and dieback. *Forest Ecology and Management* 215: 1–20.
- Jurskis, V. & Turner, J. (2002) Eucalypt dieback in eastern Australia: a simple model. *Australian Forestry* 65: 87–98.
- Kile, G.A. (1974) Insect defoliation in the regrowth forests of Tasmania. *Australian Forestry Research* 6: 9–18.
- Kile, G.A. (1980) Behaviour of an *Armillaria* in some *Eucalyptus obliqua*-*Eucalyptus regnans* forests in Tasmania and its role in their decline. *European Journal of Forest Pathology* 10: 248–296.
- King, G.C. (1985) Natural regeneration in wet sclerophyll forest with an overstorey of *Eucalyptus microcorys*, *E. saligna*, and *Lophostemon confertus*. *Australian Forestry* 48: 54–62.
- Landsberg, J. (1990) Dieback of rural eucalypts: Does insect herbivory relate to dietary quality of tree foliage. *Australian Journal of Ecology* 15: 73–87.
- Landsberg, J. & Wylie, F.R. (1988) Dieback of rural trees in Australia. *Geo Journal* 17.2: 231–237.
- Lawrence, R., Potts, B.M. & Whitham, T.G. (2003) Relative importance of plant ontogeny, host genetic variation, and leaf age for a common herbivore. *Ecology* 84: 1171–1178.
- Leuning, R., Cromer, R.N. & Rance, S. (1991) Spatial distributions of foliar nitrogen and phosphorus in crowns of *Eucalyptus grandis*. *Oecologia* 88: 504–510.
- Loyn, R.H., Runnals, R.G. & Tyers, J. (1983) Territorial bell miners and other birds affecting populations of insect prey. *Science* 221: 1411–1412.
- Marks, G.C., Kassaby, F.Y. & Fagg, P.C. (1975) Variation in population levels of *Phytophthora cinnamomi* in *Eucalyptus* forest soils of eastern Victoria. *Australian Journal of Botany* 23: 435–449.
- Marsh, N.R. & Adams, M.A. (1995) Decline of *Eucalyptus tereticornis* near Bairnsdale, Victoria: Insect herbivory and nitrogen fractions in sap and foliage. *Australian Journal of Botany* 43: 39–50.

- Mattson, W. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecological Systematics* 11: 119–161.
- McDougall, K.L., Hardy, G.E. St J. & Hobbs, R.J. (2002) Distribution of *Phytophthora cinnamomi* in the northern jarrah (*Eucalyptus marginata*) forest of Western Australia in relation to dieback age and topography. *Australian Journal of Botany* 50: 107–114.
- Medhurst, J.L. (2000) Growth and physiology of *Eucalyptus nitens* in plantations following thinning. (PhD Thesis: School of Plant Science, University of Tasmania).
- Moore, K.M. (1961) Observations on some Australian forest insects. 8. The biology and occurrence of *Glycaspis baileyi* Moore in New South Wales. *Proceedings of Linnean Society of New South Wales* 86: 185–200.
- Moore, S. & Stein, W.H. (1948) Photometric ninhydrin method for the use in the chromatography of amino acids. *Journal of Biological Chemistry* 176: 367–388.
- Neave, I.A. & Raison, R.J. (1999) Soil nitrogen availability under forests of contrasting composition and structure in south eastern New South Wales, and the effects of simulated harvesting disturbance and fire. *Australian Forestry* 62: 1–8.
- Nicholson, E. (1999) Winds of change for silvicultural practice in NSW native forests. *Australian Forestry* 62: 223–235.
- Ohmart, C.P. (1991) Role of food quality in the population dynamics of chrysomelid beetles feeding on *Eucalyptus*. *Forest Ecology Management* 39: 35–46.
- Old, K.M. (2000) Eucalypt diseases of complex etiology. In: *Diseases and pathogens of eucalypts* (eds. P.J. Keane, G.A. Kile, F.D. Podger & B.N. Brown). pp.411–425. (CSIRO Publishing: Collingwood).
- Old, K.M., Gibbs, R., Craig, I., Myers, B.J. & Yuan, Z.Q. (1990) Effect of drought and defoliation on the susceptibility of eucalypts to cankers caused by *Endothia gyrosa* and *Botryosphaeria ribis*. *Australian Journal of Botany* 38: 571–581.
- Pinkard, E.A., Beadle, C.L., Davidson, N.J. & Battaglia, M. (1998) Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. *Trees* 12: 119–129.
- Podger, F.D., Kile, G.A., Turnbull, C.R.A. and McLeod, D.E. (1980) An unexplained decline in some forests of *Eucalyptus oblique* and *E. regnans* in southern Tasmania. *Australian Forest Resources* 10: 54–70.
- Podger, F.D. (1981) Some difficulties in the diagnosis of drought as the cause of dieback. In: *Eucalypt dieback in forests and woodlands* (eds. K.M. Old, G.A. Kile & C.P. Ohmart). pp. 167–173. (CSIRO Publishing: Melbourne).
- Polglase, P.J., Attiwill, P.M. & Adams, M.A. (1986) Immobilization of soil nitrogen following wildfire in two eucalypt forests of south-eastern Australia. *Acta Oecologia* 7: 261–271.
- Rayment, G.E. & Higginson, F.R. (1992) *Australian handbook of soil and water chemical methods*. (Inkata Press: Melbourne).
- Sands, P.J. (1996) Modelling canopy production. III Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. *Australian Journal of Plant Physiology* 23: 103–114.
- SAS Institute Inc. (1987) *SAS/STAT Guide for Personal Computers, Version 6 Edition*. (SAS Institute Inc.: Cary, North Carolina).
- Schreuder, H.T. & Thomas, C.E. (1991) Establishing cause-effect relationships using forest survey data. *Forest Science* 37: 1497–1512.
- Shearer, B.L. & Smith, I.W. (2000) Diseases of eucalypts caused by soilborne species of *Phytophthora* and *Pythium*. In: *Diseases and pathogens of eucalypts*. (eds. P.J. Keane, G.A. Kile, F.D. Podger & B.N. Brown). pp. 259–291. (CSIRO Publishing: Melbourne).
- Shields, J.M. (1990) *The effect of logging on bird populations in southeastern New South Wales*. (PhD Thesis: University of Washington, Seattle, Washington).
- Steinbauer, M. (2001) Specific leaf weight as an indicator of juvenile leaf toughness in Tasmanian bluegum (*Eucalyptus globulus* ssp. *globulus*): implications for insect defoliation. *Australian Forest* 64: 32–37.
- Stewart, G.R. & Larher, F. (1980) Accumulation of amino acids and related compounds in relation to environmental stress. In: *The Biochemistry of Plants vol. 5* (ed. B.J. Mifflin). pp. 609–635. (Academic Press Inc.: New York).
- Stewart, G.R., Gracia, C.A., Hegarty, E.E. & Specht, R.L. (1990) Nitrate reductase activity and chlorophyll content in sun leaves of subtropical Australian closed-forest (rainforest) and open-forest communities. *Oecologia* 82: 544–551.
- Stone, C. (1996) The role of psyllids (Hemiptera: Psyllidae) and bell miners (*Manorina melanophrys*) in canopy dieback of Sydney blue gum (*Eucalyptus saligna* Sm.). *Australian Journal of Ecology* 21: 450–458.
- Stone, C. (1999) Assessment and monitoring of decline and dieback of forest eucalypts in relation to ecologically sustainable forest management: a review with a case history. *Australian Forestry* 62: 51–58.
- Stone, C. (2005) Bell miner associated dieback at the tree crown scale: A multi-trophic process. *Australian Forestry* 68: 237–241.
- Stone, C., Spolc, D. & Urquhart, C.A. (1995) *Survey of crown dieback on moist hardwood forests in the central and northern regions of New South Wales State Forests (psyllid/bell miner research programme)*. Research Paper No. 28. (State Forests of NSW: Sydney).
- Stone, C., Chisholm, L. & McDonald, S. (2005) Effects of leaf age and psyllid damage on the spectral reflectance properties of *Eucalyptus saligna* foliage. *Australian Journal of Botany* 53: 45–54.
- Stone, C., Wardlaw, T., Floyd, R., Carnegie, A., Wylie, R., & de Little, D. (2003) Harmonisation of methods for the assessment and reporting of forest health in Australia – a starting point. *Australian Forestry* 66: 233–246.
- Swarbrick, J., Wilson, B. & Hannan-Jones, M. (1998) *Lantana camara* In: *The biology of Australian weeds*. Vol 2. (eds. F.D. Panetta, R.H. Groves, R.C.H. Shepherd). pp. 119–136. (RG and FJ Richardson: Melbourne).
- Taylor, G.S. (1997) Effect of plant compounds on the population dynamics of the lerp insect, *Cardiaspina albitextura* Taylor (Psylloidea: Spondyliaspidae) on eucalypts. In: *Ecology and evolution of plant-feeding insects in natural and man-made environments* (ed. A. Raman). pp. 37–57. (International Scientific Publications: New Delhi).
- Tippett, J.T., Hill, T.C. & Shearer, B.L. (1985) Resistance of *Eucalyptus* spp. to invasion by *Phytophthora cinnamomi*. *Australian Journal of Botany* 33: 409–418.
- Wardell-Johnson, G. Stone, C., Recher, H. and Lynch, A.J.J. (2005) A review of eucalypt dieback associated with bell miner habitat in south-eastern Australia. *Australian Forestry* 68: 231–236.
- Waring, R.H. (1991) Responses of evergreen trees to multiple stresses. In: *Response of plants to multiple stresses* (eds. H.A. Mooney, W.E. Winner & E.J. Pell). pp. 371–390. (Academic Press, Inc.: San Diego).
- West, P.W. (1979) Rate of onset of regrowth dieback and its relation to summer drought in eucalypt forest of southern Tasmania. *Annals of Applied Biology* 93: 337–350.

- Weston, C.J. & Attiwill, P.M. (1990) Effect of fire and harvesting on nitrogen transformations and ionic mobility in soils of *Eucalyptus regnans* forests of south-eastern Australia. *Oecologia* 83: 20–26.
- White, T.C.R. (1970) Some aspects of the life history, host selection, dispersal, and oviposition of adult *Cardiaspina densitexta* (Homoptera: Psyllidae). *Australian Journal of Zoology* 18: 105–117.
- White, T.C.R. (1971) Lerps insects (Homoptera, Psyllidae) on red gum (*E. camaldulensis*) in South Australia. *South Australian Naturalist* 46: 20–23.
- White, T.C.R. (1986) Weather, Eucalyptus dieback in New England, and a general hypothesis of the cause of dieback. *Pacific Science* 40: 58–78.
- Whitehead, D. & Beadle, C.L. (2004) Physiological regulation of productivity and water use in *Eucalyptus*. *Forest Ecology and Management* 193: 113–140.
- Woodburn, T.L. & Lewis, E.E. (1973) A comparative histological study of the effects of feeding by nymphs of four psyllid species on the leaves of eucalypts. *Journal of Australian Entomological Society* 12: 134–138.
- York, A. (1999) Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. *Journal of Insect Conservation* 3: 191–199.