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Eucalypt dieback in eastern Australia: a simple model

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Summary

Eucalypt dieback is widespread throughout Australia and affects an increasing range of species. In addition to salt, a 1993 study listed 13 types of insects, five types of fungi, five kinds of vertebrate animals, four climatic perturbations and a parasitic plant that had been implicated as major agents of dieback in south-eastern Australia. Repeated defoliation by insects has usually been identified as a major factor in rural and forest diebacks, while mesic understorey development is often an important feature of forest diebacks. Different mechanisms of initiation and reinforcement have been proposed to account for many different forms of dieback. High rates of folivory leading to both rural and forest diebacks, have been related either to high resource availability and tree vigour or to low resource availability and tree stress.

A simple model of eucalypt dieback is proposed to account for both rural and forest dieback, including an increasing range of 'susceptible' species and sites. It associates eucalypt dieback with increased soil moisture and nitrogen status that stresses the roots of established eucalypt trees. These changes affect the physiology of the trees and encourage high rates of folivory and/or fungal pathogenicity. This model can encompass dieback from dryland salinity, 'high-altitude' dieback in Tasmania, 'bellbird' dieback, 'koala' dieback in Victoria and South Australia, phasmatid outbreaks in New South Wales and Victoria, and potentially extends to 'regrowth' dieback in Tasmania. Reduced application of low-intensity fire is a common agent of changed soil conditions. Additional factors that may apply are fertilisation and modifications to runoff and soil drainage.

Keywords: dieback; fire; models; *Eucalyptus;* Australia

Introduction

In the 1940s and 1950s, extensive defoliation and dieback occurred in the highlands forests of New South Wales and Victoria following outbreaks of various species of phasmatids (Newman and Endacott 1962; Mazanec 1966, 1967; Campbell and Hadlington 1967). Damage to valuable timber stands of mountain ash (*Eucalyptus regnans*) and alpine ash (*E. delegatensis*), and accelerated soil erosion in hydroelectric catchments, prompted the aerial application of insecticides to control the insects (Carne and Taylor 1978). Fire exclusion policies were implicated in the outbreaks (Carne and Taylor 1978). More recent outbreaks and consequent dieback were reported by Neumann *et al.* (1981).

During the 1950s, State Forests' Research Division received occasional enquiries about deaths of paddock trees following pasture improvement. While dieback had been noted in earlier periods (Heatwole and Lowman 1986), these enquiries increased to a flood in the 1970s. As a result, a small survey and research program was initiated in the New England region of New South Wales. Some farmers advanced the hypothesis that superphosphate applications were killing the trees but this hypothesis was dismissed since superphosphate was not toxic to trees and the problem was chronic and extensive compared to application of superphosphate. The research program concluded that repeated defoliation by insects was a major factor in 'New England dieback' which was particularly severe in depressions and poorly drained areas (Mackay *et al.* 1984). 'Rural dieback' is now widespread throughout Australia and affects an increasing range of tree species (Heatwole and Lowman 1986; Lowman *et al.* 1987; Landsberg and Cork 1997).

Also during the 1950s, State Forests of NSW investigated dieback of Sydney blue gum (*E. saligna*) in forests on the central coast associated with defoliation by psyllid insects. Dieback appeared to be associated with sites having shallow topsoil over heavy clay (Moore 1961). Further investigations followed increasing concerns, during the 1990s, that dieback associated with psyllids and bellbirds was expanding. Stone *et al.* (1995) suggested that four factors contributed to 'bellbird' dieback: local climatic conditions; stressed trees growing on suboptimal sites; inherent susceptibility of tree species; and presence of bellbirds reducing predation of psyllids by other birds (for example, Loyn *et al.* 1983). Stone (1999) proposed that inherently susceptible stand structures and disturbance by logging and fire were predisposing stresses for bellbird dieback. However, the extent of bellbird dieback continues to increase in New South Wales coastal forests and it affects all types of stand structures and most eucalypts, including species (see Fig. 1) that were previously considered resistant to the problem (Stone *et al.* 1995).

In Tasmania, Bowling and McLeod (1968) observed that regrowth areas that had been burnt at any stage during their development were less affected by 'regrowth' dieback than unburnt stands. Podger *et al.* (1980) suggested that regrowth dieback resulted from a combination of drought stress, fungal attack and insect grazing but could not explain why understorey species were not affected by drought stress. Ellis (1985) stated that rainforest had dramatically expanded at the expense of eucalypt forest on a Tasmanian plateau following a post-European reduction in fire

Figure 1. Dieback in old-growth blackbutt

application. Ellis and Pennington (1992) concluded that 'high-altitude' dieback of alpine ash (*E. delegatensis*) and succession to rainforest was associated with soil microbial factors developing in a cool moist environment in the absence of fire.

Martin (1985) studied a koala population that was contributing to heavy defoliation and dieback of *E. ovata* in coastal Victoria. Adjoining stands of other eucalypt species were unaffected. Martin (1985) suggested that succulent epicormic growth produced after defoliation was attractive to the koalas. He cited five other studies that reported eucalypt dieback from defoliation by koalas, going back to 1915. The process of repeated defoliation by koalas leading to dieback is similar to bellbird dieback where psyllid insects repeatedly defoliate the trees, and is also similar to dieback caused by phasmatids. Possingham *et al.* (1996) recommended culling, translocation and fertility control of koalas as well as tree regeneration programs to remedy eucalypt dieback on Kangaroo Island in South Australia.

Landsberg *et al.* (1990) concluded that nutrient enrichment may be a key factor contributing to rural dieback. They found higher nitrogen levels, and particularly nitrate levels, in soils of dieback sites compared with healthy sites. Landsberg (1990a) found that soil under healthy trees contained less nitrogen than soil under dieback-affected trees. Landsberg and Gillieson (1995) examined regional and local variations in insect herbivory of eucalypts according to resource availability for tree growth. They found evidence of positive relationships between resource availability, rates of leaf production and herbivory. Insect damage increased with soil moisture, nitrogen availability, nitrogen content of leaves, and leaf turnover. Landsberg and Gillieson (1995) found no evidence of an association between high herbivory and 'potentially stressful' low resource environments. They stated that the apparent level of herbivore damage on mature leaves was highest at the intermediate level of site resources, possibly reflecting interactions between resources, herbivory and rates of leaf replacement. Adams and Atkinson (1991) stated that drought stress may predispose trees to insect attack following accumulation of nitrogenous solutes as osmotica, and that nitrogen-rich amino acids may be the common thread linking drought stress, dieback and insect outbreaks in native forests and plantations.

Smith and Smith (1990) reported extensive eucalypt dieback and expansion of rainforest understorey and sheoak (*Allocasuarina littoralis*) scrub in some Sydney bushland reserves. They attributed the dieback to urban runoff and absence of fire. Lunt (1998) documented a dramatic increase in the density of *A. littoralis* understorey and dieback of the eucalypt canopy with long-term fire exclusion in a Victorian coastal reserve. He suggested that deliberate burning at short intervals may be required to reinstate an open woodland structure.

Raison *et al.* (1993) found that repeated prescribed burning in a snow gum (*E. pauciflora*) forest reduced nitrogen released from decomposing litter, nitrogen concentration in tree foliage, rates of foliage abscission and nitrogen in leaf litterfall. They suggested that repeated burning may reduce plant productivity, change the structure and floristics of vegetation, exacerbate flammability and increase the susceptibility of trees to pests and diseases. On the other hand, Jurskis (2000) suggested that eucalypt dieback may be promoted by fire exclusion that increases soil moisture, nitrogen availability, nitrogen content of leaves and leaf turnover, whilst decreasing the amount of solar radiation reaching the ground, that is, the converse of the Raison hypothesis. These changes in site resources could cause stress in ecosystems adapted to aridity, drought and low nutrient soils (Jurskis 2000).

In Bega Valley Shire, on the south coast of New South Wales, every near-coastal drainage system contains bellbird dieback (Appendix 1). Personal observations over several years indicate that dieback areas are expanding. The usual sequence is that tree crowns become thin, a thick ground litter layer develops, a dense shrub layer develops and bellbirds take control of the site. 'Bellbird dieback' on private land is particularly associated with two 'wet' vegetation types from a 'complex of grassy ecosystems' (Keith and Bedward 1999), previously described as a group of 'dry grassy eucalypt woodlands and forests' (Keith and Sanders 1990). These vegetation types, 'Brogo Wet Vine Forest' and 'Bega Wet Shrub Forest' (see Fig. 2) are remnants of woodlands and grassy forests that have been substantially cleared for agriculture (Keith and Bedward 1999). The wet types described by Keith and Bedward (1999) appear to be artefacts of post-European fire regimes (*pers. obs.*) that are causing grassy forests to develop shrubby understoreys (Jurskis 2000). In the shire's public forests, dieback is often associated with a woollybutt type (Anon. 1989) that has an open shrub layer and grassy groundcover (Keith and Bedward 1999). The shrub layer appears to be getting denser and more mesic in the dieback areas. The bellbird dieback process in the Shire appears to be following a path similar to that of high-altitude dieback in Tasmania. Incidental observations suggest that the problem extends along the entire New South Wales coast.

A model of eucalypt dieback

Post-European land management practices are altering the environment so that soils supporting natural tree communities have become unnaturally moist and fertile. Changed soil conditions affect the soil microbiology and the root dynamics of the trees, impairing their health. In some cases, especially in *Monocalyptus*, the impaired root function leads directly to dieback. The unhealthy trees produce more palatable and nutritious foliage than they did under a regime of low-intensity fire and light grazing by native macropods. The enhanced nutritional value of the foliage, especially in *Symphyomyrtus*,

Figure 2. Dieback in the ‘grassy ecosystem’ — ‘Bega Wet Shrub Forest’ (Keith and Bedward 1999)

increases the population vigour of arboreal folivores. In this situation, a combination of unhealthy roots and increased and repeated pest attack in crowns, results in dieback.

Understoreys, whether pasture or shrub, respond to the increasingly moist and fertile conditions and reinforce the soil changes through increased shade and moisture, reduced temperatures, and increased nutrient cycling, especially nitrogen cycling. These changes also increase the vigour of folivore populations. For example, lush improved pastures (resulting from fertiliser applications and sowing of legumes) provide improved habitat for Christmas beetle larvae (Carne *et al*. 1974; Landsberg and Cork 1997).

In forests and woodlands, dense mesic understoreys may provide nesting habitat for bellbirds allowing vigorous colonies to develop and possibly exclude other birds and disrupt invertebrate predators that might otherwise control folivore populations (Loyn *et al.* 1983; Stone 1996). Such understoreys may also shelter koalas from predators and harsh weather, increasing their reproductive vigour. Decline in the tree canopy accelerates the understorey changes and, in turn, changes in understorey prevent any ingress of low-intensity fire to these sites. As drier stands of eucalypts become smaller and more fragmented, they are less likely to be targeted for controlled burning and less likely to be ignited if broad-area burning is carried out, since low-intensity fires will not burn through moist areas. The environmental changes progress further across the landscape as naturally drier and more freely drained sites are affected so the range of affected tree species increases. Any wildfires that penetrate the moist sites cause further damage to the weakened eucalypt canopy, whereas understoreys quickly recover and take further advantage of the increasing site resources. The weak epicormic tree canopies on dieback sites usually carry insufficient seed (for example, Landsberg and Cork 1997) to establish effective eucalypt regeneration after wildfires.

The model explains rural, bellbird, koala and high-altitude diebacks together with phasmatid outbreaks as variations of a simple process. Different land management practices induce similar environmental changes that are reinforced by a variety of feedback mechanisms as indicated in Figure 3. Tree dieback from dryland salinity follows a similar process but includes the additional impact of saline groundwater.

Discussion

Dieback in this discussion refers to the deterioration and death of stands of trees or large areas of trees rather than individual trees. This is sometimes termed tree decline (e.g. Wylie *et al.* 1993). Some of the suggested causes, such as wood-boring insects and fungal pathogens, appear to be secondary factors that result from, and reinforce, the primary factors.

Primary factors

Fire regimes

With the exception of changed fire regimes, none of the factors that have previously been suggested as causal agents of the various forms of dieback, for example tree removal, insects, bellbirds, fertilisation, irrigation/diversion of water, fungal attack, pasture improvement, domestic grazing or cropping and climatic perturbations, are common to all types of dieback. However, the different types of dieback are all associated with reduced application of low-intensity fire (*pers. obs.*).

Prior to European settlement of Australia, natural fires were not controlled and Aborigines deliberately burnt woodlands and open forests. Long-term studies of prescribed burning in forests have indicated that topsoil moisture, nitrogen availability in soils, nitrogen

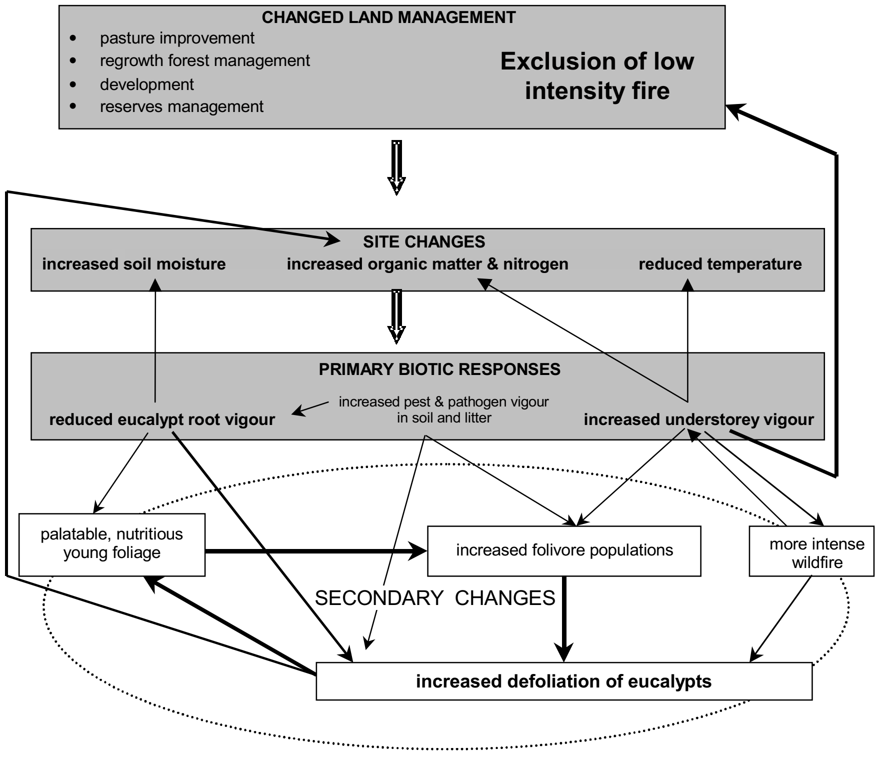

Figure 3. A simple model of eucalypt dieback

content of eucalypt leaves and leaf turnover are reduced by repeated controlled burning, whilst ground level solar radiation is increased (Raison *et al.* 1993; York 1999). Stated from a different perspective, the conclusions could be that a change from a regime of frequent, low-intensity fire to a regime of infrequent, high-intensity fire leads to greater levels of soil moisture and nitrogen, reduced soil temperatures and increased rates of turnover of eucalypt foliage. These factors are likely to promote unhealthy roots (Ellis and Pennington 1992), nitrification (Adams and Attiwill 1982), insect damage to leaves (Adams and Atkinson 1991; Landsberg and Gillieson 1995), and eucalypt dieback (Jurskis 2000).

Exclusion of low-intensity fire is increasingly the common land management practice in south-eastern Australia. Reasons for a reduction in the extent and frequency of low-intensity fire in recent decades include:

- Efficient suppression of fires caused by lightning;
- Development of improved pastures for livestock production;
- Logistic or aesthetic impediments to burning due to urban, rural residential and 'alternative lifestyle' developments and associated infrastructure;
- A desire to protect timber values in regrowth forests by excluding fire;
- Regulations that prevent burning in many areas of public forests, for example stream exclusion zones, rare old growth and rare ecosystems (Refshauge *et al.* 1999); and
- A perception amongst some public land managers that a frequent controlled burning regime may reduce biodiversity in forests (for example Lunney 1991; Keith and Bedward 1999).

Ellis and Pennington (1992) reported decline of mature alpine ash canopies in Tasmanian forests and development of rainforest understoreys (high-altitude dieback) following fire exclusion. Increasingly dense and mesic understoreys extending upslope in the absence of frequent burning regimes are a feature of coastal forests in New South Wales (Anon. 1989; Jurskis 2000). Understoreys particularly reflect local soil drainage conditions (Richards *et al.* 1990), and alterations in understoreys indicate changing soil moisture and nutrient status. Pasture improvement and livestock grazing greatly amplify understorey changes in woodlands.

Some facets of pasture improvement (cultivating, fertilising and sowing exotic grasses and legumes) and livestock grazing may have greater impacts than fire exclusion in rural woodlands. Additional factors such as stormwater and sewage disposal exacerbate the site changes in rural residential and urban bushland. Nevertheless, the conclusion that nutrient enrichment is a key factor in rural dieback (Landsberg *et al.* 1990) can be extended to the other types of dieback including high-altitude, bellbird, koala, and urban dieback.

Rural dieback extends through the coast, tablelands and western slopes of New South Wales and has been reported from many areas across Victoria and in Queensland (AUSLIG 1990; Benson 1991; *pers. obs.*). Wylie *et al.* (1993) reported dieback from all 74 local government areas that they surveyed in south-eastern Queensland and north-eastern New South Wales. They stated that dieback was particularly severe in 20 of these areas, especially on the coastal side of the Great Dividing Range. Landsberg and Cork (1997) stated that rural dieback is widespread throughout Australia. Although susceptibility varies with species, most eucalypts become susceptible to rural dieback after an extended period of insect attack (Landsberg and Cork 1997).

Mesic dieback is probably a more appropriate term for eucalypt decline in forests than the other epithets that focus attention on narrower circumstances and secondary factors. For example, Miles (2000) suggested that bellbirds could be culled to protect significant vegetation in the Bega Valley Shire whereas the model proposed in this paper indicates that more basic changes to management practices are required. The model also suggests that management of vegetation rather than koalas (for example, Possingham *et al.* 1996) should be the major focus of proposals to remedy koala dieback. Anthropogenic changes to environmental conditions resulting in reduced root efficiency of established eucalypts (Ellis and Pennington 1992) and/or increased nutrient cycling and leaf turnover (Raison *et al.* 1993) can account for the initiation of the various types of dieback.

Resource availability or stress?

Resource availability models of herbivory suggest that high levels of herbivory are more likely on vigorous plants growing in resource-rich environments, whilst plant stress models suggest the opposite, that is, high herbivory is more likely on stressed plants (Landsberg and Gillieson 1995).

Fertilisation with nitrogen can stimulate arginine production in tree foliage (Durzan 1974). Arginine is an essential compound in the diet of many, if not all, insect pests of trees (Durzan 1974). Increased nutrient availability in ecosystems may increase the nutritional value of tree foliage, allowing pest populations to increase (e.g. Xydias and Leaf 1964; Hesterberg and Jurgensen 1972; Lambert 1986). Resource availability models could provide an explanation for the time lag between agricultural clearing and rural dieback, the early association of New England dieback with fertiliser application (Humphreys unpubl.) and the slower progress of rural dieback where pasture improvement has been less vigorously pursued (*pers. obs.*). They could also account for the generally slower progression of mesic dieback compared to rural dieback (*pers. obs.*) as a result of a slower rate of accumulation of resources and change in soil conditions.

However, resource availability models of herbivory do not explain the initiation of dieback since increased resources should improve a tree's ability to sustain grazing. Alternatively, trees growing on the highest quality sites should be most affected by dieback but this is not necessarily the case. Landsberg and Gillieson (1995) suggested that insect damage may be most apparent where resources are sufficient to support high herbivory but insufficient to support compensatory rates of leaf replacement. The agents initiating rural, bellbird and koala dieback apparently cause improvements in the palatability and nutrition of eucalypt leaves. Dieback follows increased vigour of folivore populations that are using the affected trees as their primary food supply. At the same time, the vigour of the trees relative to the folivores decreases and the trees are no longer able to sustain their canopies.

Adams and Atkinson (1991) suggested that drought stress may encourage insect folivory by causing an accumulation of foliage nutrients. Landsberg and Gillieson (1995) found no evidence supporting an association between increased herbivory and tree stress. Landsberg (1990a) found no evidence that stress improved foliar nutrient status in glasshouse trials using eucalypt seedlings. Older trees, however, react to environmental changes in a different way than seedlings and young trees. Young eucalypts often react positively to soil cultivation, fertilisation and irrigation (Florence 1996), whereas established trees can be adversely affected by changed soil conditions (Hadlington and Johnston 1988). The water and nutrient uptake of eucalypts varies with age and growth stage (Florence 1996). There is evidence in stands affected by mesic dieback that trees in the large seedling – small sapling stage may be relatively little affected compared to older trees (Appendix 1; *pers. obs.*; C. Stone *pers. comm.*). Podger *et al.* (1980) found no evidence of 'regrowth' dieback in stands less than fifteen years old.

Lambert (1986) found that fertilisation with low levels of nitrogen increased the growth of Monterey pine but application of high levels of nitrogen depressed growth by inducing sulphur deficiency. The sulphur deficiency increased arginine levels in the leaves and this stimulated fungal infection (Lambert 1986). Xydias and Leaf (1964) reported that nitrogen fertilisation reduced both tree growth and insect attack in white pine. Depending on the particular adaptations of plants, nutrient enrichment may increase both plant and folivore vigour, decrease both plant and folivore vigour or affect the plant and the pest in opposite directions. It is suggested that increased site resources in eucalypt ecosystems can, at the same time, improve nutrition of folivores and place trees under stress.

Adaptations of plants

Landsberg *et al.* (1990) found higher nitrogen levels, and particularly nitrate levels, in soils of dieback sites compared to healthy sites. Adams and Attiwill (1982) suggested that ammonium is probably the predominant form of nitrogen in soils under temperate mature forest soil, and that forest trees probably obtain their nitrogen mostly through ammonifying heterotrophic fungi in their mycorrhizae rather than using nitrate. The enzyme nitrate reductase must be present in plants that utilise nitrate (Adams and Attiwill 1982). Adams and Attiwill (1982) found that there was considerable nitrate reductase activity (NRA) in mountain ash (*E. regnans*) trees on moist sites and little NRA in messmate (*E. obliqua*) trees on drier sites. Relative NRA was much higher in the leaves than the roots of both eucalypt species, whereas high NRA occurred in both the leaves and roots of silver wattle (*Acacia dealbata*). Adams and Attiwill (1986a) found consistently higher rates of nitrification in soils of wetter, high productivity forests than in drier forests. Trees adapted to drier sites and ammonifying conditions have low overall levels of NRA which occurs mainly in leaves rather than in roots (Adams and Attiwill 1982). Trees on drier sites also turn over nitrogen more slowly than trees in wet sclerophyll forests (Adams and Attiwill 1986b).

Ellis and Pennington (1989) found increasing nitrification in successional soils, developing in the absence of fire, from native grassland, through to eucalypt forests, through their decline and gradual replacement by rainforest. These authors related eucalypt decline in mature alpine ash canopies associated with development of rainforest understoreys (high-altitude dieback) to changing soil microbiology and particularly mycorrhizal development. The decline was associated with decreased soil temperatures, possible increases in soil moisture and nitrogen levels and other changes in soil chemistry.

Increased nitrogen cycling (Raison *et al.* 1993) and soil moisture (York 1999) as a result of fire exclusion could induce or increase nitrification in normally ammonifying forest soils (Adams and Attiwill 1982). Nitrification induced by fire exclusion may change the physiological processes in eucalypts adapted to these drier sites, favouring folivores and impairing root function. Adams and Atkinson (1991) reported 100-fold greater abundance of psyllids on mountain ash foliage at a site having a high soil nitrate/ammonium ratio (4.5) than at another site having a low ratio (0.7). The growth potential of understorey trees and shrubs relative to eucalypts may be improved by nitrification. Turner and Lambert (1983) found that there was a disproportionately high accumulation of nitrogen (55%) in the developing rainforest understorey of a flooded gum (*E. grandis*) plantation even though the understorey only made up 9% of the total above-ground biomass. Applying fertiliser and sowing legumes induces nitrification in improved pasture soils (e.g. Landsberg *et al.* 1990).

Increased nitrogen cycling and nitrification will reduce the competitive ability of dry-site-adapted eucalypts compared to rainforest plants, exotic weeds such as lantana and privet, and exotic pastures.

Soil conditions and roots

Increased site resources may stress trees by affecting the efficiency of their roots. Changed soil conditions may affect root efficiency in wet and/or dry conditions causing physiological changes and stress in trees. Eucalypts are adapted to cope with seasonal fluctuations in soil moisture conditions by taking advantage of deep roots in dry conditions and surface roots at other times (Jacobs 1955). Changes to the mean soil moisture conditions (Ellis and Pennington 1992; York 1999), and probably the amplitude and frequency of fluctuations in soil moisture, may be difficult to accommodate after a tree's basic root architecture is established 'in its youth' (Jacobs 1955). Any long-term changes to soil moisture conditions (either wetter or drier) will cause the death or deterioration of established eucalypts (Hadlington and Johnston 1988).

Adams and Atkinson (1991) suggested that drought stress may encourage insect folivory by causing an accumulation of foliage nutrients. Decreased root vigour in an unfavourable root environment could have a similar effect. Resultant changes in physiology are likely to increase the susceptibility of the trees to pathogens and pests (Adams and Atkinson 1991). Increases in soil moisture, changes in chemistry and decreases in temperature as a result of changed fire regimes, may alter soil microbiology and adversely affect eucalypt root function, particularly in soils that are not freely drained and in tree species that are adapted to ammonifying conditions.

Efficiency of fine roots may be deleteriously affected by changes to mycorrhizae resulting from a changed soil environment (Ellis and Pennington 1992). Hesterberg and Jurgensen (1972) suggested that mycorrhizae are generally reduced or eliminated by high levels of soil nitrogen. Mycorrhizae not only improve the efficiency of tree roots but also help to protect them from pathogens (Hesterberg and Jurgensen 1972). The soil changes may also favour antagonistic and/or pathogenic microbes (Florence 1996). Soil nitrogen levels can affect the saprophytic survival and the reproduction of root rot fungi (Hesterberg and Jurgensen 1972). Trees stressed by unhealthy roots will have enhanced foliar nutrient status due to high leaf turnover (Landsberg 1990b; Stone and Bacon 1995). Key (1991) stated that stick insects generally occur in low densities, even though their food (eucalypt foliage) is usually abundant. Supply of young foliage to first instar nymphs may limit population densities (Key 1991). Increased leaf turnover and nitrogen cycling, as a result of declining root vigour with long-term fire exclusion, would increase the supply of palatable and nutritious young foliage to first instar nymphs. The threshold food resource level for outbreak of insect populations would be more frequently or repeatedly attained and defoliation would reinforce the process.

The swamp gum (*E. ovata*) communities defoliated by koalas in the study by Martin (1985) occurred along the margins of swampy gullies. At times koalas preferred other tree species and communities on better drained sites. Although some thinning of crowns was evident in the other communities, only the *E. ovata* community suffered extreme defoliation (Martin 1985). Mackay *et al.* (1984) found that rural dieback was particularly severe in depressions and poorly drained areas. Moore (1961) stated that psyllid dieback in Sydney blue gum appeared to be associated with sites having shallow topsoil over heavy clay. Mesic dieback in south-eastern New South Wales appears to be associated with sites that are less than freely drained (*pers. obs.*). In New South Wales north coast forests, trees growing on deep well structured soils supporting well developed rainforest understoreys appear to be less affected by insect attack than trees of the same species on nearby sites with inferior soil development (*pers. obs.*). Reduced root vigour may be more prevalent or particularly debilitating where soils are not freely drained.

Water use by moist eucalypt regrowth stands increases rapidly to a maximum at about 25 years of age and declines very slowly thereafter (Bi *et al.* 2001; Vertessy *et al.* 2001). Problems associated with root vigour of regrowth trees would be likely to appear when the stands had reached their peak water demand. This may help to explain the suggested association of bellbird dieback with moist eucalypt regrowth stands (Stone 1999), and the onset of regrowth dieback in Tasmania after about 30 years (Podger *et al.* 1980). Additional adverse factors such as drought or waterlogging would reinforce the physiological changes and contribute to the decline of the regrowth stands.

Insect pests are apparently not a major factor in high-altitude dieback (Ellis *et al.* 1980) or regrowth dieback (Wardlaw 1989), but have a large role in bellbird dieback. *Monocalyptus* species such as alpine ash, mountain ash and messmate are more sensitive to soil conditions (Florence 1996) than *Symphyomyrtus* species such as Sydney blue gum, red gum, manna gum and woollybutt that may be particularly susceptible to folivorous pests (Adams and Atkinson 1991). Direct impacts of soil changes may be more debilitating to *Monocalyptus* than to other groups. It is suggested that dieback in *Monocalyptus* species may occur directly as a result of impaired root efficiency, whereas dieback in *Symphyomyrtus* is more likely to follow both root decline and increased pest attack of tree crowns.

Trees off site or site changes?

It has been suggested that some dieback situations result from increased pest and disease susceptibility of tree species that have established dense stands on sites to which they are not naturally well adapted (for example, Florence 1996). This suggestion accords with plant stress models of herbivory (see above). However, the suggestion by Moore (1961) that psyllid attack may be enhanced by stress in trees growing 'off site', contradicts his observation that Sydney blue gum trees growing on ridges (the lower extreme of site quality for blue gum) suffered low levels of attack compared with blue gum on lower slopes and creeks. Similarly, the proposal by Stone *et al.* (1995) that bellbird dieback is associated with stressed blue gum trees growing on suboptimal sites on upper slopes conflicts with Stone's (1996) statement that blue gum dieback is prevalent where there are dense mesophyll understoreys. Increasing density and vigour of understoreys on dieback sites indicates that root efficiency rather than soil moisture is limiting eucalypt growth. It appears likely that sites have moved 'off tree' in the absence of relatively frequent low-intensity fire (Ellis 1985; Anon. 1989; Lunt 1998).

Inherent susceptibility?

Stone (1999) proposed that bellbird dieback affects inherently susceptible stand structures and inherently susceptible eucalypt species. However, the extent of bellbird dieback continues to increase in New South Wales coastal forests and it affects apparently undisturbed mature stands, well stocked regrowth stands, mixed aged forests and areas identified, in a Comprehensive Regional Assessment (Anon. 1998), as old-growth forest (Appendix 1). Most eucalypts are becoming affected including species such as blackbutt (*E. pilularis*), spotted gum (*C. maculata*) and flooded gum (*E. grandis*) that were previously considered resistant to the problem (Stone *et al.* 1995). Eucalypt stands growing on soils that are not freely drained appear to be particularly susceptible (see above). Inherent susceptibility of species or stand structure to dieback (Stone 1999) does not appear to be a useful concept in attempting to explain the phenomenon.

Disturbance and bellbirds?

Stone (1999) proposed that disturbance by logging or fire could be a 'triggering stress' associated with colonisation of stands by bellbirds, and that the abundance of psyllids increases in the presence of bellbirds. In a long-term ecological research area at Eden, the size of a bellbird colony declined sharply after part of its habitat was logged and burnt. During the following ten years, eucalypt dieback and bellbird numbers have tended to increase in unburnt blocks and remain absent or stable in frequently burnt blocks (State Forests of NSW unpublished data). Mesic dieback and bellbird colonies are appearing in stands that have been undisturbed by logging or wildfire for many decades (Appendix 1). Although Stone (1999) demonstrated a correlation between canopy ill health, insect damage and presence of bellbirds, no evidence was provided that bellbirds were either causing or preceding ill health or insect damage.

On the other hand, Moore (1961) observed heavy psyllid attack preceding colonisation of a stand by bellbirds. This suggests that bellbird 'invasion' is not a primary initiation mechanism for mesic dieback. Data presented by Loyn *et al.* (1983) indicated that cyclical fluctuations in bellbird numbers lagged at least a month behind the fluctuations in psyllid numbers. It is suggested that bellbirds take advantage of increased psyllid populations responding to physiological changes in trees that follow site changes caused by the exclusion of low-intensity fire. Disturbance to unhealthy stands may intensify the process by exacerbating site changes.

Secondary factors and feedback mechanisms

Nutritional status of replacement foliage

The principal feedback mechanism for rural, bellbird, and koala dieback is the increased nutritional value of replacement foliage after defoliation (Hindell and Lee 1990; Landsberg 1990c; Fig. 3). Landsberg and Cork (1997) stated that the higher quality foliage in dieback trees compared with other trees was sufficient to cause large increases in growth rates, survival and fecundity of insect herbivores.

Secondary pests and pathogens

Monocalyptus species are generally less susceptible to damage by folivores and more sensitive to root environment than other groups (Florence 1996). Trees with unhealthy roots may also be more susceptible to disease and insect attack in their conductive tissues (for example Moore 1961; Podger *et al.* 1980).

Understorey development and flammability

According to Anon. (1989), frequent fires in Sydney blue gum stands produce a grassy understorey whilst a rainforest understorey usually develops in the absence of fire. The pattern of bellbird dieback, associated with dense mesophyllic understoreys, in Sydney blue gum stands (Stone 1996) following fire exclusion is similar to the development of high-altitude dieback in alpine ash and the development of mesic dieback in red gum (Jurskis 2000) and other forest types (see above) on the south coast of New South Wales.

Felling the understorey in bellbird dieback-affected stands has not had any apparent impacts on tree health (Stone 1996; C. Stone *pers. comm.*). Ellis *et al.* (1980) reported recovery of alpine ash from high-altitude dieback following felling and burning of the understorey, but felling alone was ineffective. Felled and unburnt understorey would probably have a mulching effect that would not ameliorate unfavourable soil conditions for established eucalypts. It is suggested that mesic understorey development reinforces site changes resulting from fire exclusion.

Decreased flammability of mesic understoreys following a period of fire exclusion is an important feedback mechanism in mesic dieback (Fig. 3). Mesic understorey development prevents the ingress of low-intensity fires to these sites. Wildfires that are sufficiently intense to penetrate these sites are likely to cause further damage to the unhealthy eucalypt canopy. Reduced seed production in dieback canopies (Landsberg and Cork 1997) and reduced resprouting ability in weakened trees is likely to prevent effective eucalypt regeneration on sites burnt by wildfire. On the other hand, intense fire will stimulate prolific germination or resprouting of many understorey species, and the increased site resources will allow these to rapidly re-establish. Intense fire can stimulate invasion by lantana in north coast forests (Duggin and Gentle 1998). Dense regeneration of leguminous or other nitrogen-fixing shrubs (for example, *Acacia* and *Allocasuarina*) will increase nitrogen fixation and may intensify nitrification.

Improved habitat for folivores

Pasture improvement enhances habitat quality for Christmas beetle larvae that feed on the roots of pasture plants (Landsberg and Cork 1997). Increased vigour of beetle populations accelerates tree decline which in turn promotes pasture growth through reduced competition from trees. Carne *et al.* (1974) reported that severe defoliation and dieback in eucalypt plantations on the north coast of NSW, arising from Christmas beetle feeding, was limited to trees planted on old pastures that were considered to provide a favourable breeding place for the insects. Survival of phasmatid eggs may also be enhanced in accumulating litter on long-unburnt forest floors (Carne and Taylor 1978). This would produce large populations of first instar nymphs to take advantage of the improved food resources provided by the foliage of the trees on these long-unburnt sites.

The establishment of mesic understorey enhances habitat quality for bellbirds by improving nesting habitat and shelter from predators. Vigorous bellbird colonies may exclude some other birds and disrupt invertebrate predators that might otherwise control insect folivores (Loyn *et al.* 1983; Stone 1999). Psyllid populations fell dramatically following removal of bellbirds from an unhealthy stand by Loyn *et al.* (1983), but psyllid populations also fluctuated widely at the unhealthy control site. Total bird populations were substantially higher at the unhealthy sites compared with the healthy site during most of the study, whilst other than bellbird populations were similar at the healthy and unhealthy control sites. This suggests that bellbirds were not substantially affecting populations of other birds but were taking advantage of high psyllid populations that had developed in response to changed environmental conditions at the unhealthy sites. Bellbirds appear to reinforce rather than initiate forest health problems.

Increasingly dense and mesic understorey may contribute to a similar feedback mechanism in koala dieback, where increased shelter from predators and weather extremes (for example Ough *et al.* 1988; Jurskis and Potter 1997) may increase the reproductive vigour of koala populations. The highest koala activity level (Phillips *et al.* 1996) detected from surveys of more than 100 sites in the Bega Valley Shire occurred at a site affected by mesic dieback (C. Allen *pers. comm.*).

Climatic stress

Stress due to climatic fluctuations (Podger *et al.* 1980; Stone 1999) is an unlikely agent of progressive forest decline since otherwise healthy trees and stands usually either recover or succumb totally to extreme conditions such as drought (*pers. obs.*). Moore (1961) found indications that the severity of psyllid attack may have been related to unfavourable soil drainage during wet seasons. Stone and Bacon (1995) found that drought stress in river red gum trees reduced the average leaf age of stressed trees by increasing the rate of leaf abscission and leaf initiation. Since

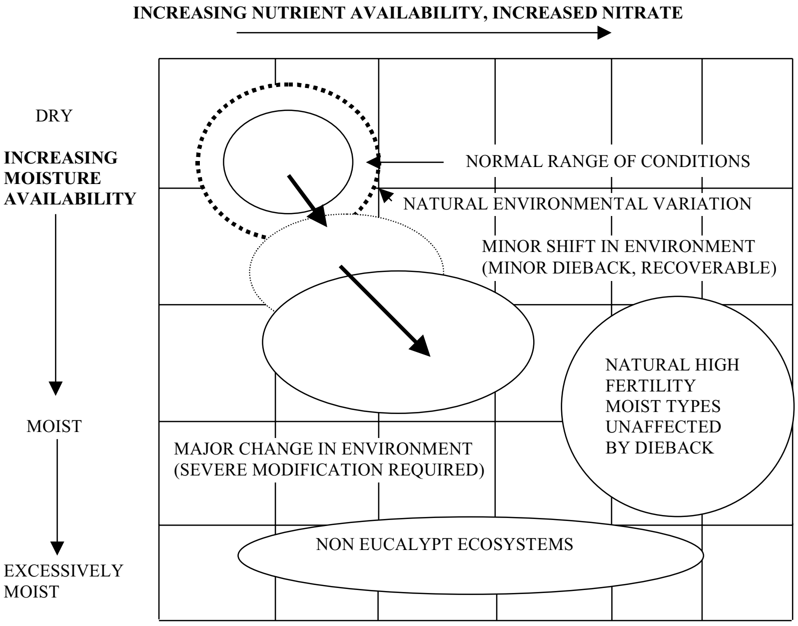

Figure 4. Site changes and dieback

young leaves have a higher foliar nutrient status than older leaves (Kavanagh and Lambert 1990; Landsberg 1990b), the drought stress would encourage herbivory. Insects consumed a higher proportion of the foliage from drought stressed trees than from healthy trees (Stone and Bacon 1995). Adams and Atkinson (1991) stated that drought stress may predispose trees to insect attack following accumulation of nitrogenous solutes as osmotica. Drought or waterlogging would reinforce the stress initiated by impaired root health and physiological changes in trees.

Management implications

Exclusion of low-intensity fire from forests that evolved with fire is leading to their progressive decline. Any massive disturbance by wildfire is unlikely to regenerate these eucalypt forests because insufficient seed is available and the weakened trees are less able to resprout. Loss of the structurally dominant taxa from extensive areas of native vegetation and replacement of eucalypt ecosystems by viney scrubs that may be infested with noxious weeds, such as lantana and privet, are likely outcomes of regulations and policies that restrict prescribed burning. These regulations and policies, however, are mostly intended to conserve natural biodiversity. It may be appropriate to review some of these policies.

Unhealthy trees are prone to attack by various fungi and wood-boring insects (see, for example, Moore 1961; Podger *et al.* 1980) that can reduce the economic value of their wood or render them useless. Excluding fire from regrowth forests and plantations to protect timber values may, ironically, result in biological degrade of timber in trees weakened by mesic decline or dieback. The benefits of excluding fire from regrowth forests and plantations to prevent timber degrade need to be balanced against the potential timber degrade of trees weakened by mesic decline processes as well as the inevitable wildfire damage that will occur in some regrowth stands and will be exacerbated in long-unburnt stands. Until this model is fully tested, low-intensity controlled burning of open forests adjacent to dieback areas is suggested as a precautionary approach to fire management for both conservation (Jurskis 2000) and timber production. It is suggested that there should be no deliberate exclusion of low-intensity fire from regrowth timber-producing forests.

Intensive disturbance such as clearing and plantation establishment would be required to re-establish eucalypt ecosystems on sites where mesic dieback is well advanced (Fig. 4). Ripping and mounding may be necessary to ameliorate soil conditions. Follow-up weed control would be essential in young stands prior to canopy closure. Following canopy closure and either self thinning or deliberate thinning, prescribed burning may be necessary to prevent increasing soil moisture and mesic understorey development. Eucalypt species native to dieback sites and having resistance to both fire damage and insect attack should probably be selected for rehabilitation plantings. A possible example from the north coast of New South Wales is tallowwood (*E. microcorys*). Genetic improvement programs could increase the growth potential of such species relative to more favoured plantation species that have less resistance to damage by defoliating insects and fire.

Testing the model

Validation of changed processes in forest soils and litter as well as physiological changes in trees, including roots and leaves, on dieback sites as compared to healthy sites would confirm the model. Soil analyses could compare nitrogen concentrations, nitrate/ammonium ratios and/or nitrification rates (e.g. Adams and Attiwill 1986a; Adams and Atkinson 1991) between soils in dieback-affected and healthy forest stands, as was done for woodlands by Landsberg *et al.* (1990). Carefully designed sampling of tree roots might ascertain whether there are any gross differences in fine root structure and mycorrhizal associations between healthy and dieback stands. NRA in roots might be compared between dieback resistant and susceptible tree species and growth stages as well as invasive understorey shrubs such as *Pittosporum* (Gleadow and Ashton 1981) and lantana (Duggin and Gentle 1998). Pot trials using soils from stands with different stages of understorey development to raise eucalypt seedlings could test microbial factors in a similar way to the studies of Ellis and Pennington (1992). Effects of different soil moisture and temperature regimes on root efficiency would be more difficult to evaluate. Monitoring tree health after cutting and burning understorey vegetation in mesic dieback areas on the New South Wales coast could be used to test the model. Operational trials of contrasting burning regimes around the periphery of dieback sites would provide a robust test in the medium term. Opportunities for operational trials of this type are becoming increasingly limited as mesic dieback continues to expand.

Potential extension of the model

Regrowth dieback in Tasmania is possibly explained by this model. Podger *et al.* (1980) described a phenomenon affecting stands of messmate (*E. obliqua*) and mountain ash (*E. regnans*) older than about 30 years. Attempts to ameliorate regrowth dieback by thinning and fertilisation may have exacerbated the dieback by inducing high levels of leaf beetle defoliation (Wardlaw 1989). Fertilisation of these dieback affected *Monocalyptus* trees may have changed their physiology to the extent that their foliage resembles *Symphyomyrtus* in nutritional value and palatability to folivores.

Podger *et al.* (1980) stated that multi-aged stands of *E. obliqua* have developed in southern Tasmania following low-intensity fires. However, they did not indicate whether these were affected by regrowth dieback. Bowling and McLeod (1968) observed that regrowth areas that had been burnt at any stage during their development were less affected by dieback than unburnt stands. However, Podger *et al.* (1980) were unable to distinguish fire damage from regrowth dieback. Indications are that fire is deliberately excluded from these regrowth stands and that regrowth dieback may involve a similar process to the other types of dieback encompassed in this model. Any problems associated with root vigour of regrowth trees would be likely to appear when the stands had reached their peak water demand. This coincides (Bi *et al.* 2001; Vertessy *et al.* 2001) with the timing of the onset of regrowth dieback in Tasmania.

The proposed hypothesis is that exclusion of fire from regrowth forests established since intensive utilisation of the forests for timber production commenced is leading to changed soil and microclimatic conditions. The *Monocalyptus* species are particularly sensitive to their root environment and their root efficiency deteriorates in the increasingly mesic conditions. Declining root vigour induces stress as maximum water demand occurs after age 25. Resultant changes in physiology increase their susceptibility to pathogens and pests. Any adverse factor such as drought, fungal infection or other pest attack reinforces the physiological changes and contributes to their irretrievable decline. The hypothesis explains that the unhealthy trees are more susceptible to drought stress than the understoreys which are favoured by fire exclusion.

Conclusion

The simple proposed model accounts for a range of apparently dissimilar eucalypt dieback phenomena through a common process of soil moistening, eutrophication and nitrification, leading to impaired root function and changed physiology of eucalypts. It accommodates dieback involving heavy folivory as well as dieback where other factors or combinations of factors such as fungal infection and drought may be more important. The model reconciles the resource availability and stress models of herbivory by proposing that increased resources may improve foliar nutrient status whilst stressing the tree roots and initiating dieback by changing the balance between the vigour of the folivores or pathogens and the vigour of the eucalypt trees.

Unless management practices change, many currently mesic communities will be replaced by scrub, while currently grassy forests will become more mesic and decline.

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Appendix 1. Observations of eucalypt dieback in Bega Valley Shire

Catchment	Location	Tree species[1]	M[2]	OG[3]	Tenure[4]	Notes
Merrica River	tributary gully	*lon, glo*	✓		NPWS	
Wonboyn River	Collins Ck	*A. flo, lon, cyp*	✓		PP	
Wonboyn River	Watergums Ck	*ela*			LALC	
Wonboyn River	bridge	*vim*	✓		SF	trees 90 cm dbh
Scrubby Creek	picnic area	*lon, cyp, mue*		✓	SF3B	
Towamba River	Snake Track	*cyp, mue, ela*	✓	✓	SF3A, PP	
Towamba River	Whelans Swamp	*lon*	✓		SF3A, PP	
Nullica River	Boydtown	*lon, bos, tri, bau*	✓	✓	PP	
Nullica River	Old Highway	*bos, bau, cyp*			PP	
Mangaema Creek	Quarantine Bay	*lon, bos, tri, mue, mai, ela, cyp, sie*	✓	✓	PP, Shire Council	young ti tree on ridgetop
Freshwater Creek	Eden	*cyp*			PP	
Palestine Creek				✓	SF3A, 4	
Bellbird Creek		*smi*	✓		NPWS	
Jigamy Creek		*smi*, unknown			SF, LALC	distant view
Pambula Lake	Broadwater	*lon*	✓		PP	rapid progress
Yowaka River	Nethercote		✓	✓	PP, SF	
Pambula River	Stone trial	*cyp, mue, A. flo, ela*	✓	✓	PP, SF	trees 100 cm +
Pambula River	Pambula	*pil*			PP	
Merimbula Lake	Merimbula Beach	*pil, ter*	✓	✓	VCL	
Merimbula Lake	Boggy Creek	*ela, cyp, tri, glo, C. gum*		✓	NPWS, PP	sapling regrowth healthy
Merimbula Creek		*bot*			PP	
Merimbula Creek	Yellow Pinch	*mai, ela*	✓		NPWS, PP	
Sandy Beach Creek	Sapphire Drive	*lon, C. gum, glo*			PP	drainage?
Jellat Jellat Creek	Various	*smi, bau*		✓	NPWS	
Wallagoot Lake		*lon*	✓	✓	NPWS	progress rapid
Bondi Lake		*amp, agg, C. gum, cyp, A. flo*		✓	NPWS	no bellbirds in dry forest
Benooka Lake	western VCL	*sie, A. flo, lon*			VCL	dammed; only mature *sie* dead
Tathra Beach		*bos*			Shire Council	
Tathra Beach		*B. int*			Shire Council	no bellbirds

Appendix 1. (continued)

Catchment	Location	Tree species[1]	M[2]	OG[3]	Tenure[4]	Notes
Bega River	Mogareeka	*C. mac*			PP	
Bega River	Dr George Mtn	*smi, bau, ela, ter*			NPWS, PP	mature & regrowth stands
Bega	Brogo Pass	*ela*			PP	
Nelson Lagoon			✓		NPWS	distant view
Nelson Lagoon	Bermagui Road	*C. mac, glo*			NPWS	regrowth
Middle Lagoon	Bega Road	*lon, mue, bos*			NPWS	early mature
Middle Lagoon					PP	distant view
Bunga Lagoon	Bermagui Road	*ter*				
Bunga Beach	Bermagui Road		✓	✓	LALC, PP	distant view
Brockelos Creek	Bermagui Road	*bot, cyp, lon*		✓	PP	
Murrah River	Benny Gowings Road	*lon, bos*			SF, PP	
Barragoot Beach		*lon, bot*			PP	no bellbirds
Barragoot Lake					PP	distant view
Bermagui River	Nutleys Creek Rd				PP	bellbirds heard
Bermagui River		*bot*			SF	
Wallaga Lake	Scenic Drive	*C. mac*			SF	
Wallaga Lake	north side	*ter, tri*			VCL	
Wallaga Lake	Dignams Creek	*bot*			NPWS	

Notes [1]*Eucalyptus* or *A.* = *Angophora*, *B.* = *Banksia*, *C.* = *Corymbia* plus first 3 letters of specific name

[2]Identified as mature forest in Comprehensive Regional Assessment

[3]Identified as old growth forest in Comprehensive Regional Assessment

[4]NPWS = National Park or Nature Reserve; PP = private property; LALC = Local Aboriginal Land Council; SF = State Forest; VCL = vacant crown land; 3A, 3B, 4 = Forest Management Zones (Anon. 1999)