Review

Eucalypt decline in Australia, and a general concept of tree decline and dieback

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Abstract

Decline and dieback of eucalypts have been attributed to an exotic pathogen, various native organisms, climatic factors and agricultural or urban pollution. Where particular biotic or abiotic factors could not be singled out, they have been regarded as predisposing, inciting or contributing factors in 'diseases of complex etiology'. Ongoing monitoring of eucalypt decline during recent droughts in eastern Australia, together with extensive one-time observations across temperate Australia, provided opportunities to further examine some hypotheses of decline and dieback that were largely based on retrospective investigations.

Episodes of dieback can be distinguished from the process of chronic decline. Dieback episodes were associated with natural climatic extremes whereas chronic decline was associated with human management. Decline of forests in nature reserves was associated with exclusion of fire and grazing, while decline of rural trees was mostly associated with pasture improvement. Trees growing low in the landscape on soils with poor drainage and aeration were especially predisposed to decline. It appears that chronic abiotic stress causes tree decline when the function of roots is impaired by changes in soils. Climatic extremes can accelerate chronic declines associated with human management. A variety of pests, 'pathogens' and parasites can take advantage of trees that are stressed by environmental changes, especially eutrophication. Similarities between diebacks and declines in the Atlantic and Pacific regions suggest a simple unifying concept of tree decline and dieback. The implications for management of forest health are discussed.
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Keywords: Tree decline; Dieback; *Eucalyptus*; Abiotic stress; Eutrophication; Fire regimes

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1. Introduction

1.1. Suggested causes of tree decline

Two major 'waves' of rural tree decline in temperate Australia were accompanied by outbreaks of a wide range of folivores and by infestations of mistletoes (e.g. MacPherson, 1886; Norton, 1887; Landsberg and Wylie, 1988; Reid and Yan, 2000; Jurskis and Turner, 2002). The first wave during the late 19th century followed the initial agricultural development by settlers. The second wave commenced in the mid-20th century (e.g. Mackay et al., 1984) and increased dramatically later on (Wylie et al., 1993). Both were mostly attributed to the folivores (e.g. MacPherson, 1886; Kile, 1981a), however they were alternatively attributed to agricultural development (e.g. Norton, 1887; Landsberg et al., 1990). Forest 'diebacks' also became prominent in Australia around the mid 20th century (e.g. Hopkins, 1974), especially those associated with *Phytophthora cinnamomi* and *Armillaria*.

The 'germ theory', that pests or diseases singularly cause the death of trees, has been modified to recognise that tree decline and death are governed by the interaction of the host, the pest or pathogen, and the environment (e.g. Smith, 2004). This theory has been further elaborated by proposals that reduced 'predation' causes pest outbreaks (e.g. MacPherson, 1886; Neyland, 1996; Stone, 1999). There is continuing debate whether 'germs' initiate or respond to tree decline (Lowman and Heatwole, 1992; Farrow, 1999; Jurskis, 2004d), however a widely held view is that declines are caused by complex interactions between 'germs' and abiotic factors (e.g. Landsberg and Wylie, 1988; Manion, 1991; Manion and Lachance, 1992; Neyland, 1996; Old, 2000; National Forest Inventory, 2003). Alternatively, White (1993, 2004) proposed a general ecological principle that predators and 'herbivores' are limited by the nutritional value of their prey or their food plants. He argued that 'herbivores' and their predators increase when sick trees provide them with better food. This principle contradicts the germ theory and its embellishments, as well as the concept of 'complex interactions'.

'Rural dieback' in Australia is associated with chemical changes in soils caused by agriculture (e.g. Landsberg et al., 1990; Granger et al., 1994; Marsh and Adams, 1995). Unnatural chemical imbalances in the atmosphere, soils and waters have widely been proposed as causes of tree decline in Europe, North America and Japan (e.g. Kandler, 1992; Kreutzer, 1993; Ohrui and Mitchell, 1997), whereas natural causes have usually been proposed for declines and diebacks in the Pacific Rim (Huettl, 1993). However, climatic stress and/or global climate change have been put forward as the primary causes of 'diebacks' and declines in both polluted and unpolluted regions of the world (White, 1986; Auclair et al., 1992).

In Hawaii, Mueller-Dombois (1993) proposed a 'cohort senescence' theory that older stands of

Metrosideros are predisposed to die during climatic extremes in a natural process of succession. Some examples of eucalypt decline in Australia have been similarly portrayed as natural succession to rainforest (e.g. Ellis and Pennington, 1992; Stone et al., 1995). Alternatively, these and other declines in Australia have been attributed to changes in biogeochemical cycles as a result of unnatural fire regimes (e.g. Mount, 1969; Ellis and Pennington, 1992; Jurskis and Turner, 2002).

Debate continues about the relative importance of climate, biotic factors and human impacts as causes of tree decline or vegetation change (e.g. Mueller-Dombois, 1988; Houston, 1992; Kandler, 1992; Manion and Lachance, 1992; Huettl, 1993; McCulley et al., 2004). Australia's recent State of the Forests Report (National Forest Inventory, 2003) suggests that a wide range of crown 'dieback' syndromes in native forest in all States is caused by complex interactions between biotic and abiotic factors. The report does not contain maps or quantitative data on the extent of declining forest because of "the heterogeneity of data, the variety of causes and lack of spatial information" (National Forest Inventory, 2003). An attempt to indicate the reported extent of eucalypt declines in Table 1 presented similar difficulties.

Few options are available to manage the health of native forests (Simpson and Podger, 2000), and some attempts to arrest decline have been unsuccessful (e.g. Wardlaw, 1989) because the cause was not correctly identified (Jurskis and Turner, 2002). Continuing observations of chronic decline (Moore, 1961; Stone et al., 1995; Jurskis and Turner, 2002; Jurskis et al., 2003; Jaggers, 2004; Jurskis, 2004a), together with extensive, one-time observations throughout temperate Australia (Jurskis, 2004b) provided an opportunity to re-examine various hypotheses of tree decline and dieback. The roles of climate, human impacts and biotic factors are discussed in the context of ecological principles. A general concept of tree decline and dieback is presented and the implications for managing forest health are discussed.

1.2. Definitions

Australian use of the term "dieback" usually refers to protracted malfunction in stands of trees due to the persistent action of damaging factors (Podger, 1981). However, the term is also applied to relatively sudden deaths of trees and patches of understorey associated with root rots, drought or waterlogging (e.g. Davison, 1997; Fensham and Holman, 1999; Rice et al., 2004). Both uses may include the symptoms defined as dieback by the Society of American Foresters (Podger, 1981). Decline will be used in this paper to refer to protracted malfunction, and dieback will refer to

Table 1
Extent of some eucalypt decline syndromes in temperate Australia

Syndrome	Region	Extent	Reference
Severe eucalypt 'dieback'	Dandenong Ranges VIC	9% of forest	Ward and Neumann (1982)
Severe eucalypt 'dieback'	Coastal East Gippsland VIC	6000 ha	Ward and McKimm (1982)
Defoliation by *Uraba lugens*	Central Murray river system	Extensive, widespread	Parsons et al. (1991)
Rural tree decline	South east QLD	Widespread in most of region	Wylie et al. (1993)
Rural tree decline	TAS	All low rainfall districts	Neyland (1996)
Rural tree decline	Australian dryland farmland	Widespread and of great concern	Farrow (1999)
'Phytophthora dieback'	Jarrah forest WA	14% of total	Shearer and Smith (2000)
'Phytophthora dieback'	Public forest VIC	10% of total	Shearer and Smith (2000)
E. gomphocephala decline	Yalgorup WA	1000 ha	Tuart Response Group (2002)
E. wandoo decline	South west WA	Entire range	York Land Conservation District Committee (2002)
Defoliation by *Uraba lugens*	Southern jarrah forests WA	90000 ha	Farr et al. (2004)
Forest decline	Coastal NSW	100000s ha	Jurskis (2004a)
Forest 'diebacks'	TAS	>30000 ha	Jurskis (2004b)
'Armillaria root disease'	Central VIC	~2000 ha	Smith (2004)
Defoliation by insects	Central highlands VIC	Extensive, repeated	Smith (2004)
E. fasciculosa decline in woodland reserves	Mount Lofty Ranges, SA	48% average canopy loss	Ward (2005)

immediate impacts of acute stress. For example 'drought scorch' is a type of dieback that occurs when the leaves of eucalypts suddenly die and turn brown as if they had been scorched by heat from a fire. It is quite distinct from decline.

Improved pastures are areas where open forests or woodlands were partially or substantially cleared and exotic plants were introduced and fertilised to increase the carrying capacity for domestic livestock.

Natural fire regimes were those that applied immediately before European settlement of Australia. There were frequent ignitions by lightning and Aboriginal people, and the extent of fires was limited by climatic and edaphic factors and previous fires (e.g. Jurskis et al., 2003).

2. Eucalypt decline and dieback in temperate Australia

2.1. Recent observations

Eucalypt decline increased dramatically throughout Australia in the late 20th Century (Day, 1981; Wylie et al., 1993; Keane et al., 2000). For example, in coastal New South Wales during the early 1980s there were mostly isolated small patches of declining forest in sheltered gullies (Stone et al., 1995). A targeted survey north of Sydney in 1992 identified more than 2000 ha of declining forest in small scattered patches averaging 16 ha (Stone et al., 1995). In the far north coast, the area of declining forest increased from less than 1000 ha in 1992 (Stone et al., 1995) to at least 20,000 ha in 2004 (Forests NSW, unpublished data). By 2002, there were estimated to be more than 100,000 ha of severely declining stands in coastal state forests and the average patch size was about 40 ha (Jurskis, 2004a). As drought intensified during 2002, the area of unhealthy forest expanded rapidly and an increasing range of forest types in increasingly high topographic positions declined in health. By 2004, around 100,000 ha (about 20%) of forest in a single region in the far south were in decline (Jaggers, 2004), and a similar proportion of forest in an adjacent region was also declining (Jurskis, 2004a). By extrapolating the results of these regional surveys, using the proportions of susceptible forest types that are substantially affected by tree decline (e.g. Jurskis, 2004a), it is estimated that the total area affected in coastal New South Wales may be in excess of a million hectares.

I observed drought scorch in various parts of eastern Australia on five occasions from 1980 to 2004. It typically occurred on skeletal soils overlying bedrock or on coarse-grained soils in low rainfall areas. Saplings and shrubs as well as trees were affected. In some young, even aged eucalypt stands there were obvious contrasts between thinned and unthinned stands. Retained trees in thinned stands had vigorous crowns whereas in dense, unthinned stands, the dominant trees had suffered severe drought stress, and the subdominant trees had died. Drought scorch mostly occurs in higher and more exposed positions whereas decline is usually associated with lower and more sheltered positions in the landscape. Saplings and shrubs in declining stands are usually healthy, except in some cases involving *P. cinnamomi*.

2.2. Common features of eucalypt decline in temperate Australia

There are some common features of declining stands that relate to site quality, geography and forest type (Jurskis, 2004a,b,c,d). Declining stands have dense shrub and vine understoreys or dense grass or heavy litter on the ground. The shrubs, vines and grasses may be exotics or natives, and the shrubs may be mesic or sclerophyllous. Mesic shrubby or viney stands occur on sites that are not prone to drought, waterlogging or frost. In south-eastern mainland Australia they often contain colonies of bellbirds (*Manorina melanophrys*). The dry shrubby understoreys are often dominated by a few native weeds, such as sheoak, *Allocasuarina littoralis* or native cherry (*Santalaceae* spp., root parasites of eucalypts). They usually occur on sites that are subject to drought, waterlogging and/or frost. Declining stands in dry forests often carry high populations of mistletoes, or, in some areas, dense koala (*Phascolarctos cinereus*) populations (e.g. Martin, 1985).

Decline is usually associated with concave topography and depositional soils around dams, waterholes, swamps, drainage features and alluvial flats. Throughout coastal New South Wales it commonly occurs on Quaternary alluvium deposits in low, water accumulating sites with soils that are not well drained

or aerated. In multiple use public forests decline is prevalent in reserves along drainage features, and is usually more prevalent below roads traversing side-slopes than above them. Woodlands and open forests in valleys throughout temperate Australia are declining while dry forests on convex upper slopes and ridges mostly remain relatively healthy.

In declining stands, there are often differences between the health of eucalypts according to their species, subgenus and genus. There are about 600 species of eucalypts in 10 genera or subgenera that do not interbreed (e.g. Florence, 1996, pp. 4–5). In mixed stands in south-western Australia, *Corymbia calophylla* generally have better crowns than *Eucalyptus marginata*, *E. gomphocephala*, or *E. wandoo*. On the New South Wales coast, *C. maculata* and *E. microcorys* remain relatively healthy compared to their associates in declining stands (e.g. Stone et al., 1995). Near Melbourne *E. radiata* die out whilst *E. rubida* remain healthy. However, the health of any particular species of eucalypt in a region may vary according to the soils and topography. Stands on well structured, soils often remain healthy whilst nearby stands of the same species on less well-developed soils decline.

Declines and diebacks directly related to roots, including drought scorch, waterlogging, root rots and sudden deaths of trees or patches of shrubs, mainly occur in stands dominated by trees of the subgenus *Monocalyptus*, such as *E. obliqua*, *E. marginata* and *E. sieberi*. In one case, a rising watertable caused immediate and complete dieback of mature *E. sieberi* while *E. longifolia* and *Angophora floribunda* (another type of eucalypt) started to decline slowly (Jurskis and Turner, 2002). Decline involving arbivory in tree crowns often affects trees in the subgenus *Symphyomyrtus*, such as *E. saligna*, *E. longifolia*, *E. viminalis*, *E. camaldulensis*, *E. rudis* and *E. gomphocephala*. However, as decline intensifies in a region or locality, *Monocalyptus* crowns may also be heavily attacked. For example, *E. sieberi* and *E. pilularis* in declining stands have been uncharacteristically attacked by foliovores and *E. pilularis* has suffered unusual infestations of mistletoes.

The age of declining trees ranges from decades to centuries, but saplings in declining stands are usually healthy compared to poles or mature trees in the same stands. Saplings of *E. sieberi* were unaffected when mature trees were killed by a rising water table (Jurskis and Turner, 2002). In declining stands of *E.*

Fig. 1. Contrasting health between a grazed privately owned stand on the left and a long unburnt public forest on the right. The line indicates the cadastral boundary.

marginata, lignotuberous regrowth stems appear relatively healthy compared to coppice regrowth, whilst mature crowns are relatively poor.

Declining trees are usually evident in ungrazed and unburnt areas along roadsides and gullies. These retained strips often have dense understoreys of grass, shrubs and/or young trees. Retained trees in unimproved grazing paddocks or paddocks where crops have been harvested are often healthy compared to similar trees in improved pastures.

Stands that have been regularly grazed, burnt or slashed usually have healthy trees and an open grassy structure. Declining stands typically show no evidence of recent fires. Thus, there are many sharp contrasts between forest structure and health in relatively undisturbed conservation reserves, state forests and domestic water supply catchments compared to adjacent private lands. The reserves and public forests typically contain dense shrubbery and declining trees. Fig. 1 illustrates such a contrast. Similar contrasts are visible in a long-term fire study area in south-east Queensland (Jurskis, 2004c). Parts of the study area that have not been burnt for half a century contain many dead and dying stands whereas stands that have been burnt annually are relatively healthy.

3. Discussion

3.1. Theories of tree decline

Manion (1991) reviewed tree decline in North America, and identified some ''common denominators'' that are consistent with observations of tree decline in France (Landmann, 1993), *Metrosideros* dieback in Hawaii (Mueller-Dombois, 1986, 1993; Akashi and Mueller-Dombois, 1995) and eucalypt decline in Australia (Landsberg and Wylie, 1988; Jurskis and Turner, 2002):

- site or climate, especially physically unfavourable soils are predisposing or inciting factors;
- decline affects trees that are genetically suited to the site;
- fungi and insects usually contribute to tree decline rather than inciting it;
- feeder roots and mycorhizzae degenerate before the crowns of trees;

- declines set in as trees approach physiological maturity.

Five types of theories have been proposed to explain tree decline: germ theory, climatic impacts, cohort senescence or natural succession, human impacts and complex interactions of factors. These can all be tested against the foregoing observations and the literature on tree decline.

3.2. Germ theory

The germ theory proposes that individual biotic agents cause tree decline or dieback. For example, the introduction of chestnut blight (*Endothia parasitica*) from Asia early in the 20th Century almost eliminated chestnut (*Castanea dentata*) forests from North America (Heather and Griffin, 1978). However, tree decline associated with outbreaks of native pathogens or pests cannot be explained so simply. Disease epidemics occur when there is major environmental change, usually caused by humans (Heather and Griffin, 1978). Very few of the enormous variety of insects that eat eucalypts become pests (e.g. Carne and Taylor, 1978). Trees are not susceptible to substantial damage by native pests and pathogens (hereafter arbivores) unless they are stressed by factors such as drought, flood, frost, intense fire, radiation, fertilizers, herbicides, industrial emissions and/or competition from other plants (Carne and Taylor, 1978; Day, 1981; Ward and Neumann, 1982; White, 1984; Manion, 1991).

It is generally accepted that *P. cinnamomi* was very recently introduced to Western Australia and that it causes 'dieback' of *E. marginata*, jarrah (e.g. Shearer and Smith, 2000). However, the expression of disease associated with *P. cinnamomi* throughout temperate Australia varies with environmental conditions (Shearer and Smith, 2000). Dieback has been associated with very wet and/or dry seasons on poorly drained sites affected by human management such as tree cutting, earthworks and severe fires (Marks et al., 1975; Fagg et al., 1986; Davison, 1997; Shearer and Smith, 2000). Whether or not *Phytophthora* is exotic in parts of its range (Pratt and Heather, 1973), root disease is associated with human disturbance. It first became apparent after heavy machinery and intensive logging operations were introduced into forests on

subdued topography with poorly drained soils (Marks et al., 1975; Shearer and Smith, 2000). Intensive logging operations and severe fires can change soils directly by modifying runoff, drainage and aeration, and indirectly by reducing transpiration. They can also cause direct physical damage to trees. These are obvious impacts of human management (e.g. Jurskis et al., 2003). However, outbreaks of *Phytophthora* may also be caused by more subtle human interference, such as unnatural exclusion of fire in relatively undisturbed forests (e.g. Jurskis, 2004a,b,c). There is severe or extensive 'dieback' involving *Phytophthora* in many conservation reserves (e.g. Martin et al., 2001; Weste, 2003).

Outbreaks of *Phytophthora* have occurred in Victorian East Gippsland, but not in similar forests across the state border near Eden in New South Wales (Hopkins, 1974; Gerrettson-Cornell et al., 1979; Bridges et al., 1980). The fungus is common and widespread on both sides of the border (Pratt and Heather, 1973; Marks et al., 1975; Gerrettson-Cornell et al., 1979; Bridges et al., 1980) but intensive logging and climatic extremes did not incite epidemics in New South Wales (e.g. Hopkins, 1974; Bridges et al., 1980). The differences in expression of disease may relate to different forest management. Intensive forestry operations, including fire suppression, were introduced into East Gippsland much earlier than at Eden, and hazard reduction burning in regrowth forests has become routine at Eden but not in East Gippsland.

Davison (1997) suggested that there had been no conclusive evidence that jarrah were killed by *Phytophthora* and she reported a case where water-logging as a result of human activity was the cause of death. She suggested that crown decline in jarrah forest required further investigation. Waterlogging, '*Phytophthora* dieback' and other declines and die-backs are associated with water gaining sites on shallow soils with impeded drainage (e.g. Pratt and Heather, 1973; Ward and McKimm, 1982; Manion, 1991; Shearer and Smith, 2000; Weste, 2003). This suggests that dysfunction of tree roots is the general cause of decline. The germ theory does not provide a satisfactory explanation for eucalypt dieback or decline involving *Phytophthora* because the fungus is found in healthy stands and is not necessarily the cause of disease and death in unhealthy stands (Pratt

and Heather, 1973; Ward and McKimm, 1982; Davison, 1997). The same situation occurs with *Metrosideros* dieback in Hawaii (e.g. Akashi and Mueller-Dombois, 1995) and 'gully dieback' in Tasmania (Palzer, 1981a) where it is generally accepted that *Phytophthora* is a secondary or contributing factor.

Armillaria luteobubalina is a native root rot fungus that has been involved in decline and dieback of eucalypts in central Victoria and south-western Australia. Logging increases the level of inoculum by increasing the food supply provided by dead stumps and roots, and this supposedly triggers disease in healthy live trees (Kile, 1981b; Robinson, 2003). However, '*Armillaria* root disease' occurs in unlogged forests (Kile, 2000), and there is conflicting evidence whether the expression of disease is related to logging intensity, and therefore inoculum levels, in cutover stands (e.g. Kellas et al., 1987; Robinson, 2003). In cutover forests, the correlation of disease with the frequency rather than the intensity of logging operations (e.g. Kile, 2000) points to soil compaction and physical damage to trees, rather than the level of inoculum as likely causes of tree decline (Jurskis, 2004b).

'Diebacks' and declines attributed to *Armillaria* by Kile (1981b) were attributed to drought, logging, fire and poisoning by Edgar et al. (1976). Not all trees showing crown dieback had *Armillaria* infections and not all seedlings innoculated with *Armillaria* developed disease (Kile, 1981b). This contradicts the germ theory. Regrowth trees usually died suddenly, whereas mature trees usually declined slowly (Kile, 1981b) suggesting that *A. luteobubalina* takes advantage of conductive tissues affected by drought or mechanical injuries, and also contributes to decline by attacking unhealthy roots in unfavourable soils. Unfavourable soil conditions may be created in unlogged stands by unnatural exclusion of fire, and in cutover stands by compaction and reduced transpiration. *Armillaria* was regarded as a secondary pathogen in 'gully dieback' and 'bell miner dieback' (e.g. Bird et al., 1975; Carter et al., 1981; Palzer, 1981a; Stone et al., 1995). Various species of *Armillaria* commonly contribute to decline syndromes in North America (Manion, 1991).

Houston (1992) considered that declines in North America typically involved 'secondary attack' by various fungal diseases following environmental

stress, but he regarded outbreaks of defoliating and sucking insects as causes rather than effects of stress. In Australia, the germ theory has been similarly applied to declines supposedly caused by a wide range of native folivores (e.g. Wylie et al., 1993), however these pests cannot logically be responsible for the demise of hosts that have evolved with them over millennia, because either the pests and their hosts would have become extinct or they would have reached a balance that allowed them to exist together. Also, the germ theory cannot explain the observed contrasts in health of eucalypt stands separated only by fences or narrow roads (e.g. Jurskis, 2004a,b) or small cliffs (e.g. Moore, 1961) because these do not prevent the passage of arbivores from one stand to another.

3.3. Climate and weather

Climatic stress has been proposed as the primary cause of diebacks and declines around the world (e.g. White, 1986; Wardlaw, 1990; Auclair, 1993). However, there were very low indices of climatic stress between 1977 and 1984 (White, 1986) when there were high rates of tree decline and mortality in New England (Lowman and Heatwole, 1992), and trees continued to decline through periods of low climatic stress in other rural areas and forests throughout Australia (Podger, 1981; Landsberg and Wylie, 1983).

Drought is considered to be the major cause of rural and forest declines in Tasmania (Palzer, 1981a; White, 1986; Wardlaw, 1990; Neyland, 1996), however Palzer (1981b) suggested that it may be used as a 'scapegoat' when the causes of tree decline could not be identified. Dry and exposed ridgetop forests are generally unaffected by declines (Hopkins, 1974; Podger, 1981; Jurskis, 2004b) suggesting that agricultural practices in valleys and exclusion of fire from moist forests are the causes of tree decline (Jurskis, 2004b). Extensive drought deaths in Queensland mostly occur in drier inland areas (Fensham and Holman, 1999) where there is significantly less tree decline than in wetter coastal areas (Landsberg and Wylie, 1983; Wylie et al., 1993). This is consistent with the pattern of drought scorch and decline at a local scale. Mesic understoreys and young eucalypt stands are not affected by declines, tree decline is not related to stand density, and it is not ameliorated by thinning

(Hopkins, 1974; Podger, 1981; Wardlaw, 1989). These observations do not support the drought stress hypothesis for tree decline because understoreys and eucalypt saplings are prone to drought stress, and thinning can prevent drought stress.

Rice et al. (2004) considered that drought stress caused dieback by inducing cavitation and also rendered trees more susceptible to arbivory. They reported that trees with lower water potentials were more vulnerable to drought than other trees, but they did not distinguish between decline and dieback. Nor did Fensham and Holman (1999), who found that patchy deaths during a drought were not closely related to local rainfall deficits. Failure to distinguish between dieback caused by drought, and tree decline caused by other factors may have confounded their analyses. A number of studies have reported lower water potentials, under climatic stress or salinity, in healthy eucalypts than in declining eucalypts (e.g. Landsberg, 1985; Marsh and Adams, 1995; Zubrinich et al., 2000). Lowered water potentials during drought may cause dieback in healthy trees (e.g. Rice et al., 2004), whereas high water potentials may occur in unhealthy trees as a result of reduced leaf area and transpiration.

Auclair (1993) considered that waterlogging, drought and frost were the likely causes of eucalypt declines and White (1986) suggested that declines were associated with harsh sites. Episodes of drought scorch or waterlogging are associated with harsh sites but decline often occurs on moist and sheltered sites that are not prone to drought, waterlogging or frost. Chronic decline in eucalypt forests appears as a consistent wave moving outwards and upwards from flats and drainage systems with some vacillation around the edges according to climatic fluctuations. This is inconsistent with the constantly changing pattern that would be produced by climatic fluctuations (White, 1993). Natural climatic variations do not alter the competitive balance between trees and other plants, so dieback caused by climatic extremes is followed by recovery or regeneration of the same species (e.g. Jacobi et al., 1988). On the other hand, eucalypt stands suffering chronic decline are eventually replaced by low scrub because the competitive balance is upset by environmental changes. Contrasts between the health of similar stands and between trees and understoreys within a stand indicate that human

land management rather than climatic stress causes tree decline.

It is not certain whether management impacts can initiate tree decline in the absence of climatic extremes, however climatic extremes will inevitably recur during the normal lifespan of trees. For example, there were at least seven periods of extreme climatic stress in New England within 120 years (White, 1986). Norton (1887) saw no evidence of pre-European tree decline in the landscape, and the natural distribution of eucalypt ecosystems in south-eastern Australia has been relatively stable for the last 5000–10,000 years (e.g. Kirkpatrick et al., 1973; Barlow, 1981; Singh et al., 1981). These ecosystems have persisted through countless short-term climatic extremes as well as longer term climatic fluctuations such as the Medieval Warm Period and the Little Ice Age (e.g. Whitlock et al., 2003). Climatic fluctuations are not a satisfactory explanation for chronic tree decline.

3.4. Succession and cohort senescence

Wardle et al. (2004) reported increased nitrogen to phosphorus ratios in the soils of declining forests around the world, and suggested that tree decline was the ultimate stage of succession in the long-term absence of catastrophic disturbance. However, natural succession does not occur in eucalypt forest because eucalypts always remain the dominant species in their natural environment. For example, wet eucalypt forests are "highly resilient" to infrequent catastrophic fires, whilst drier eucalypt forests are "resistant" to frequent low intensity fires (Attiwill, 1994). Natural fires recurred in wet eucalypt forests at intervals less than the lifespan of the eucalypt trees (e.g. Turner, 1984). Prolonged absence of fire from drier forests is an unnatural disturbance (Jurskis et al., 2003) that can increase the availability of nitrogen and reduce the availability of phosphorus to eucalypt trees (e.g. Raison et al., 1993; Guinto et al., 2001) leading to their decline and premature death (Jurskis and Turner, 2002).

Although 'high altitude dieback' and 'bell miner dieback' have been portrayed as a natural succession to rainforest (Stone et al., 1995; Old, 2000), they both occur on sites that cannot support rainforest, and 'bell miner dieback' does not occur on sites with a well developed rainforest subcanopy (Jurskis, 2004a,b).

Eucalypts may be affected by decline from about 20 to 30 years of age, but their natural lifespan is measured in centuries (e.g. Jacobs, 1955; Burrows et al., 1995; Hickey et al., 1999), consequently, their death cannot be explained by senescence and natural succession (Landsberg and Wylie, 1988; Jurskis, 2004a). Trees start to decline as they approach physiological maturity (e.g. Podger, 1981; Manion, 1991; Landmann, 1993; Jurskis, 2004b). Only mature trees, not saplings, of *E. sieberi* were killed by a rising watertable, indicating that the saplings were better able than mature trees to adapt their root systems to changing soil conditions (Jurskis and Turner, 2002). The adaptive and regenerative capacity of young root systems can explain why young trees are not susceptible to decline (e.g. Manion, 1991; Mueller-Dombois, 1993; Jurskis and Turner, 2002; Bi, 2004a).

Decline may begin in moist eucalypt stands soon after the peak in sapwood basal area (Bi et al., 2001; Jurskis and Turner, 2002). This is when their evapotranspiration begins to decline along with the area of sapwood and leaves (Vertessy et al., 2001). Dysfunction of tree roots as a result of changing soil conditions (e.g. Manion, 1991; Ellis and Pennington, 1992) will reduce the ability of trees to compete with understoreys as sapwood area declines because more water will be available in the soil, and the trees will be less able to use the water, and less able to cope with excessively damp soil. Understoreys flourish in declining eucalypt stands (e.g. Podger, 1981; Wardlaw, 1989; Jurskis, 2004b), and may replace the forest (e.g. Jurskis et al., 2003). There is no evidence that this type of 'succession' occurred prior to European settlement, and it does not appear to be a natural process. On the other hand 'cohort senescence' in *Metrosideros* may occur naturally (Mueller-Dombois, 1993) when cohorts with declining sapwood area suffer prolonged waterlogging during climatic extremes.

3.5. Human impacts

Unlike many declining forests in the Northern Hemisphere, Australian forests are largely free of air pollution (National Forest Inventory, 2003), and White (1986) considered that tree decline in Australia was not the result of human environmental impacts. However, rural tree decline is associated with

agriculture (Landsberg et al., 1990; Granger et al., 1994; Marsh and Adams, 1995; Farrow, 1999) and it occurred after graziers substantially improved their pastures (e.g. Norton, 1887; Mackay et al., 1984). Eucalypts are poorly adapted to environments changed by European agricultural practices (Farrow, 1999), and decline is more severe with more intensive agriculture (Landsberg et al., 1990; Lowman and Heatwole, 1992; Wylie et al., 1993; Farrow, 1999). Trees in an improved pasture supported the highest density of koalas (a folivore dependent on eucalypts) found in New South Wales (Braithwaite, 1993).

The 'Phytophthora diebacks' were mostly associated with earthworks, intensive logging and intense wildfires (Marks et al., 1975; Fagg et al., 1986; Davison, 1997). Tasmanian forests declined after their natural fire regimes were disrupted (e.g. Ellis and Pennington, 1992; Jurskis et al., 2003), and burnt stands were less affected than unburnt stands (Bowling and McLeod, 1968). Mundulla yellows is a new 'disease' affecting eucalypts and other plants in highly disturbed sites across Australia (Hanold et al., 2002). It is caused by chemical changes in soils and its symptoms can be "reversed" by applying iron and manganese (Luck et al., 2004).

On the other hand, some declines of E. obliqua have been incorrectly ascribed to particular human impacts. They were thought to be caused by soil erosion and nutrient depletion, unnaturally dense regeneration and expansion of E. obliqua onto suboptimal sites as a consequence of intensive logging and burning (Florence, 1996). The hypothesis was that dense regrowth stands on poor sites may exhaust the available resources and fail to adequately self-thin. Conversely, Huettl (1993) suggested that increasing atmospheric carbon dioxide could provide better growing conditions that would increase competition between trees and reduce their vigour. However, E. obliqua declined on their favoured sites, after self-thinning, irrespective of stand density, basal area and the dominance of individual trees (Edgar et al., 1976; Palzer, 1981a; Podger, 1981; Wardlaw, 1989; Jurskis, 2004b). Thinning and fertilizing exacerbated the decline (Wardlaw, 1989) because they exacerbated the changes in soils that had initiated the decline (Jurskis and Turner, 2002). Self-thinning is driven by stand density, and the mortality of subdominant trees, the growth of dominant trees and the maximum

biomass of plants all decrease with site quality (Bi, 2004a). Conversely, dominant trees and subdominant trees are equally affected by declines due to environmental changes (Bi, 2004b).

Subtle impacts of passive human interference may be responsible for forest decline, and they may be overlooked on the assumption that they are natural (Jurskis, 2004c) leading to unnecessarily complicated theories of decline focussing on many secondary factors.

3.6. Complex etiologies

Tree decline has frequently been attributed to complex interactions of biotic and abiotic factors (e.g. Landsberg and Wylie, 1988; Manion, 1991; Manion and Lachance, 1992; Neyland, 1996; Old, 2000; Haswell and Walker, 2003; National Forest Inventory, 2003), although Kandler (1992) suggested that German forest declines attributed to complex interactions were really a complex of diseases whose biotic agents were yet to be identified.

Haswell and Walker (2003) considered that the causes of decline in E. gomphocephala (tuart) forests were not clear because there were a number of interrelated contributing factors. However, unnatural eutrophication was the simple explanation for algal 'blooms' and the decline of stromatolites in some waterbodies within the same forests (Monastersky, 1998; Jurskis, 2004b). Eutrophication can also explain the decline of the tuart forests, the 'bloom' of their understoreys, and the outbreaks of arbivores (Jurskis, 2004b). The variety of factors that contribute to tree decline should not confuse the search for its primary cause.

Norton (1887) saw no need to develop complex explanations of rural tree decline, although he recognised that it was difficult to consider the causes of tree decline retrospectively. Auclair et al. (1992) suggested that complex multiple-factor hypotheses of decline were "simply too difficult to test". The concept of 'bell miner dieback' (Stone, 1999; Old, 2000) in eastern Australia illustrates the difficulties of overly complex explanations based on retrospective investigations. Stone (1999) suggested that disturbing forests promotes dense understoreys that provide nesting habitat that attracts bellbirds, which initiate psyllid outbreaks by excluding other predators that

would otherwise control the psyllids. The psyllid outbreaks are supposed to eventually kill the trees.

However, bellbirds are increasing mostly in 'undisturbed' forests and the dynamics and timing of tree decline, understorey development and invasion by psyllids and bellbirds do not support Stone's hypothesis (Moore, 1961; Jurskis and Turner, 2002; Jurskis, 2004d). Tree crowns develop epicormic shoots before there are any obvious outbreaks of pests, and before bellbirds move in (e.g. Jurskis and Turner, 2002) indicating that feeder roots and mycorhizzae are degenerating (e.g. Manion, 1991) in response to changing soil conditions. The birds are a tertiary factor, responding to increased food provided by outbreaks of pysllids feeding on flushes of young epicormic leaves.

Frequent fires maintained grassy understoreys in forests of *E. saligna* (Sydney blue gum), whilst exclusion of fire promotes mesic understoreys (Anon., 1965). Recent retrospective studies have assumed that mesic understoreys and infrequent, intense fires are natural features of these forests (Stone et al., 1995) and have failed to recognise many of the contrasts between healthy and declining stands under different management. Psyllid plagues, borers, root rots, *Armillaria*, *Phytophthora*, bellbirds and logging have invaded or extended throughout the forests (Hopkins, 1974; Bird et al., 1975; Carter et al., 1981; Higgins et al., 2001; Jurskis, 2004a) making the retrospective separation of cause and effect very difficult.

'Waldsterben' presents similar difficulties in Europe. It occurs in forests with unnatural species compositions and long histories of intensive management including tree planting, harvesting of litter and humus, and salvage of declining trees (Kandler, 1992). The forests have suffered declines since at least the 19th Century, and various episodes of climatic stress and air pollution have occurred in various regions (Kandler, 1992). Since about the 1950s, there have been widespread increases in nitrogen supply, which have caused increased growth or decline in different situations (Kreutzer, 1993).

By observing the early stages of eucalypt decline in relatively undisturbed Australian forests some of the problems of retrospective observations and multiple factors may be avoided. It will be easier to separate cause and effect, and distinguish secondary factors or symptoms.

Complex decline theories may forestall management actions (e.g. Tuart Response Group, 2002; National Forest Inventory, 2003) or lead to ineffective actions. For example, installing 'possum guards' on rural trees in Tasmania, and removing bellbirds or noisy miners (*Manorina melanocephala*) from declining stands on the mainland have failed to arrest declines (e.g. Clarke and Schedvin, 1999; Jurskis, 2004b) and consumed resources that might have otherwise been available for more effective actions. Creating 'habitat' features such as shrubby understoreys that supposedly attract predators of pests can actually increase the stress on trees by favouring the competing vegetation and reinforcing the changes in soils and microclimate that cause tree decline (e.g. Jurskis, 2004b).

3.7. Fire, grazing and eucalypt decline

A wide variety of pests and diseases afflict different types of eucalypt forest in supposedly undisturbed and unpolluted reserves (Martin et al., 2001; Weste, 2003; Jurskis, 2004a,b). This chronic and debilitating arbivory by native organisms in relatively undisturbed forests indicates that some insidious but widespread, unnatural factor is affecting the forests (e.g. Carne and Taylor, 1978; Heather and Griffin, 1978; Day, 1981; White, 1984; Manion, 1991). Spatial analysis of tree decline in one nature reserve indicated that infection by *Phytophthora*, invasion by bellbirds and 'cohort senescence' could not explain the patterns of decline (Martin et al., 2001). Most reserves have been 'protected' from fire for long periods and have unnaturally dense understoreys or ground covers (Jurskis, 2004b), but this insidious disturbance has largely been overlooked. The history of structural changes and decline in Australian forests parallels changes in fire regimes at very broad scales and at very fine scales (Jurskis, 2004c,d; Jurskis et al., 2003).

There were sharp boundaries in natural fire regimes corresponding to sharp physical changes in soils and microclimates according to parent materials and topography (Jurskis, 2000). Natural vegetation boundaries also corresponded to these edaphic boundaries. For example, Turner (1984) found evidence of only one fire about 1000 years earlier in a rainforest stand on krasnozem soil, whilst there was evidence of eight fires at intervals of about 300 years in the surrounding

wet sclerophyll stand on brown forest soil. With post-European human interference, moisture and shade loving plants and infrequent intense fire regimes are expanding out of their restricted natural 'habitat' into naturally drier and more open forests (Turner, 1984; Jurskis et al., 2003), and decline of 'undisturbed' eucalypt forests are a consequence of these changes. However, unnatural exclusion of fire has rarely been considered as a cause of eucalypt decline in Australia because many ecologists fail to recognise passive management as human interference (Jurskis, 2000,2002,2004c).

For example, Florence (1996) considered that it was natural for eucalypts to regenerate in small gaps, but he paradoxically regarded the long-term absence of fire as a natural phenomenon. Frequent low intensity fire is critical to regeneration of eucalypts in small gaps because germinants must access mineral soil to survive, seedlings must have light to develop and lignotubers must have light and freedom from understorey competition to survive (Jacobs, 1955). Frequent low intensity fire maintains the competitive advantage of mature eucalypts over other plants in dry and moist forests, and maintains their capacity to regenerate when they are burnt or blown down or die of old age. Infrequent high intensity fire in wet forests allows eucalypts to regenerate and maintain their dominance over other slower growing plants that 'love' moisture and shade.

When fire is kept out, profound changes occur in dry and moist eucalypt forests including: increased nitrogen content in trees' foliage, increased rates of leaf fall, increased weight and nutrient content of litter on forest floors, increased organic matter, nitrogen and moisture in topsoils, increased rates of mineralisation and cycling of nitrogen in soils and vegetation, increasingly dense groundlayers or understoreys, increased ratios of nitrogen to phosphorus in litter and topsoils and reduced availability of phosphorous to trees (e.g. Raison et al., 1993; York, 1999,2000; Guinto et al., 2001; Wardle et al., 2004). These changes inhibit mycorrhizae, stimulate unfavourable microbes in the soil (e.g. Marks et al., 1973, 1975; Ellis and Pennington, 1992; Florence, 1996; Davison, 1997; Shearer and Smith, 2000) and make the sap and leaves of trees more nutritious, palatable and accessible to pests, parasites and pathogens (e.g. Landsberg et al., 1990; Granger et al., 1994; Turner,

2004). Problems associated with increasing nitrification in soils have also been reported from a variety of forests in other parts of the world (e.g. Hesterberg and Jurgensen, 1972; Balchi and Halmschlager, 2003). These types of changes in soils, nutrient cycles and vegetation result in forest decline following exclusion of fire, and rural tree decline following pasture improvement (e.g. Landsberg et al., 1990; Ellis and Pennington, 1992).

Dense understoreys or thick layers of 'mulch' hinder the propagation of fires in mild conditions, and prescribed burning becomes more difficult after a period of fire exclusion. Fires propagate relatively slowly downhill, and lower slopes are less exposed to sun and wind. The general reduction in the use of low intensity fires in recent decades (Jurskis et al., 2003) has particularly affected drainage features and slopes and flats below roads and cliffs. The pattern of decline mirrors the pattern of fire regimes. The area of frequently burnt forest is contracting towards ridge-tops and convex upper slopes as the area of declining forests expands outwards and upwards from flats, drainage features and concave slopes.

Suppression of wildfires becomes difficult and dangerous after a period of fire exclusion because dense understoreys and thick ground layers can sustain very intense fires under severe climatic conditions (e.g. Jurskis et al., 2003; Shaw et al., 2004). Increases in the occurrence and extent of intense wildfires reinforce the process of forest decline. High intensity wildfire, like pasture improvement, can increase nitrogen cycling in soils and understoreys (Jurskis et al., 2003) and cause long lasting hydrological changes because of the diminished regenerative capacity of declining forests (Jurskis and Turner, 2002).

Exclusion of fire has been recognised as a factor in some cases of eucalypt decline. Bowling and McLeod (1968) found that burnt stands were less affected by 'regrowth dieback' than unburnt stands. 'High altitude dieback' is a consequence of fire exclusion, and can be remedied by felling and burning understoreys (Ellis et al., 1980; Ellis and Pennington, 1992). Farr et al. (2004) found some evidence that prescribed burning moderated outbreaks of gumleaf skeletoniser (*Uraba lugens*) in the southern jarrah forests. Guinto et al. (1999) found that annual burning enhanced the growth of *E. tereticornis*, whereas there was severe tree

decline in some parts of their experimental areas where fire has been excluded for 50 years (Jurskis, 2004c). Infestations of mistletoes in another fire study area increased more rapidly in areas that had little or no fire compared to frequently burnt areas (Forests NSW, unpublished data). Bradshaw (2000) recommended that understoreys should be cleared and burnt to promote regeneration in declining tuart forests, and he suggested that more natural open conditions could be maintained in future by using frequent low intensity fire regimes.

Some forests where fire had been excluded for long periods remained healthy and open while they were regularly grazed by domestic stock, but are declining and suffering shrub invasion since grazing was withdrawn (e.g. Jurskis, 2002, 2004b). Grazing has been withdrawn from areas that were recently dedicated as conservation reserves or fenced to encourage regeneration, and from roadsides and travelling stock reserves because of increasing dangers of traffic or because the surrounding land use has changed from grazing to cropping or 'hobby farms' (e.g. Jurskis, 2004b,c). Retained trees in cropped paddocks are often healthy. It appears that grazing and cropping can substitute for the natural function of frequent low intensity fires that prevents accumulation of nitrogen and moisture, changes in forest structure and microclimatic changes in the soil (Jurskis, 2004c).

McCulley et al. (2004) found higher pools of organic carbon and nitrogen, more microbes and higher potential rates of nitrogen mineralisation and nitrification in soils in Texas where shrubs had invaded grasslands as a result of changed fire and grazing regimes. These are the same changes that occur in eucalypt forests when fire and/or grazing are excluded. If ecologists fail to recognise these changes (e.g. Jurskis, 2000, 2002; Keith and Henderson, 2002) and focus instead on pests and diseases as agents of decline (e.g. Heatwole and Lowman, 1986; Wylie et al., 1993), there will continue to be little progress towards managing forest health. Widespread forest decline involving many contributing factors has been associated with post-European changes in fire and grazing regimes in North America (Koonce and Roth, 1980; Anderson et al., 1987; Bergeron and Leduc, 1998; Dwire and Kauffman, 2003; Hessburg and Agee, 2003). As a result, ecologists have called for the reintroduction of natural fire regimes to improve forest

health and fire protection in dense unhealthy forests (Shaw et al., 2004).

3.8. Ecological context of eucalypt decline

Physiological responses to unnatural environmental changes vary between eucalypt species and subgenera (e.g. Bowling and McLeod, 1968; Mount, 1969; Palzer, 1981a; Neyland, 1996; Jurskis and Turner, 2002; Turner, 2004). A common agent of decline would not be expected to produce synchronous regional declines across different tree species and sites as suggested by Kandler (1992). For example, increased nitrogen supply in Central European forests has caused large increases in growth of some species and stands as well as declines in health of other stands, whilst some stands with a low level of premature needle cast have also shown increased growth (Kreutzer, 1993).

'Gully dieback', 'high altitude dieback', 'regrowth dieback', waterlogging, drought and 'root diseases' particularly affect *Monocalyptus* (Mount, 1969; Palzer, 1981a; Florence, 1996; Davison, 1997) because their roots are very sensitive (e.g. Florence, 1996) to physical changes in soils. *Symphyomyrtus* are particularly adapted to chemically fertile sites (Florence, 1996) and become increasingly attractive to folivores (e.g. Stone et al., 1995; Neyland, 1996) when nutrient cycling accelerates in 'rural dieback' and 'bell miner dieback' (Landsberg et al., 1990; Jurskis and Turner, 2002). *Corymbia* are intermediate in their adaptations and generally resistant to pests in their roots stems and leaves (e.g. Carne and Taylor, 1978; Wylie et al., 1993; Stone et al., 1995; Florence, 1996). Within individual species, susceptibility to decline varies with site conditions. Monocalypts are particularly vulnerable where they grow on water gaining sites, over impervious subsoils or shallow water tables (e.g. Shearer and Smith, 2000).

Arbivores have particular habitats and particular responses to environmental changes caused by humans. *Phytophthora* and *Armillaria* are not involved in 'high altitude dieback' because the climate is too cold (e.g. Ellis and Pennington, 1992; Shearer and Smith, 2000). However, both of these fungi as well as various psyllids and borers are able to take advantage of 'bell miner dieback' (Bird et al., 1975). Plants that compete with the eucalypts also

have particular environmental requirements and responses to human disturbance. Exclusion of fire favours *Lantana camarum* and *Ligistrum* spp. in northern New South Wales, native vines and shrubs in southern New South Wales, Tasmania and south-western Australia and some grasses and ferns in central Victoria (e.g. Jurskis, 2004a,b). Mesic shrubs and thick groundcover vegetation reinforce microclimatic changes in topsoils caused by exclusion of fire. Legumes in improved pastures fix atmospheric nitrogen and reinforce nitrification in soils.

Folivores can reinforce eucalypt decline because defoliation stimulates new epicormic leaves that are more nutritious and palatable to the folivores than mature leaves (Landsberg, 1990). Parasitic plants including mistletoes, cherries and dodder laurel vines (*Cassytha* spp.) may respond to high water potentials in stressed trees (e.g. Landsberg, 1985; Marsh and Adams, 1995; Zubrinich et al., 2000) because pronounced negative gradients towards the parasites will enhance their access to water and nutrients (e.g. Fisher, 1983). Trees will lose their capacity to fight the 'infection' as they lose resources to the parasites.

Some eucalypt species in declining stands are attacked by parasites or pests that do not usually affect them. Increased pest populations in the landscape as a result of pasture improvement or exclusion of fire from forests can exaggerate the spatial and temporal patterns of responses by pests to trees that are suffering climatic stress (e.g. Jurskis and Turner, 2002; Dwire and Kauffman, 2003; Hessburg and Agee, 2003; Shaw et al., 2004). Thus, environmental changes caused by human management can increase the range of species and sites that are 'predisposed' to decline, and stress caused by climatic extremes may initiate chronic decline in formerly 'resistant' trees. Any pest or competitor that is favoured by the same environmental changes that stress eucalypts will contribute to the decline of the trees. There is nothing complex about these responses and interactions. They are predictable consequences of human impacts on the environment of the tree and its competitors and 'predators'.

Manion and Lachance (1992) cautioned that a concept of forest decline should not "pool an array of problems identified by generic symptoms that are best understood as distinct problems". Landsberg and Cork (1997) stated that no single theory adequately explained the various relationships between 'herbivory' of eucalypts and environmental disturbance. On the other hand, White (1993) suggested that ecologists must search for general rules which explain the variability we observe rather than retreating into the "protective jungle of complexity".

Eucalypt decline in Australian forests has many similarities with other declines in Pacific and Atlantic forests, suggesting that too much emphasis has been placed on climate change, air pollution, 'germs' and their 'complex interactions', at the expense of more basic factors in tree decline. The commonalities between declines and diebacks around the world suggest that declines are caused by chronic abiotic stress. Biotic factors merely contribute to and reinforce physical or chemical stress to trees (except where exotic pathogens are introduced to new hosts). Particular species of trees are predisposed to decline because their physiological responses, and their competitors' responses to environmental changes, are more dramatic than those of other species. Similarly, the relative impact of physical and chemical changes will vary with site and soil conditions. For example, hydrophobicity, reduced evapotranspiration, or reduced porosity as a result of intense fires or compaction of soils will affect poorly drained sites more than freely drained sites.

4. A simplified perspective of decline and dieback

Human activities, such as clearing, earthmoving, polluting, fertilising, sowing exotic legumes and imposing unnatural fire regimes, can make the environment less suitable for some trees and more suitable for their competitors and 'predators'. Plants that are genetically better adapted to the new conditions will outcompete or replace those that are disadvantaged by the changes.

Manion's (1991) concept can be simplified (Fig. 2), and factors involved in dieback or decline can be more consistently classified as follows: Predisposing factors are genetics and site. Physical or chemical factors incite diebacks and declines. Natural weather extremes lead to temporary outbreaks of pests and dieback of trees followed by recovery or regeneration. Unnatural (post-European) human impacts incite
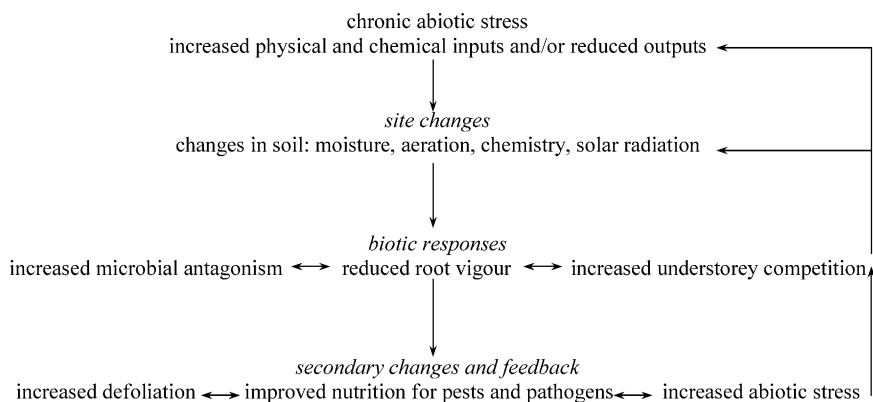
chronic abiotic stress
increased physical and chemical inputs and/or reduced outputs ←

↓

site changes
changes in soil: moisture, aeration, chemistry, solar radiation ←

↓

biotic responses
increased microbial antagonism ←→ reduced root vigour ←→ increased understorey competition

↓

secondary changes and feedback
increased defoliation ←→ improved nutrition for pests and pathogens ←→ increased abiotic stress

Fig. 2. A simplified perspective of tree decline.

chronic decline by changing the environment, causing stress to trees, and favouring other plants and animals. Arbivores including fungi in roots, stems and leaves, parasitic plants, boring, sucking and leaf eating insects, and leaf eating vertebrates are contributing factors. They respond to improved food quality in the sick trees (White, 1993, 2004), and directly to the site changes, but they cannot suddenly flourish for no reason. Diebacks may be a direct result of injuries to trees whereas declines involve one or many contributing factors.

Two examples of supposedly different and complex eucalypt 'diseases' (Old, 2000) can be used to illustrate this simplified perspective. Old (2000) considered that 'bell miner dieback' was associated with insect pests whereas 'high altitude dieback' was associated with successional changes. However, both declines appear to be caused by unnatural exclusion of fire from grassy forests (Ellis and Pennington, 1992; Jurskis and Turner, 2002).

In the case of 'bell miner dieback', 'mulch' builds up after fire is excluded (e.g. York, 1999; Jurskis and Turner, 2002), changing the soil conditions (e.g. Raison et al., 1993; York, 2000; Guinto et al., 2001; Jurskis and Turner, 2002; Wardle et al., 2004) and inhibiting tree roots and mycorrhizae (e.g. Ellis and Pennington, 1992; Jurskis and Turner, 2002). As the roots decline and die, 'root rot' fungi increase (e.g. Bird et al., 1975). The stressed trees shed their leaves prematurely (e.g. Stone and Bacon, 1995) adding to the 'mulch' on the ground. They sprout young epicormic leaves (Stone, 1999) that sustain outbreaks of folivorous insects (e.g. Landsberg, 1990), which

add frass to the 'mulch' and further promote premature shedding of leaves. Young leaves are soft and rich in nitrogen (Landsberg, 1990), which is quickly returned to the soil and taken up by competing vegetation (Turner, 2004). Colonies of territorial bellbirds are attracted by the insects (Jurskis and Turner, 2002) and they exclude other predators that would otherwise 'damp' the increasing populations of insects (Stone, 1999). Reduced canopy and increased nutrient cycling promote mesic shrubs and vines, including exotic weeds (Stone, 1999), which shade the ground and further accelerate the cycling of nutrients (Turner, 2004). Borers multiply in the inner bark and sapwood of the declining trees (Moore, 1961; Bird et al., 1975; Stone, 1999), and also contribute to the process. The moist and shady understorey can no longer sustain low intensity fires (Jurskis et al., 2003). The sparse epicormic shoots in the eucalypt crowns are repeatedly replaced. They do not produce flowers and set seed because development of shoots over several years is required to sustain the lengthy process from initiation of flower buds through to ripening of seed (e.g. Florence, 1996). Severe wildfire eventually destroys the stand and the remaining nutrients in the trees are returned to the soil. The mesic understorey regenerates vigorously and 'controls' the site (Jurskis and Turner, 2002).

In 'high altitude dieback', exclusion of fire from naturally grassy stands of *E. delegatensis* also causes changes in the soil conditions and understorey (Ellis and Pennington, 1992). The roots and mycorrhizzae degenerate, and the canopy thins but there are no root rot fungi or gregarious folivores adapted to the cool

environment (Ellis et al., 1980; Ellis and Pennington, 1992). Native understorey plants respond to the changes in the soil and the microclimate under the reduced canopy (Ellis and Pennington, 1992). They reinforce these changes and contribute to the process of decline (Jurskis and Turner, 2002). Although the feedbacks and contributing factors are very few and subtle compared to the previous example, the process is essentially the same.

5. Implications for management

Considerable resources are being devoted to research of contributing factors in tree decline but few corrective actions are being applied in eucalypt forests other than quarantine and hygiene measures to restrict the spread of *Phytophthora* (Simpson and Podger, 2000; Tuart Response Group, 2002; National Forest Inventory, 2003). Management of abiotic inputs and outputs as well as management of competing understoreys would have more direct impacts on forest health than management of parasites, pests and diseases (e.g. Fig. 2; Ellis et al., 1980; Monastersky, 1998; Luck et al., 2004). For example, measures to reduce SO_2 emissions allowed conifers to recolonise the Ruhr (Kandler, 1992).

Manipulation of silvicultural practices is the only option available to manage eucalypt 'diseases' in native forests (Simpson and Podger, 2000) but conventional silviculture may exacerbate forest decline (e.g. Wardlaw, 1989; Jurskis and Turner, 2002; Robinson, 2003). Prescribed burning appears to be the only silvicultural practice that can have widespread application in conservation reserves and timber producing forests. Passive management of nature reserves in Australia has failed to maintain healthy ecosystems, especially in the case of the grassy forests that were most depleted by clearing for agriculture and are now mostly declining in health and changing in structure (e.g. Wylie et al., 1993; Neyland, 1996; Bradshaw, 2000; Jurskis, 2000, 2004b; Jurskis et al., 2003).

To conserve healthy dry and moist eucalypt forests it will be necessary to restore more natural outputs of nitrogen and moisture by using frequent low intensity fire (e.g. Bradshaw, 2000) and/or grazing (Jurskis et al., 2003; Jurskis, 2004c). Ecological burning

regimes should be integrated with hazard reduction burning to protect forest health as well as social and economic values. In situations where fire has been excluded, but grazing has maintained healthy open forests, any withdrawal of grazing should be accompanied by re-introduction of frequent low intensity fire regimes (Jurskis, 2004c). Where management aims to maintain or re-establish stands of native eucalypts outside forests, provision should be made to prevent accumulation of 'mulch' and proliferation of competing vegetation by using fire, grazing, slashing or herbicides, and by not sowing exotic pastures or adding fertilisers (e.g. Neyland, 1996; Jurskis, 2004b). Deliberate planting of native understorey species to create diversity is generally unnecessary because they mostly regenerate aggressively, and it may be counter productive because they compete with the trees and reinforce the primary causes of decline (Jurskis, 2004b).

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