

The uniqueness of habitats in old eucalypts: contrasting wood-decay fungi and saproxylic beetles of young and old eucalypts

T. Wardlaw^{1,2*}, S. Grove², A. Hopkins³, M. Yee¹, K. Harrison⁴ and C. Mohammed^{2,4,5}

¹Forestry Tasmania, GPO Box 207, Hobart, Tasmania 7001

²Co-operative Research Centre for Forestry, College Road, Sandy Bay, Tasmania 7005

³Forest Protection, Scion, Private Bag 3020, Rotorua 3010, New Zealand

⁴Department of Agricultural Science, University of Tasmania, College Road, Sandy Bay, Tasmania 7005

⁵CSIRO Sustainable Ecosystems, College Road, Sandy Bay, Tasmania 7005

*e-mail: tim.wardlaw@forestrytas.com.au (corresponding author)

Abstract

Over the past decade, considerable research has been done in Tasmania to better understand the ecological value of old eucalypts in temperate wet forests with respect to communities of wood-decay fungi and wood-inhabiting (saproxylic) beetles. Old eucalypts provide unique habitats for these organisms, and support a high species diversity and distinctive assemblage composition. However, the value of old eucalypts in providing unique habitat extends well beyond the time the trees are alive. Once fallen, their dead remains may take several centuries to decompose, providing further habitat for fungi and invertebrates which are the most species-rich component of forest biodiversity, including rare species with very restricted ranges.

The development of communities of wood-decay fungi and saproxylic beetles in living eucalypts at different stages of their life can be understood in terms of the stages of crown development. Thus, young trees in the crown-lifting phase are characterised by white-rot fungi colonising as small branches are shed. In contrast, older trees in the crown-retraction phase harbour a diverse suite of fungi, many of them causing brown rot, associated with sizeable wounds resulting from failure of large branches, dieback or fire.

A similar transition is seen for beetles, with a diverse community of obligately saproxylic beetles only appearing in mature trees that contain brown rot. The switch that provides conditions suitable for the colonisation of mature trees by fungi that cause brown rot, while ecologically significant, remains unresolved.

Importantly, research to date has shown that there is a continuum of habitats for decay fungi and saproxylic beetle assemblages in mature trees and the logs that these generate. Maintaining the habitats provided by large logs therefore requires a perpetuation of the mature growth stage of living trees. This in turn can only be achieved through maintaining a diversity of forest ages across the landscape, and allowing a proportion of those forests to reach maturity at appropriate scales of space and time.

Introduction

The management of old-growth eucalypts has divided the Australian public for at least the past two decades. In Tasmania, particularly, this debate has been hotly contested, and rarely does an election pass without the management of old-growth eucalypts becoming a political issue. The main focus of the old-growth debate in

Tasmania has been the tall, wet eucalypt forests dominated by *Eucalyptus regnans*, *E. obliqua* and *E. delegatensis*. Together, these three species sustain Tasmania's hardwood sawmilling and veneer industries, with supply from Crown (State) forest mandated through government legislation (Forestry Act 1994). While the massive size attained by these three species makes them very valuable for timber products, it also provides a powerful symbol for environmentalists: individual trees are anthropomorphised with mystical names such as "Icarus' Dream", "Gandalf's Staff" and "El Grande" (see www.gianttrees.com.au).

For over half a century, foresters have argued, on ecological grounds, that these wet eucalypt forests exist only as a result of periodic catastrophic disturbance resulting from wildfires. Stand-replacing wildfire producing even-aged regeneration was the accepted paradigm for wet eucalypt forests. The silvicultural practice of clearfell harvesting followed by high-intensity burning and aerial sowing of seed (CBS) was thus adopted widely, and was touted as emulating this wildfire disturbance. Increasingly, however, it is being recognised that in certain aspects CBS does not emulate wildfire, and that when done on regular, 80-100 year cycles CBS will result in forests that are much simpler in structure than those resulting from natural wildfires (Lindenmayer and McCarthy 2003). This is because wildfires in wet eucalypt forests are often not completely stand-replacing, particularly in areas where there has been a long fire-free interval resulting in a mixed forest consisting of a mature eucalypt overstorey with a rainforest understorey (Turner *et al.* 2009). This knowledge has significant implications for forest management, where the goal is to sustain not just wood supply but also the many other values that forests provide, including the provision of sufficient suitable habitat at appropriate spatial scales to allow the perpetuation of forest-dependent species across their range (Forestry Tasmania 2008).

The public and scientific focus on the value of old-growth eucalypts for species dependent on the habitats they provide has tended towards charismatic mammal and bird species. However, in the wet eucalypt forests of Tasmania and elsewhere, these groups make up a very small proportion of the forest biodiversity. Studies around the Warra Long-Term Ecological Research (LTER) site in southern Tasmania, and based mostly in wet eucalypt forests, have found that total species richness is dominated by much smaller life-forms, particularly the beetles (and other invertebrates) and the fungi (Figure 1). Not only do these two groups dominate the richness of species lists in these wet eucalypt forests, they also provide vital roles in ecosystem function as 'ecosystem engineers' (creating habitat for other species), nutrient recyclers (Edmonds and Marra 1999) and soil builders (Lavalle *et al.* 1997).

Over the past decade, a substantial research effort has therefore been devoted to a better understanding of invertebrate and fungal diversity in wet eucalypt forests in southern Tasmania, particularly those elements that are dependent on old trees and on structures originating from such trees. In this paper, we review that body of research and draw conclusions that may guide future management of these forests.

Patterns of tree development associated with ageing of eucalypts

Under natural conditions, eucalypt seedlings in wet forest establish as an age cohort following a disturbance event sufficiently intense to create large openings in the dense canopy of the standing forest, expose mineral soil, and reduce populations of seed-feeding ants and browsing herbivores. Typically, such disturbance events are extensive wildfires. While small-scale disturbance, such as tree-falls, can trigger eucalypt regeneration, the seedlings typically become suppressed due to shading from the surrounding intact forest (Alcorn 2002).

Regardless of whether temperate wet eucalypt forests regenerate from stand-replacing wildfires producing single-aged

forests, or from non-stand-replacing fires producing multi-aged forests, each cohort of eucalypt regeneration typically follows

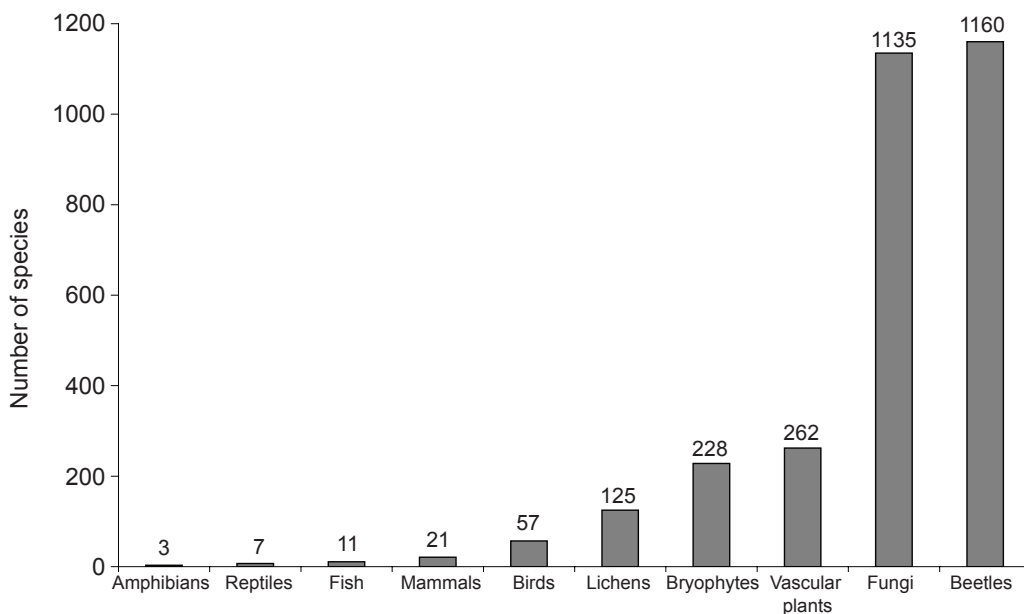


Figure 1. Number of species in different life-form groups recorded in the Warra Long-Term Ecological Research (LTER) site, southern Tasmania (www.warra.com). The number of species shown for the different life-forms is not based on equal sampling effort for each life-form across the range of ecological zones present in Warra. The numbers of species shown for vascular plants and lichens, in particular, are likely to be underestimates.

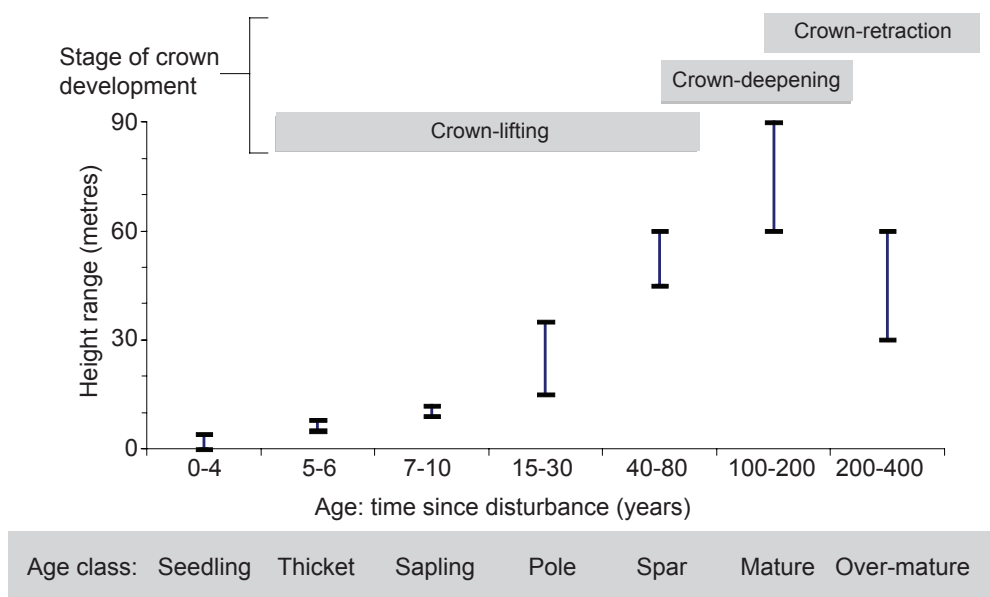


Figure 2. Stages in the development of *Eucalyptus regnans* across its natural life-span (illustrated as height ranges at particular age-classes). Adapted from Ashton (1975).

a characteristic pattern of development (Figure 2). After seedlings have become established three distinct phases of crown development can be recognised: *crown-lifting*, *crown-deepening* and *crown-retraction* (Figure 3).

The *crown-lifting* phase, which occupies most of the first century of development, is a “race to the sky”, as the light-demanding eucalypts get their heads above their neighbours and above the dense layer of regenerating understorey species. Attrition rates are high for individuals, and barely one tree in ten will make it past the first 30 years (Jackson 1968). During this period of rapid height growth, branches at the base of the crown have a relatively short life as they quickly become shaded. As these branches die, they are quickly lost through an efficient branch-shedding mechanism (Jacobs 1955),

resulting in a straight, branch-free trunk - an attribute much admired by sawmillers.

After about 70-100 years since disturbance, the crowns of the surviving eucalypts are growing in a more open light-environment; branches at the base of the crown persist, and the rate of crown-lifting slows. This marks the beginning of the *crown-deepening* phase. Further height growth over the next 100-200 years results in the development of deep crowns (Bar-Ness 2005). Because natural branch senescence induced by shading slows down or stops altogether, the branches can grow to large sizes. Mortality of these large branches is much less predictable, and follows stochastic events such as wildfires (Bar-Ness 2005), dieback episodes triggered by climatic stresses such as drought (Wardlaw 1989), or mechanical failure while the branches



Figure 3. The three distinct phases of crown development in eucalypts: *crown-lifting* (left), *crown-deepening* (centre) and *crown-retraction* (right).

are still alive. In this mature stage (100-300 years after disturbance), the breakage of large branches, either dead or alive, or the killing of patches of the stem following wildfire, produces large wounds that may eventually develop into hollows.

By about 200 years after disturbance, the eucalypts have reached their maximum height (Ashton 1976), and further aging results in a progressive decline in height through dieback or top breakage. This is the *crown-retraction* phase, which continues until the oldest survivors of the cohort reach their maximum life-span of about 450 years. While old trees decline in height during the latter stages of their life, they do continue to increase in diameter (Ashton 1975), and some grow to become massively “fat” trees of immense volume (see www.gianttrees.com.au).

The terms “regrowth” and “mature” are widely used in forestry to group growth stages. The crown-lifting and transition to the crown-deepening phase correspond with regrowth, while mature corresponds with the majority of the crown-deepening and crown-retraction phase. The term “over-mature” corresponds with the crown-retraction phase.

Throughout the natural life-span of a cohort of eucalypts, a proportion of the standing trees (either dead or alive) fall over or suffer stem breakage, and in doing so provide a supply of downed logs to the floor of the forest. Once on the forest floor, the downed logs, commonly called coarse woody debris (CWD), slowly decay until they are eventually fully consumed and returned to the soil organic matter pool. This process of decay follows a recognisable sequence of decay stages (Grove *et al.* 2009):

- Decay class 1: Structurally intact or almost so; bark or small branches still attached; few signs of wood-decay; wood mostly retains original colour.

- Decay class 2: Structurally less intact but still hard when kicked; small branches absent; little or no bark present; early signs of wood-decay or discoloration.
- Decay class 3: Clearly decaying but still supports its own weight; may be slightly soft when kicked; may be hollow in places; no bark; moss and fungi may be prominent.
- Decay class 4: Cannot support its own weight; soft to kick (but may still be hard in places, in which case may be extensively hollow); moss, fungi and invading roots likely.
- Decay class 5: No longer retains original shape; wood very soft or largely disintegrated; sometimes only outline visible beneath moss and invading roots.

Large eucalypt logs can persist on the forest floor for a long time: studies in southern Tasmania have found that the progress of eucalypt logs through these five stages of decay and on to the soil organic matter pool may take more than two centuries (Grove *et al.* 2009). Because of their longevity and the ongoing injection of fresh CWD, the volumes of CWD on the floor of temperate wet eucalypt forests can be among the largest globally, commonly exceeding 800 m³ ha⁻¹ (Grove and Meggs 2003).

Successional patterns in wood-decay fungi

Wood-decay fungi establish quite early in the life of a eucalypt. Studies in regrowth forests by Wardlaw (1996, 2003) found that, by age 20-40 years, more than 90% of vigorous, unsuppressed *E. obliqua*, *E. regnans* and *E. delegatensis* trees had at least one column of wood decay within the lower stem. Extensive columns of decay had developed in about 20% of these trees. The overwhelming majority of decay columns in these young trees become established during the branch-shedding process via

dead branches (Wardlaw 1996, 2003) (Figure 4), with an increasing probability of decay establishment with increasing branch size (Wardlaw 2003).

Species within the family Hymenochaetaceae and a species of *Dichostereum* dominate the communities of wood-decay fungi establishing through dead branches in young eucalypts, and accounted for 50% of the isolates of wood-decay fungi obtained in cultures taken from decay columns that originated from dead branches in Tasmanian wet eucalypt regrowth forests (Wardlaw 2003). Davidson and Tay (2008) also found a species of *Hymenochaete* was common in discoloured wood in young karri (*E. diversicolor*) in Western Australia. *Armillaria* (putatively *A. novae-zelandiae*) is the dominant wood-decay fungus establishing through the roots, where it

causes a white rot of the heartwood. Enzyme tests suggest that the majority (>80%) of wood-decay fungi establishing in young eucalypts in Tasmania cause white rot (T. Wardlaw, unpublished data); taxa within the Hymenochaetaceae all cause white rot (Hawksworth *et al.* 1995).

A chronosequence study in a mixed-age stand of *E. obliqua* within the Warra LTER site found low levels of wood decay in 69- and 105-year-old cohorts of trees (Hopkins *et al.* 2006). However, there was a significant increase in both the amount of wood decay and the diversity of wood-decay fungi in the oldest cohort (>150 years), which had declining crowns characteristic of the crown-retraction phase. This study found little overlap in species composition of wood-decay fungi between the two younger age-cohorts and the oldest cohort. Several

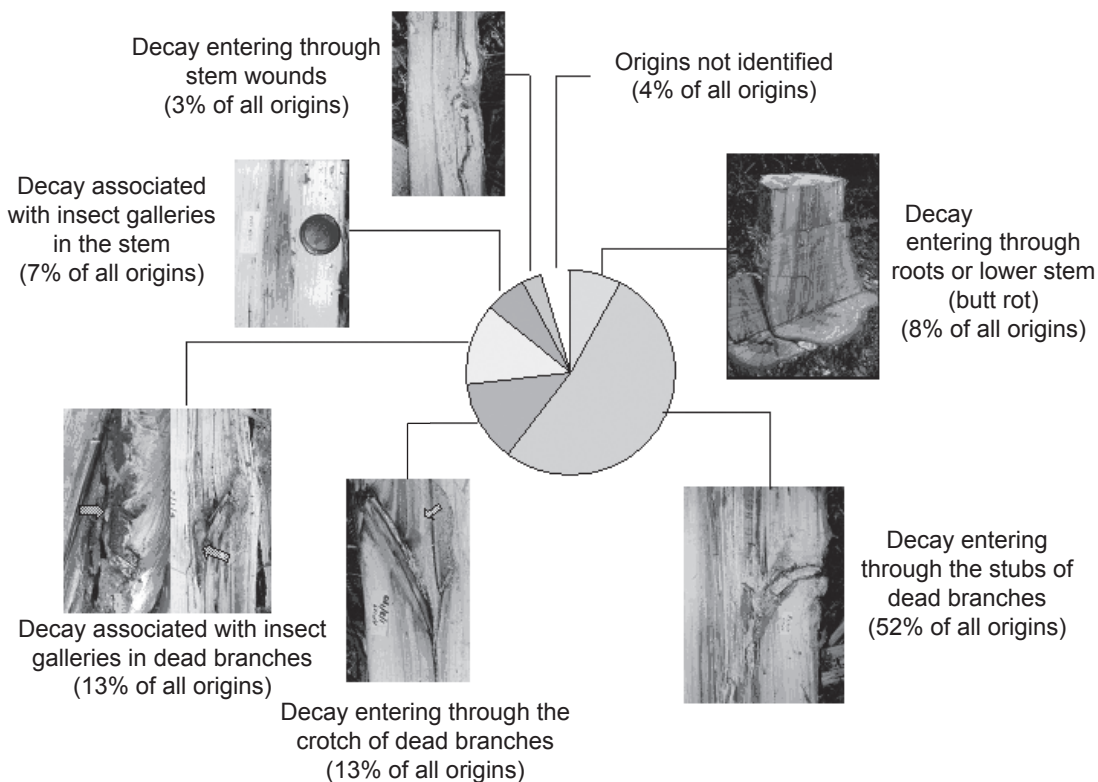


Figure 4. The origins of decay columns that had established in the stems of young (20-40 year old) *Eucalyptus* spp. in Tasmania. Based on Wardlaw (2003).

species from the genus *Postia* predominated in the communities of wood-decay fungi within the trees over 150 years old, but were largely absent from younger trees. Although two species of the Hymenochaetaceae were found in trees over 150 years old, their general paucity in the chronosequence study contrasted with the findings of Wardlaw (2003) in younger trees in Tasmanian forests.

The contrasts in the assemblages of wood-decay fungi inhabiting younger and mature *E. obliqua* were also reflected in contrasts of the type of wood decay. In regrowth trees, the great majority of decay columns were white rot (Figure 5), either simultaneous white rot or white pocket rot (Hopkins 2007; T. Wardlaw, unpublished data). Brown rot was rare in regrowth *E. obliqua*, but became more common in mature trees (Hopkins 2007). The increase in abundance of brown rot in mature trees coincided with the prevalence of *Postia*, a genus widely considered to cause brown rot.

The pattern of types of rot found in regrowth and mature *E. obliqua* trees was mirrored in downed logs. Yee (2005) found significantly more brown rot in large logs originating from mature trees than in smaller logs originating from regrowth trees (Figure 6). In that study, Yee found that columns of brown rot were primarily confined to the central heartwood region of the logs, suggesting that the decay columns had established while the tree was still standing. This idea was supported by Hopkins (2007), who found that one species of *Postia* was common to decay columns in both living trees and dead and/or downed logs. Smaller logs originating from younger regrowth trees were dominated by white ("pale") rot and white pocket rot decay types, typically spreading from the outside of the log inwards, suggesting that decay columns in these logs had established after the tree had died (Yee 2005).

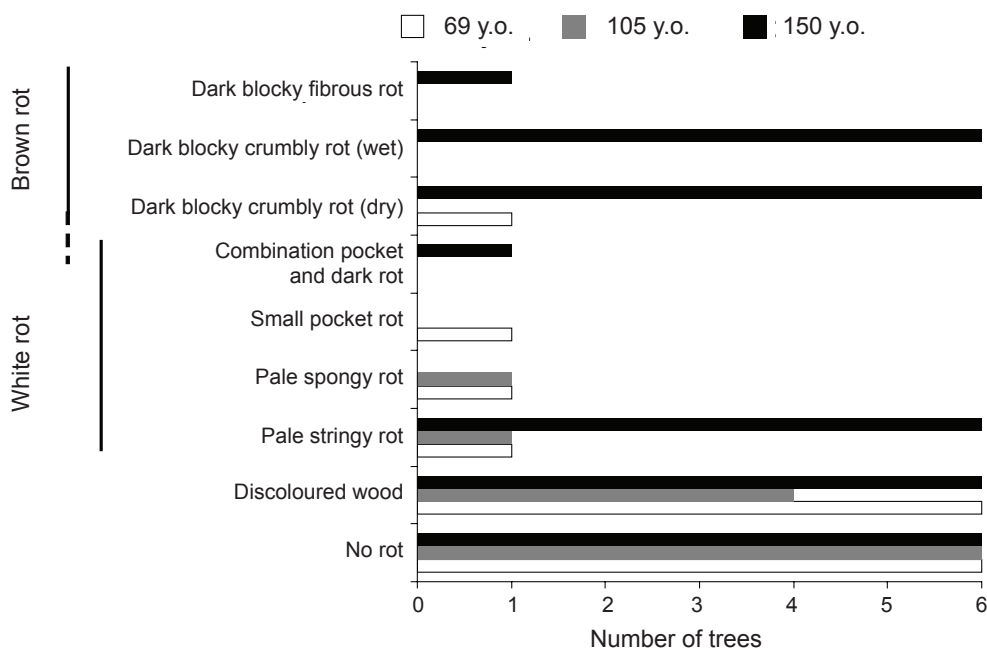


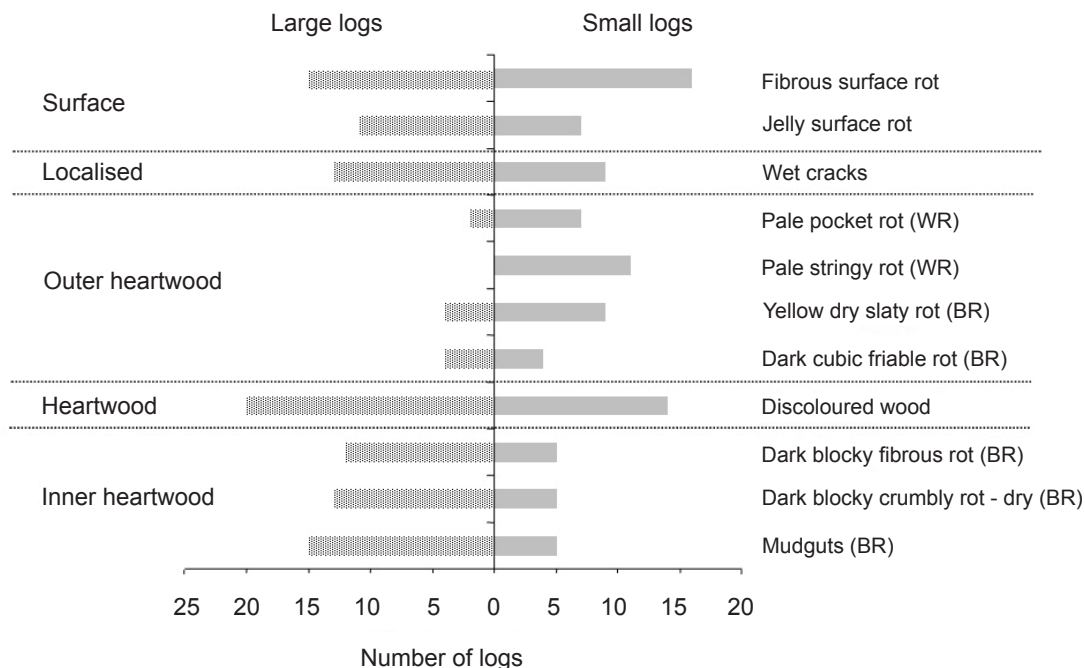
Figure 5. Frequency of occurrence of rotten wood types in six trees each of 69-year-old regrowth, 105-year-old regrowth, and >150-year-old mature *E. obliqua*. Adapted from Figure 5.3.4 in Hopkins (2007).

Succession patterns of saproxylic beetles

Little is known about the diversity of saproxylic (dead-wood-dependent) insects in young regrowth eucalypts. However, Wardlaw (2003) found ample evidence of stem-borers associated with decay columns in 20-40 year-old eucalypt regrowth. Nearly 20% of the encountered decay columns contained galleries of wood-boring insects (Figure 4). Nearly two-thirds of the borer galleries were associated with dead branches, typically in the crotch of the branch. Cerambycid beetles of the genera *Phoracantha* and *Epithora* are thought to be the main wood-boring insects in these branch-crotch galleries (Dick Bashford, pers. comm.). The genus *Phoracantha* contains many species known to attack young eucalypts in both native forest and plantation situations, occasionally achieving pest status and causing considerable economic damage (Elliott *et al.* 1998). These species are seldom found in mature eucalypts, suggesting that they are

specialists on young trees, although their initial attraction may be to stressed trees.

Older regrowth and mature *E. obliqua* trees support a rich diversity of beetles. Harrison (2007) recorded a total of 143 species of saproxylic beetles within the same eighteen *E. obliqua* trees sampled for fungi by Hopkins (2007). The process of tree aging strongly influences the assemblages of beetles inhabiting living *E. obliqua* trees. In particular, the transition from regrowth habit (<110 years) to maturity (>150 years) is associated with marked shifts in beetle assemblages, with mature trees having a much richer diversity of species compared to regrowth trees (Harrison 2007). Nearly 40% of the total beetle diversity was unique to mature trees (Figure 7). The distinctiveness of mature trees is due mostly to obligately saproxylic beetles that live within the stem wood (Harrison 2007). A substantial proportion of that unique saproxylic beetle fauna in mature trees was associated with hollows and dead tops.



Harrison (2007) found that species diversity among the saproxylic beetles was strongly associated with different rot-types within *E. obliqua* trees. A greater number of species occurred more commonly in wood containing brown rot than in wood containing white rot (Figure 8). The great diversity of saproxylic beetle species restricted to mature trees is correlated with the strong association between saproxylic beetles and the brown rots that Hopkins (2007) found to be most prevalent in mature *E. obliqua*.

Yee (2005) found similar saproxylic beetle species richness in small and large *E. obliqua* logs, with nearly 50% of the species in each of the small and large log size-classes being unique to that size-class. As with mature living trees, regions of brown rot, primarily located in the inner heartwood, contained particularly rich saproxylic beetle communities (Figure 9). There was also a saproxylic beetle

community associated with fibrous rot on the outer surface of the logs. This zone, which typically occurs at the soil-log interface, is known to be an important larval habitat for soil-dwelling species (Grove 2006).

There are some common elements in the saproxylic beetle communities associated with brown rot in the inner heartwood of mature *E. obliqua* trees and large logs arising from such trees. Six of the seven beetle species that Harrison (2007) found to be significantly associated with mature trees were also commonly encountered in large logs (Yee 2005). Interestingly, some of these species, which are common in Tasmanian forest (e.g. *Prostomis atkinsoni*, *Pycnomerus* TFIC sp. 2, *Cossonus simsoni*), have relatives in European forests that have become endangered or regionally extinct following a long history of intensive forestry and land clearance. The sensitivity to intensive forestry of saproxylic beetle species reliant

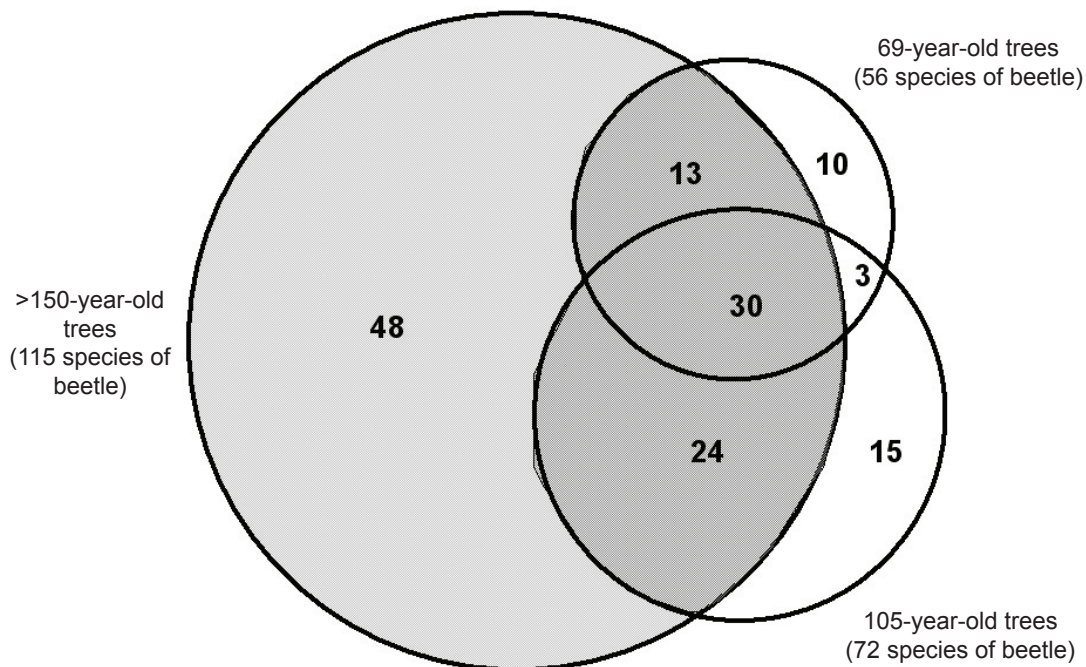


Figure 7. Venn diagram showing the total number of saproxylic beetle species extracted from six living *E. obliqua* trees in each of three age classes (young = 69 years old, medium-aged = 105 years old and mature = >150 years old). Adapted from Figure 5.1 in Harrison (2007).

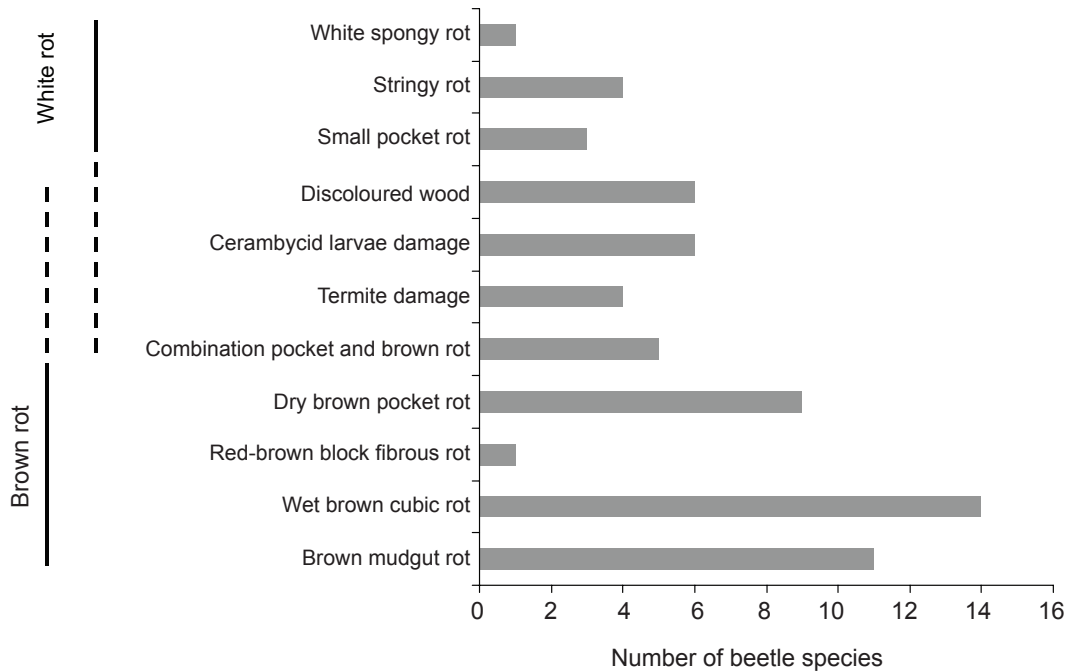


Figure 8. Number of saproxylic beetle species collected from different rotten wood types occurring in 18 *E. obliqua* trees across a range of ages. Figure 6.4 in Harrison (2007).

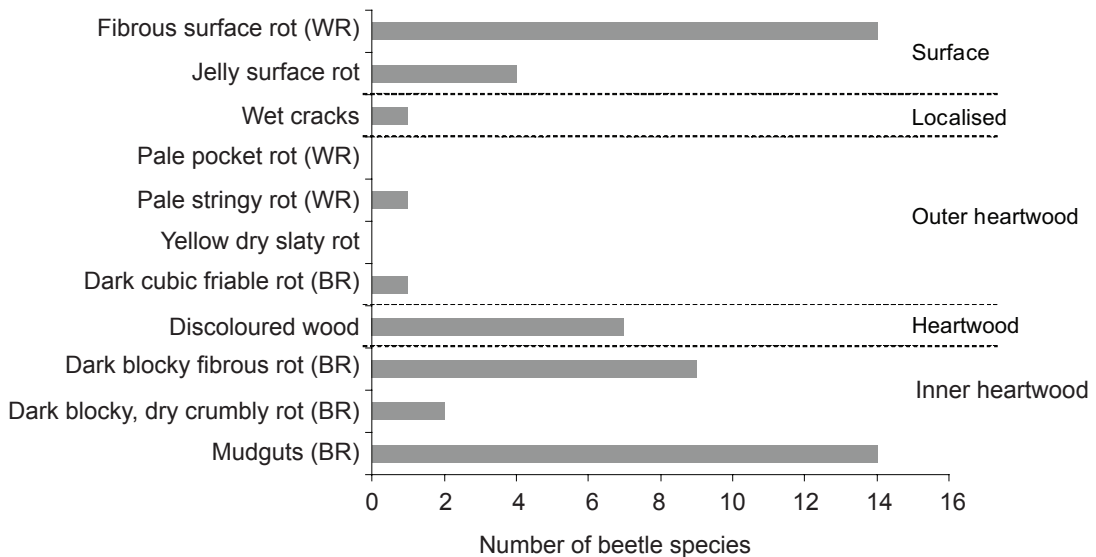


Figure 9. Number of saproxylic beetle species that were recovered on more than two occasions each for particular types and locations of rot in small and large *E. obliqua* logs. Adapted from Table 5.1 in Yee (2005). (BR) = brown rot types; (WR) = white rot types.

Table 1. Key attributes of different age-classes of *E. obliqua* trees and logs, and (italic dot-points) proposed consequence with respect to wood-decay fungi and saproxylic beetles.

Age-class	Standing trees	Fallen logs
Young regrowth (20-40 years old)	<p>Crown-lifting: regular senescence of lower branches, many small dead branches.</p> <ul style="list-style-type: none"> • <i>Many decay columns (mostly small), Hymenochaetaceae and Dichostereum spp. predominate</i> • <i>White rot prevalent</i> • <i>Cerambycid (Epithora, Phoracantha) galleries in crotches of dead branches</i> 	<p>Low heartwood extractives content.</p> <ul style="list-style-type: none"> • <i>Decay progresses from the surface of the log inwards</i> • <i>White rot prevalent</i> • <i>Little/no overlap between wood-decay fungi in standing tree and fallen log</i>
Regrowth (70-100 years old)	<p>Crown-deepening: senescence of lower branches stops.</p> <ul style="list-style-type: none"> • <i>Few decay columns establish, few species of wood-decay fungi present</i> • <i>Rot, when present, is white rot</i> • <i>Relatively low diversity of saproxylic beetles</i> 	As above (initially)
Mature (>150 years old)	<p>Crown-retraction: branches persist and grow to large size; branch breakage, fire damage and branch death (from dieback) creating large wounds.</p> <p>Large stem diameter.</p> <ul style="list-style-type: none"> • <i>Larger volume of decay</i> • <i>Suitable conditions for hollow formation</i> <p>Heartwood becomes less suitable for white-rot fungi.</p> <ul style="list-style-type: none"> • <i>Brown rot becomes more prevalent, higher diversity of wood-decay fungi than in regrowth trees</i> • <i>Diversity of saproxylic beetles (associated with brown rot) increases</i> 	<p>High heartwood extractives content.</p> <ul style="list-style-type: none"> • <i>Surface decay restricted to sapwood</i> <p>Brown rot in inner heartwood (established when tree was standing).</p> <ul style="list-style-type: none"> • <i>High saproxylic beetle diversity associated with standing trees is maintained</i> <p>Large log diameter.</p> <ul style="list-style-type: none"> • <i>Persistent and stable environment for saproxylic beetles with poor dispersal abilities</i>

on habitat that develops in mature trees (and large logs arising from them) is reflected in the preponderance of this group among European red-listed species – nearly 45% of Sweden’s 1000+ known saproxylic beetle species are red-listed (Jonsell and Nordlander 2002). Tasmania, with a much shorter history of forestry, is fortunate to have very few CWD-dependent species listed as endangered. In the southern forests, where we know most about the biodiversity dependent upon mature trees and CWD, only one saproxylic beetle species, *Lissotes menalcas*, is listed as vulnerable, chiefly because of its restricted distribution (Meggs and Taylor 1999). Recent research has

confirmed that this log-dwelling species also has a strong association with brown rot in the centre of logs (Belinda Yaxley, pers. comm.).

Interdependencies among eucalypts, wood-decay fungi and saproxylic beetles

In providing habitat for wood-decay fungi and saproxylic beetles, characteristics of eucalypts during their development are of fundamental importance. We would expect patterns in branching characteristics to be a key driver of assemblage composition for wood-decay fungi and saproxylic beetles, because of the importance of branches as

entry points for these organisms. Across the age-span examined in the studies by Wardlaw (1996, 2003), Hopkins (2007) and Harrison (2007), three distinct phases in crown development occur: crown-lifting, crown-deepening, and crown-retraction. Table 1 summarises the key findings from these studies and their linkage to the three stages of crown development. Studies by Yee (2005) were of logs generated from mid-aged regrowth trees and mature trees, likely reflecting the crown retraction and crown-deepening phases respectively.

During the crown-lifting stage, when young trees achieve rapid height growth, there is ongoing senescence of relatively young and small branches in the lower crown. The great abundance of dead branches being shed provides numerous potential entry points for wood-decay fungi and stem-boring insects. In particular, several species of decay fungi from the family Hymenochaetaceae appear well-adapted to infecting the bole as small branches are being shed. In addition, Hopkins (2007) found that 69-year-old trees tended to be colonised by wood-decay fungi from genera that are regarded by Northern Hemisphere workers as primary colonisers. Some species of cerambycid beetles from the genera *Phoracantha* and *Epithora* are similarly opportunistic in establishing galleries in the crotches of dead branches during this phase of crown development.

By mid-age, when crown-lifting stops (Bar-Ness 2005) and the eucalypts commence a period of crown-deepening, branches persist to much older ages and grow to larger sizes. The lower levels of wood decay and lower diversity of wood-decay fungi in mid-aged eucalypts reported by Hopkins (2007) is consistent with a greater branch persistence and hence with fewer opportunities for wood-decay fungi to gain entry into the stem of the eucalypt. These low levels of decay are also reflected in a lower diversity of saproxylic beetles relative to mature eucalypts, particularly those taxa that are obligately saproxylic (Harrison 2007).

There is an interesting contrast between the prevalence of wood-decay fungi in the young trees reported by Wardlaw (1996, 2003), and the paucity of such fungi and their associated decay in mid-aged trees as found by Hopkins (2007). In particular, trees with extensive decay columns, which were common in young eucalypts, were not encountered in the mid-aged trees sampled by Hopkins (2007). We would expect a proportion of the young trees with extensive decay columns to break off or fall over before they reached mid-age. This has been observed by the authors in young wet eucalypt forests, in which trees with extensive butt-rot due to *Armillaria* infection may be particularly vulnerable. Some young eucalypts with extensive decay do, however, reach mid-age (T. Wardlaw, unpublished observation). Their absence from the mid-aged trees sampled by the studies reported by Hopkins (2007) probably reflects the small sample size relative to the natural degree of variation in decay amount (Wardlaw 1996, 2003).

In mature eucalypts, the crown-deepening phase continues until the trees attain their maximum height, a process which may be truncated prematurely by stochastic events such as fire, storm or crown dieback episodes, the latter triggered by stress events such as severe drought (Wardlaw 1989). Branches persist for much longer in this phase and can become so large that they fail mechanically or succumb to the stochastic events just mentioned. The wounds created when such branches break, die or are burnt provide large entry-points for wood-decay fungi and saproxylic beetles (Lindenmayer *et al.* 1993). Over the long time-span that mature trees persist, the accumulation of such events produces large volumes of rotten wood in the stem and branches with a high diversity of wood-decay fungi and saproxylic beetles. This rich diversity is not just a function of the large volumes of available habitat (dead wood), but also of the distinctiveness of the habitat. While physically distinct structures such as hollows and dead tops contribute to this, the

shift to a greater prevalence of brown rots in the heartwood of mature trees is also a significant factor. All of the seven saproxylic beetle species that Harrison (2007) found to be indicative of mature eucalypts were associated strongly with brown rot.

The ultimate cause of the age-related shift from decay fungi that cause white rots to those that cause brown rots remains unclear. One possible factor is an age-induced change in the chemical properties of the heartwood. For example, more extractives are deposited in the heartwood of older eucalypts (Wardlaw 1990). These render the heartwood more resistant to microbial attack, and would provide an explanation for the tendency for wood decay to spread from the outer heartwood inwards in small eucalypt logs, while in large logs or mature trees the spread is from the inner heartwood outwards (Yee 2005; Hopkins 2007). It is uncertain, though, whether it is the increase in heartwood extractives in older trees that favours brown-rot fungi over white-rot fungi, or some other chemical change.

The composition of lignin also has a powerful effect on selecting for white- or brown-rot fungi. Most brown rot fungi occur in conifers, whereas most white rot fungi occur in angiosperms (Nakasone 1996). Conifer lignin is dominated by guaiacyl lignin, which is quite resistant to degradation by wood-decay fungi (Highley 1982). This renders conifer wood an unfavourable substrate for white rot fungi, which attack both lignin and cellulose. Angiosperm lignin, on the other hand, contains a mixture of guaiacyl and syringyl lignin in varying proportions. The syringyl lignin is more susceptible to decay by white rot fungi than is the guaiacyl lignin (Highley 1982; Obst *et al.* 1994), so angiosperm wood with a high syringyl:guaiacyl ratio may thus tend to be degraded more readily by white rot fungi. Although poorly understood, there is evidence that the lignin in mature heartwood of *E. regnans* differs qualitatively from the lignin in younger trees (Bland 1960). It would be of great ecological

interest if it were demonstrated that such qualitative differences between young and mature eucalypt wood reflected changes in the syringyl:guaiacyl lignin ratio, and if it could be determined whether such changes render mature wood less favourable as a substrate for white-rot fungi.

The distinctive wood-decay fungi and saproxylic beetle communities that develop in mature eucalypts also appear in large eucalypt logs after the trees fall to the forest floor. This is particularly so for the saproxylic beetle fauna, where five of the seven species found by Harrison (2007) to be significantly associated with mature eucalypts were among the common species inhabiting brown-rotted regions of the inner heartwood of large downed logs (Yee 2005). While Hopkins (2007) found some overlap in the wood-decay fungi of mature eucalypts and large downed logs, the association was much stronger for the saproxylic beetle fauna. Taken together, these elements of commonality in communities of saproxylic beetles and wood decay fungi in mature trees and large logs strongly suggest that the communities that develop in the standing tree persist after the tree falls to the forest floor. The large size of the downed logs generated from mature eucalypts and their long residence time on the forest floor (Grove *et al.* 2009) provides for a very stable habitat that is well-buffered from fluctuations in moisture and fire (Yee and Grove 2007). This persistent and stable habitat is particularly important for those saproxylic species that are thought to have limited dispersal abilities, allowing them to go through many generations without having to move out of the log. Several invertebrates (e.g. stag beetles and velvet worms) listed as rare or endangered under Tasmania's Threatened Species Act (1999) fall into this category.

In contrast with the continuum between mature trees and large downed logs, there appears to be little linking the communities of wood-decay fungi and saproxylic

beetles of young trees and small logs. Because of their low heartwood extractive content (Wardlaw 1990), small logs decay readily from the surface inwards, allowing predominance by fungi that colonise after the tree falls to the forest floor. While we could find no evidence of a continuum in the communities of wood-decay fungi in regrowth trees (particularly those in the active crown-lifting phase) with the communities in mature trees, we cannot conclude that such a continuum does not exist. Our knowledge of the communities of wood-decay fungi in older regrowth trees commencing the crown-deepening phase, and in mature trees, has developed from a small sample of trees in a restricted area. In addition, evidence of latent colonisation of apparently sound wood by wood-decay fungi (Hopkins 2007) suggests that sampling focussed just on decay columns (as was done in the young regrowth trees) may overlook decay fungi that bridge the growth stages.

The lack of evidence linking the wood-decay fungi and saproxylic beetle biota of young trees with those of mature trees does not greatly impact on management considerations. Prescriptions for mid-rotation thinning of native forests aim to selectively cull trees with high levels of internal decay. However, the area of native forest targeted for such management is less than 2% of the area of State forest (Forestry Tasmania 2007). In addition, thinning will never remove all trees containing internal decay (Wardlaw and Bashford 2007). Therefore, even if future research does uncover a successional link in the communities of wood-decay fungi and/or saproxylic beetles between young regrowth trees and mature trees, the consequence of any disruption to that link by thinning is likely to be minimal.

The link between the biota colonising mature trees and that of large logs indicates the need to ensure the continuity of mature trees in space and time throughout forested landscapes, at appropriate scales to allow natural dispersal of the dependent biota. A forest landscape with a diversity of age-classes, including mature trees, will achieve this. The system of Comprehensive, Adequate and Representative (CAR) reserves provided through the Tasmanian Regional Forest Agreement, coupled with complementary management outside reserves, is designed to cater for the conservation needs of forest-dependent species in production forests. The challenge for management is to understand the scales at which forest age-classes need to be dispersed in space and time in order to achieve the this continuity.

Two research projects have commenced within the Warra LTER to provide this understanding. One is examining the spatial arrangement of reserved mature forests within the production forest landscape, and testing whether that arrangement is successfully maintaining species dependent on mature forests. The other is using molecular methods to resolve how saproxylic beetles, including species strongly associated with mature trees or large logs, move through the production forest landscape to colonise suitable habitat.

Acknowledgements

The work presented here evolved from an oral presentation given by the senior author at the Inaugural Asia-Pacific Conference of the International Society of Arboriculture, held in Brisbane 9-13 May 2008. Comments on earlier drafts of this manuscript by Dr Steve Read and two anonymous referees are gratefully acknowledged.

References

- Alcorn, P. J. (2002). *The effects of light availability, canopy gap size and within gap position on the growth of Eucalyptus obliqua seedlings*. Honours thesis, School of Resources, Environment and Society. Canberra, Australian National University.
- Ashton, D.H. (1975). The root and shoot development of *Eucalyptus regnans* F. Muell. *Australian Journal of Botany* 23: 867-887.
- Ashton, D.H. (1976). The development of even-aged stands of *Eucalyptus regnans* F. Muell. in Central Victoria. *Australian Journal of Botany* 24: 397-414.
- Bar-Ness, Y.D. (2005). *Crown structure and the canopy arthropod biodiversity of 100 year-old and old-growth Tasmanian Eucalyptus obliqua*. MSc Thesis, University of Tasmania.
- Bland, D.E. (1960). Methanol lignin from *Eucalyptus regnans* F. Muell. and its purification by countercurrent distribution. *Biochemistry Journal* 75: 195-201.
- Davison, E.M. and Tay, F.C.S. (2008). Causes of incipient rot and rot in regrowth *Eucalyptus diversicolor* (karri) trees. *Plant Pathology* 57: 1097-1102.
- Edmonds, R.L. and Marra, J.L. (1999). Decomposition of woody material: nutrient dynamics, invertebrate / fungi relationships and management in northwest forests. In: Meurisse, R.T., Ypsilantis, W.G. and Seybold, C. (Editors) *Proceedings: Pacific Northwest Forest and Rangeland Soil Organism Symposium. General Technical Report PNW-GTR-461*. USDA Forest Service, Pacific Northwest Research Station, Portland Oregon.
- Elliott, H.J., Ohmart, C.P. and Wylie, F.R. (1998). *Insect pests of Australian Forests: Ecology and Management*. Inkata Press, Melbourne, Australia.
- Forestry Tasmania (2007). *Sustainable high quality eucalypt sawlog supply for Tasmanian State forest*. Forestry Tasmania, Hobart.
- Forestry Tasmania (2008). *Sustainability Charter: Forest Management Plan 2008*. Forestry Tasmania, Hobart.
- Grove, S.J. (2002). Saproxyllic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33: 1-23.
- Grove, S.G. (2006). What lives under logs in Tasmanian eucalypt forest? *The Tasmanian Naturalist* 128: 23-25.
- Grove, S. J. and J. Meggs. (2003). Coarse woody debris biodiversity and management: a review with particular reference to Tasmanian wet eucalypt forests. *Australian Forestry* 66: 258-272.
- Grove, S.J., Stamm, L. and Barry, C. (2009). Log decomposition rates in Tasmanian *Eucalyptus obliqua* determined using an indirect chronosequence approach. *Forest Ecology and Management* 258: 389-397.
- Hawksworth, D.L., Kirk, P.M., Sutton, B.C. and Pegler, D.N. (1995). *Ainsworth and Bisby's Dictionary of Fungi*. Eighth Edition. CAB International, Wallingford, UK.
- Harrison, K. (2007). *Saproxyllic beetles associated with habitat features in Eucalyptus obliqua trees in the wet eucalypt forests of southern Tasmania*. PhD Thesis, University of Tasmania.
- Highley, T.L. (1982). Influence of type and amount of lignin on decay by *Coriolus versicolor*. *Canadian Journal of Forest Research* 12: 435-438.
- Higuchi, T. (2002). Biochemistry of wood components: Biosynthesis and microbial degradation of lignin. *Wood Research* 89: 43-51.
- Hopkins, A.J.M., Harrison, K.S., Grove, S.J., Wardlaw, T.J. and Mohammed, C.L. (2006). Wood-decay fungi and saproxyllic beetles associated with living *Eucalyptus obliqua* trees: early results from studies at the Warra LTER Site, Tasmania. *Tasforests* 16: 111-122.
- Hopkins, A.J.M. (2007). *The taxonomy and ecology of wood decay fungi in Eucalyptus obliqua trees and logs in the wet sclerophyll forests of southern Tasmania*. PhD Thesis, University of Tasmania.
- Jacobs, M.R. (1955). *Growth Habits of the Eucalypts*. Forestry and Timber Bureau, Canberra.
- Jackson, W.D. (1968). Fire, air, water and earth: an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia*, 3: 9-16.
- Jonsell, M. and Nordlander, G. (2002). Insects in polypore fungi as indicator species: a comparison between different forest sites differing in amounts and continuity of dead wood. *Forest Ecology and Management* 157: 101-118.
- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. and Dhillon, S. (1997). Soil function in a changing world: The role of invertebrate ecosystem engineers. *European Journal of Soil Biology* 33: 159-193.

- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Tanton, M.T. and Nix, H.A. (1993). The abundance and development of cavities in Eucalyptus trees: a case study in the montane forests of Victoria, southeastern Australia. *Forest Ecology and Management* 60: 77-104.
- Lindenmayer, D. and McCarthy, M.A. (2003). Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. *Forest Ecology and Management* 155: 319-335.
- Meggs, J.M. and Taylor, R.J. (1999). Distribution and conservation status of the Mt Mangana stag beetle, *Lissotes menalcas* (Coleoptera: Lucanidae). *Papers and Proceedings of the Royal Society of Tasmania* 133 (1): 23-28.
- Nakasone, K.K. (1996). Diversity of Lignicolous Basidiomycetes in Coarse Woody Debris. In: *Biodiversity and Coarse Windy Debris in Southern Forests. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity*. Athens, Georgia, October 18-20, 1993.
- Obst, J.R., Highley, T.L. and Miller, R.B. (1994). Influence of lignin type on the decay of woody angiosperms by *Trametes versicolor*. Pages 357-374. In: Llewellyn, G. C., Dashek, W. V., O'Rear, C. E., Eds. *Biodeterioration research 4: Mycotoxins, wood-decay, plant stress, biocorrosion, and general biodeterioration: Proceedings of 4th meeting of the Pan American Biodeterioration Society; 1991*. Plenum Press, New York.
- Turner, P.A.M., Balmer, J. and Kirkpatrick, J.B. (2009). Stand replacing wildfires? The incidence of multi-aged and even-aged *Eucalyptus regnans* and *E. obliqua* forests in southern Tasmania. *Forest Ecology and Management* 258: 366-375.
- Wardlaw, T.J. (1989). The management of Tasmanian forests affected by regrowth dieback. *New Zealand Journal for Forestry Science* 19: 265-276.
- Wardlaw, T.J. (1990). *White pocket rot in plantation and naturally regenerated Eucalyptus regnans*. BSc(Hons.) Thesis. University of Tasmania.
- Wardlaw, T.J. (1996). The origin and extent of discolouration and decay in stems of young regrowth eucalypts in southern Tasmania. *Canadian Journal of Forest Research* 26: 1-8.
- Wardlaw, T.J. (2003). *The extent impact and management of stem decay in regrowth eucalypt forests scheduled for thinning in Tasmania*. PhD Thesis, University of Tasmania.
- Wardlaw T.J. and Bashford, R. (2007). The effectiveness of thinning in reducing losses from stem boring insects and fungal rots. Presentation to the Institute of Foresters of Australia Borers and Rot Conference. 5-7 November 2007, Perth, Western Australia.
- Yee, M. (2005). *The ecology and habitat requirements of saproxylic beetles native to Tasmanian wet eucalypt forests: potential impacts of commercial forestry practices*. PhD Thesis, University of Tasmania.
- Yee, M. and Grove, S.J. (2007). Giant velvet worm (*Tasmanipatus barrettii*) and post-harvest regeneration burns in Tasmania. *Ecological Management and Restoration* 8: 66-71.
- Yee, M., Grove, S.J., Richardson, A.M.M. and Mohammed, C.L. (2006). Brown rot in inner heartwood: why large logs support characteristic saproxylic beetle assemblages of conservation concern. In Grove, S.J. and Hanula, J.L. (Editors): *Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology*. Gen. Tech. Rep. SRS-93, USDA Forest Service, Southern Research Station, Asheville, NC.