# The decay of coarse woody debris

Final Consultants' Report

to the Australian Greenhouse Office

(September 1999)

by

Jens Mackensen and Jürgen Bauhus

ANU, Department of Forestry, Canberra, ACT 0200

Email:

jmacken@gwdg.de

Juergen.Bauhus@anu.edu.au

Conservation Library
Dept. of Parks and Wildlife
Kensington, W.A.

925189

# **Executive Summary**

13

This consultancy was undertaken to evaluate the current IPCC default used to calculate the decay of woody debris, to review decay models and the importance of individual factors in the decomposition process, and to determine decay rates in several Australian tree species. We focussed on the decay of coarse woody debris (CWD), assuming that this will constitute the majority of litter following clearing or harvesting of forests.

The literature review revealed that the number of studies on decomposition rates of CWD in Australia is insufficient to derive reliable data at a regional or national scale. However, by referring to international studies on decomposition rates and to durability studies on Australian timbers, it was concluded that an assumed turnover time of 10 years (IPCC default) for all litter may be a considerable overestimation of decay rates if the majority of the litter is in the form of CWD.

Indeed, the sampling of decaying wood from three different tree species *Pinus radiata* (non-durable softwood), *Eucalyptus regnans* (non-durable hardwood), and *E. maculata* (durable hardwood), suggested turnover times ( $t_{0.95}$ , time at which 95% of material has been lost) for these species of 24, 43, and 62 years, respectively. Single-component negative exponential decay models were fitted to data on wood density loss during decomposition of three species. However, measurement of  $CO_2$  loss and chemical characterisation of wood samples at different stages of decay suggest that a two-component model, accounting for the different decay resistance in sapwood and heartwood, may be more appropriate in some species. To assess how accurate the 10 year default is as an average for all forms of residual biomass, including fine litter, more information on the proportion of different litter fractions following clearing and harvesting is needed.

Based on this study and on transformations of data derived from studies on the durability and decay resistance of Australian timbers it was concluded that CWD-turnover will in most cases exceed 25-30 years and more. As a first approximation of turnover times for Australian timber species it is recommended that  $t_{0.95}$ -values be calculated according to the durability assessment of Thornton *et al.* (1997). Thornton *et al.* 's durability classes 1, 2, 3 and 4 are expected to have minimum turnover times  $(t_{0.95})$  of 54, 39, 26 and 11 years. Further, durability decreases substantially north of 30° latitude, which is largely due to the increasing importance of wood destroying agents such as termites. The adjusted turnover times for these conditions are >30, 20, 11, and 4 years for the durability classes 1, 2, 3, and 4.

However, results on turn-over times according to long-term decomposition studies are likely to provide higher values.

Abiotic factors such as moisture and temperature regime determine the general conditions for decomposition, whereas factors such as substrate quality influence abiotic conditions as well as regulate the specific conditions for decomposition. However, quantitative information on the relative importance of these key drivers for decomposition is lacking. In this study, the respirational carbon loss from wood could not be explained by wood density, moisture content, or the carbon-to-nitrogen ratio. Because of the importance of temperature and moisture regimes and the presence-absence of wood-destroying invertebrates, particularly termites, turnover rates of woody debris must be considered in a regional context. Decomposition drivers such as wood quality, charred surfaces, positioning of wood and wood diameter have to be evaluated at a local scale before they can be incorporated into future decomposition models. It is strongly recommended that a large scale experiment be set up to quantify the influence of the above factors on decay of different size classes of above- and below-ground fractions of important tree species, and that the methodology to assess CWD decay be further developed.

### 1. Background

Currently the release of carbon from land use change and forestry activities through the decomposition of residual biomass - fine litter as well as coarse woody debris such as snags, fallen logs, branches, stumps, and coarse roots - is calculated according to the Intergovernmental Panel on Climate Change (IPCC) default linear decay over 10 years following clearing or harvesting.

Recent estimates for CO<sub>2</sub>-emissions from land use changes and forestry activities are subject to large uncertainties (NGGIC, 1997b). These uncertainties result from a range of sources, such as the area being cleared, carbon density of vegetation, fraction of cleared biomass burned, and rate at which remaining biomass decays.

For example, current calculations take the fraction of above-ground biomass left on site following clearing and burning as 10% of the initial biomass (NGGIC, 1997a). It can be assumed that burning consumes most of the fine litter, and therefore most of the residual mass consists of coarse litter. However, clearing is often carried out without burning, or only smaller fractions of biomass are burned. Although the total amount of carbon released from the site may be the same for the different clearing scenarios in the long term, emissions from decomposition on previously cleared land may become important for the calculation of emissions in the baseline year (1990).

In the absence of reliable surveys, below-ground biomass is currently estimated as 25% of above-ground biomass (NGGIC, 1997a). However, this value may be higher in much of the drought-prone and nutrient-poor environment of Australia, where trees allocate more carbon to below ground structures to facilitate exploitation of limiting soil and water resources. The decay of coarse roots following clearing is currently calculated in the same way as that of above-ground coarse litter.

The IPCC default for decomposition of above- and below-ground litter appears to be a rough estimate of actual carbon losses from decay. It does not consider the climatic and environmental variables controlling decomposition nor does it take into account other variables linked to decay, such as size distribution of litter, density, content of extractives and the situation in which wood is decaying.

The 10 year linear decay default applies to both fine and coarse litter. However, this study will concentrate on coarse woody debris (CWD), because we assume that it will constitute most of the

residual biomass following clearing or harvesting and burning. This assumption is based on studies of logging slash following harvesting and burning (Stewart and Flinn, 1985) and the percent consumption of different fuel fractions in high intensity fires (Cheney *et al.*, 1980).

# 2. Study objectives

The objectives of this study are to:

- review the current IPCC decay default;
- examine the feasibility of an improved estimation of CWD decomposition rates and thereby adjust the current default decomposition rate to Australian conditions; and
- identify the main drivers of CWD decomposition, which may need to be considered if it becomes necessary to model CO<sub>2</sub> release from CWD at a regional or national scale.

This is a preliminary study to identify if and where knowledge gaps exist, and what future research may have to be undertaken to improve the National Carbon Accounting System. It is based on two approaches: a literature review on decay of CWD and an experimental study of CWD decomposition.

# 3. Literature review

A literature review was conducted to identify key drivers of decay and common decay patterns. The review included laboratory and field studies on the durability of Australian timber species. Studies on the decay of CWD in streams were not considered (see Melillo *et al.*, 1983; Harmon *et al.*, 1986). To allow a better comparison of the various parameters, available information was summarised in table form (Appendix 1). In some instances statistical analysis of the data set or parts of it were carried out to extract desirable information.

#### 3.1 Definitions

Decomposition is the process whereby the complex organic structure of biological material such as wood is reduced to its mineral form. Swift (1977) proposed that the respiration of sugar molecules was a simple model for biochemical decomposition:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + Energy$$
 (equation 1)

However, Swift (1977) points out, that decomposition not only deals with the catabolism of molecules but a complex mixture of different substrates such as proteins, cellulose, hemicelluloses and lignins and that it does not only include the transformation of carbon but of all elemental constituents including

macro- and micronutrients. It should also be noted that hemicelluloses or lignins represent heterogeneous chemical groups themselves.

Apart from the biochemical aspects of decomposition the term is often used in a wider context that includes the physico-chemical deterioration of organic matter due to photodegradation, leaching, and fragmentation. Unless otherwise stated, in this study we refer to decomposition or, alternatively, decay as the sum of these processes.

No universally accepted standard definition exists for the term CWD (coarse woody debris). The minimum diameter for CWD in some studies is as small as 2.5 cm (Wei *et al.*, 1997), although many studies consider only larger material (>10 cm in diameter).

#### 3.2 Decomposition processes

#### Respiration

Respirational loss of organic matter is the main process behind the complex phenomenon of decomposition. During the decomposition process, microbes, transform organically bound carbon (C), which accounts for approximately 50% of the organic material, into  $CO_2$  through respiration. The cellulose in wood is encrusted in lignin. Unlike most bacteria, certain fungi have the ability to break down lignin, which gives them a key role in the decomposition process. Fungal lignin degrading enzymes provide access to cellulose for other decomposers. The biological activity of decomposing organisms can be evaluated by measuring  $CO_2$  emission from organic matter.

## **Biological Transformation**

Microbes, and to a lesser extent invertebrates, metabolise organic matter. Studies on this topic indicate that the quantity of metabolised organic matter is comparable to the extent of respirational losses (Swift, 1973). Metabolised organic matter is either further mineralised by other organisms in the short term, or may become stabilised in complex organic molecules, such as parts of the soil organic matter, which can be highly resistant to decay. The quality of metabolised organic matter in the substrate is usually lower than that of the original substrate.

#### Fragmentation

It is common to distinguish between physical and biological wood fragmentation (Harmon et al., 1986). Physical causes of wood fragmentation include gravity, shrinkage and swelling, freezing and thawing cycles, formation of cracks, wind-blown particulate matter, and flowing water. The use of machinery in managed ecosystems is also an important agent of wood fragmentation through traffic or deliberate crushing of woody residues. Physical fragmentation is accelerated by decay organisms that destabilise wood and bark. The main agents for biological fragmentation are wood-boring insects, such as bark and ambrosia beetles, and other invertebrates. Wood-boring insects facilitate faster colonisation of wood by microbes and thus accelerate decomposition. Vertebrates, such as birds, feeding on wood inhabiting invertebrates can also fragment decaying wood. The fragmentation of decaying wood accelerates the decomposition process because it increases the surface-volume-ratio and may bring fragmented wood and bark pieces into direct contact with soil.

#### Leaching

Leaching is considered to be of minor importance in wood decomposition, and there have been very few studies on this topic (Mattson & Swank, 1984). Water percolating through CWD dissolves and transports soluble substances, which results in weight loss. However, the percentage of easily soluble substances in wood is low, especially during the first stages of decomposition. Nevertheless, leaching may be more significant in advanced stages of decomposition, during which polymers are transformed into soluble material (Harmon *et al.*, 1986).

#### Weathering

Weathering is the chemical and physical disintegration of wood by atmospheric elements (Jemison, 1937). The process of weathering alone, where it can be distinguished from decay, is practically insignificant as an agent in reducing the mass of coarse litter (Jemison, 1937). Thus the mass loss of standing dead trees or suspended coarse organic matter is negligible unless the material is colonised by wood destroying agents such as fungi and termites.

#### 3.3 Controlling factors

Microbial activity, as the main force behind wood decomposition, depends on controlling factors such as moisture, temperature, and substrate quality. The inter-dependence of these factors is complex and so far the relative importance of individual factors is known only qualitatively. Studies emphasising single factors have been restricted to laboratory tests (Boddy, 1983) and there is no agreement on which factor

may be the prime determinant of decomposition. For example, Swift *et al.* (1979) concluded that substrate quality is the key driving factor for decomposition, but Bunnell *et al.* (1977) and Mikola (1960, *fide* Brown *et al.*, 1996) found that moisture and temperature regimes were the major determinants.

Decomposition also depends on which micro-organisms and invertebrates are involved. Details on the biology of wood-inhabiting organisms, their biochemical interaction with wood components, and further references relating to Australian fungi are given by Simpson (1996) and in a more general manner by Harmon *et al.* (1986), Rayner and Boddy (1988), and Blanchette (1995).

#### Moisture

With increasing decomposition, maximum moisture content increases. This is because the moisture content of sound wood is negatively correlated with wood density. The maximum amount of water which can be held in cell cavities  $(M_{\text{max}})$  is a function of the fibre saturation point  $(M_f)$  and dry-volume specific gravities of gross wood  $(G_o)$  and cell walls  $(G'_o)$  (Skaar, 1972):

$$M_{\text{max}} = M_f + 100 (G'_{\text{o}} - G_{\text{o}}) / (G_{\text{o}} G'_{\text{o}})$$
 (equation 2)

Moisture content in CWD and its daily and seasonal fluctuations also depend on the seasonal precipitation regime, log size, log position and degree of shading (microclimate). Studies by Hayes (1940) and Brackebusch (1975, *fide* Harmon *et al.*, 1986) indicate that both drying and wetting proceed from the outer regions toward the inside of logs. However, logs in contact with the soil are more likely than raised logs to maintain their level of moisture saturation, even during drier periods.

Below the fibre saturation point of 30% moisture content (of dry mass), water is generally not available for fungi, other decomposing micro-organisms and insects, whereas a very high moisture content limits aeration and imposes a physiological barrier for fungal growth. Käärik (1974, *fide* Harmon *et al.*, 1986) found that a moisture content of 30-160% of dry matter weight is most suitable for the growth of basidiomycetes. Other fungi such as ascomycetes and fungi imperfecti and bacteria can tolerate higher amounts of moisture in CWD. Fungi can tolerate lower moisture contents than bacteria. Some insects, however, are reported to cope with extremely dry wood (Harmon *et al.*, 1986).

#### **Temperature**

The temperature within CWD is strongly influenced by factors such as surrounding temperature, moisture content, log diameter, surface-to-volume ratio and bark cover. Because of the very high thermal capacity of water, log moisture content will also significantly influence temperature (Rayner & Boddy, 1988). Temperatures on log surfaces which are fully exposed to sunlight may greatly exceed air temperatures (Graham, 1925; Wengert et al., 1966) and spatio-temporal temperature gradients are to be expected with increasing log depth (Savely, 1939).

Most wood-decaying fungi, the major agents of wood decomposition, are mesophilic, i.e., cannot grow above  $40^{\circ}$ C (Käärik, 1974, *fide* Harmon *et al.*, 1986). The optimal temperature for fungal growth in wood is between 25-30°C. Between 13°C and 30°C the  $Q_{10}^{*}$  for fungal respiration was found to be between 2 and 3, which means that respiration increases by a factor of 2-3 for every 10°C increase in temperature (Deverall, 1965, *fide* Harmon *et al.*, 1986). Wood-inhabiting insects were found to have similar upper temperature limits (Savely, 1939).

#### Woody substrate quality

CWD is a complex substrate consisting of outer and inner bark, sapwood and heartwood. The proportion of these components varies with species, size and age. The inner bark, which contains the cambium and phloem, is rich in sugars and generally decomposes more rapidly than the other wood components (Smith & Zavarin, 1960, *fide* Harmon *et al.*, 1986). Heartwood, which in many species, particularly eucalypts, forms the largest proportion in CWD, decomposes relatively slowly compared to other wood components, mainly because it contains fungi- or insect-toxic extractives, may have a higher density, and has a lower nutrient content. Nitrogen in particular, which is found in very small concentrations, can limit wood decaying fungi (Cowling, 1970).

The decay resistance of heartwood varies considerably between species, depending on the occurrence and type of extractives (Scheffer & Cowling, 1966; Rayner & Boddy, 1988; Eaton & Hale, 1993). For some species it has been shown that such heartwood decay resistance decreases within the tree from the pith outward and from the base of the bole to the top (Scheffer & Cowling, 1966). Protection from decay through extractives eventually decreases with time. Scheffer & Cowling (1966) list four mechanisms for inactivation of decay-inhibiting compounds: deactivation of extractives by enzymes; self-oxidation; microbial degradation and loss via leaching; and volatilisation.

Rate of decomposition also depends on the percentage of the main wood components such as lignins, cellulose, and hemicelluloses. Lignins decompose more slowly than celluloses (Crawford, 1981), which results in an increase in the lignin-cellulose ratio as decay proceeds.

# 3.4 Determination of decomposition rates

The decomposition rate is generally expressed through a constant k (Harmon  $et\ al.$ , 1986). Although there are several processes involved in decomposition, the following definition for k has been proposed:  $k = k_{\rm m} + k_{\rm p}$  where k is the overall decomposition constant,  $k_{\rm m}$  refers to mass losses due to respiration and leaching and  $k_{\rm p}$  refers to mass loss due to fragmentation (Lambert  $et\ al.$ , 1980).

#### Long-term studies

Long-term studies provide the most reliable method for the determination of decomposition rates. Monitoring of changes in volume, weight and density of CWD samples over a long period allows the assessment of losses due to respiration and leaching  $(k_{\rm m})$  as well as fragmentation  $(k_{\rm p})$ . However, most studies have used small diameter samples or have monitored samples only over a relatively short period of time.

#### Chronosequences

Most investigations of CWD decomposition are unable to continue over a long period. It is therefore common practice to take samples of a range of known ages, or of different decay classes, and establish a chronosequence. The reliability of this method depends largely on the ability to accurately determine the age of the CWD and to identify sample sites with comparable conditions. Different approaches have been followed to determine the age of CWD (see Harmon *et al.*, 1986). However, harvesting records of managed forests provide the most reliable method of age determination.

Generally, in chronosequence studies the decomposition rate is derived from the change in wood density over time. Unless the weight or volume of CWD samples is monitored over a long period, fragmentation losses can only be estimated. Most chronosequence studies therefore neglect fragmentation losses or apply a factor to estimate loss.

<sup>\*</sup>  $Q_{10}$  describes the factor by which biological processes accelerate over a 10° C temperature increase. For the same biological

#### Input-biomass ratio

The decomposition constant k can also be estimated from the ratio between CWD-input and the pool of CWD mass in an ecosystem (Christensen, 1977; Sollins, 1982). However, this method assumes that the pool of CWD and the input to the pool are in steady state. Only a few old-growth forests are likely to be in a steady state. Hence, this method is unlikely to be applicable to most forest types, and certainly not managed forest stands.

#### 3.5 Decay models

Various mathematical models have been used to describe decomposition patterns. In particular, models that have been successfully applied to fine litter decomposition, have also been used in CWD studies. The four most common models are listed in Table 1.

The single-exponential model is the most common model used to describe decomposition patterns. It is based on the assumption that the decomposition rate is proportional to the amount of matter remaining (Olson, 1963). The multiple-exponential model considers the fact that CWD is not an homogeneous substrate, but consists of various components (Minderman, 1968). If some components are susceptible to decay, while others are resistant, actual decay curves can differ significantly from the single-exponential model. It is very easy to fit multiple exponential models to decay data. However, the question always remains whether these models provide a significantly better fit. The lag-time model is based on the observation that during a transition time decay is slowed down until decomposers finally succeed in colonising the debris (Harmon *et al.*, 1986).

Table 1. Commonly used decomposition models. Variable X is proportion of initial mass, density or volume (X<sub>0</sub>) at time t. X<sub>1-3</sub> are partitioned parameters (such as bark, sap- heartwood), N is lag-time constant. References are: (1) Jenny *et al.* (1949); (2) Olson (1963); (3) Wieder & Lang (1982); (4) Means *et al.* (1985); (5) Harmon *et al.* (1986); (6) Minderman (1968); (7) Lambert *et al.* (1980).

Model	Expression	References	
Single-exponential model	$X = X_0 e^{-kt}$	1, 2, 3, 4, 5, 7	
Multiple-exponential model	$X = X_{0,1} e^{-k_1 t} + X_{0,2} e^{-k_2 t} + X_{0,3} e^{-k_3 t}$	3, 4, 6	
Lag-time model	$X = 1 - (1 - \exp[-kt])^{N}$	5	
Linear model	$X = X_0 - kt$	3, 7	

Assuming an exponential decay model, the time to decompose 50% ( $t_{0.5}$ ) and 95% ( $t_{0.95}$ ) can be calculated according to equations 4 and 5 (Olson, 1963):

$$X/X_0 = e^{-kt}$$
 (equation 3)

where X = e.g. present wood density,  $X_0 = initial$  wood density, k = decomposition constant, t = time.

$$t_{0.5} = -\ln(0.5) / k = 0.693 / k$$
 (equation 4)

$$t_{0.95} = -\ln(0.05) / k = 3 / k$$
 (equation 5)

According to the applied method (see above), k should be referred to as  $k_{\rm m}$  and  $k_{\rm f}$  respectively.

#### 3.6 Studies on decomposition rate of CWD

Studies on the decomposition rate of CWD are listed in Appendix 1. In addition to decomposition rates, other important parameters such as climate, species name, sample dimension, study duration and methodology are listed. However, since these parameters are highly variable, studies are not readily comparable. It should be noted that studies on the dynamics of CWD that did not directly determine a decomposition rate are not considered (e.g. Jemison, 1937; McFee & Stone, 1966; Eslyn & Highley, 1976; Christensen, 1977, 1984;. Berg, 1984; Raphael & Morrison, 1987; Harmon & Hua, 1991; Keenan et al, 1993; McCarthy & Bailey, 1994; Scheu & Schauermann, 1994; Stewart & Burrows, 1994; Torres, 1994; Temnuhin, 1996; Sturtevant *et al.*, 1997; Brown *et al.*, 1998).

#### Australian studies on CWD decomposition

Only 2 studies were found that investigated the decomposition rate of CWD from Australian trees (Brown *et al.*, 1996; O'Connell, 1997, Appendix 1). Using the decay constants provided for *E. diversicolor*, the 95% turnover time ( $t_{0.95}$ ), at which the material has virtually disappeared, is 17 and 136 years, respectively. This difference between the studies is astonishingly high considering the comparable climate (southwest Western Australia) and methodology (long-term study). Brown *et al.* (1996) found a significant impact of climate on decomposition, however, absolute differences between sites were small. The high value given by O'Connell (1987) might indicate that a 2-year period is too short to extrapolate to a long-term decomposition rate. Complicating factors such as termites, which might have enhanced decomposition at the site used by Brown *et al.*, were not mentioned.

O'Connell's results on decomposition of small E. diversicolor branches indicate a turnover-time  $(t_{0.95})$  of 25 years. Turnover-times  $(t_{0.95})$  for E. marginata and E. calophylla were reported to be 45 and 14 years, respectively (Brown et al., 1996) and those of associated species were 23 to 24 years for Trymalium spathulatum and Banksia grandis (O'Connell, 1997) and 61 years for P. pinaster (Brown et al., 1996).

Both O'Connell and Brown *et al.* reported a significant, inverse relationship between sample size (diameter) and decomposition rate. Considering that sample size in both studies is on the lower end for CWD, it must be expected that turnover-times  $(t_{0.95})$  for all studied species will increase with increasing size of debris. In addition, it can be assumed that the proportion of sapwood, which decays usually faster than heartwood, was higher in those small samples. According to both studies single-exponential decay models adequately described decomposition. Further, double- exponential models gave the best fit for the decay of leaf fractions, bark and small-diameter understorey wood (O'Connell, 1997), while the linear model failed to describe decomposition properly (Brown *et al.*, 1996).

Considering the foregoing, the minimum turnover-time for CWD in *E. diversicolor* and *E. marginata* stands in south-western Western Australia is expected to be at least 17-45 years. The possible influence of termites is not considered in this assumption.

# Overseas studies on CWD decomposition

More than 60% of all studies on CWD decomposition (Appendix 1) were conducted in forest ecosystems in North America. One third of these studies investigated the decomposition of *Pseudotsuga menziesii* in the Pacific Northwest of the USA and British Columbia, making it the best-studied species world-wide. Considering the different approaches and parameters studied, it is relevant for this review to explore the results of decomposition studies on *P. menziesii* in more depth.

The turn-over-time  $(t_{0.95})$  for CWD of *P. menziesii* ranged from 15-17 years to 430-770 years (Appendix 1). Variation in the decomposition rate depended on factors such as log diameter, log position, study period and methodology. In terms of methodology the long-term study by Stone *et al.* (1998) is unique because it covered a period of 65 years. The authors reported decomposition constants between 0.012 and 0.067 with a mean value of 0.022. This equals turnover-times  $(t_{0.95})$  of 45 to 250 years, with an average of 136 years. However, by measuring volume, Stone *et al.* (1998) accounted for decomposition of bark and outer sapwood and heartwood (including losses due to fragmentation), but did not necessarily include density loss in the log centre. The error associated with this method is unknown.

Most studies have used chronosequences (Erickson et al., 1985; Means et al., 1985; Edmonds et al., 1986; Sollins et al., 1987; Spies et al., 1988). While Edmonds et al. (1986) and Spies et al. (1988) measured mass loss and thus included mass loss due to fragmentation, other authors used density loss over time to estimate decomposition rates.

The single-exponential decay model was widely applied in these studies. However, Means *et al.* (1985) found no difference between a single-exponential model and a multiple-exponential model, which included the individual decay of lignin, cellulose and ADSF (acid detergent soluble fraction). Graham and Cromack (1982), in a study on *Tsuga heterophylla* and *Picea sitchensis*, and Lambert *et al.* (1980), found no difference between single-exponential, linear and logarithmic decay models. Sinsabaugh *et al.* (1992) reported that mass losses generally followed linear, rather than exponential, decay curves.

The relation of log diameter to the rate of decomposition was a focus in many studies. However, results are by no means convergent. Whereas Erickson *et al.* (1985) and Edmonds *et al.* (1986) reported a significant correlation between both parameters for *P. menziesii*, this was not corroborated by Marra & Edmonds (1994, 1996) using a gas emission technique. Other chronosequence studies, such as those by Graham and Cromack (1982), Foster and Lang (1982), Johnson and Greene (1991), and Fahey and Arthur (1994), also failed to demonstrate a correlation between log diameter and decomposition rate.

Compiling the data from studies on *P. menziesii* and *T. heterophylla*, we found that approximately 60% of the variation in decomposition rate can be explained by log diameter (Figure 1). The lower decomposition rate of large diameter logs can be explained by the lower surface-volume ratio, reducing access to decomposers and lowering gas and water exchange in proportion to volume (Abbott & Crossley, 1982; Harmon *et al.*, 1986). In addition, an increasing proportion of more slowly decomposable heartwood is found in bigger logs (Hillis, 1977, *fide* Harmon *et al.*, 1986; Harmon *et al.*, 1995).

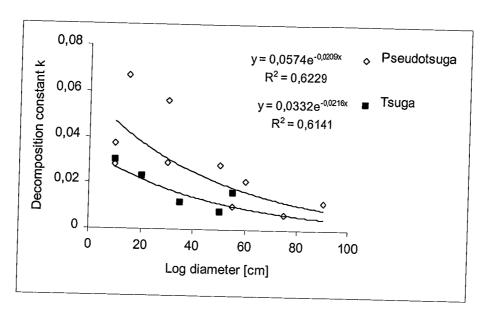


Figure 1. Correlation between log diameter and decomposition rate for *P. menziesii* and *T. heterophylla* in northwestern USA. Data by Grier, 1978; Graham & Cromack, 1982; Sollins, 1982 (estimated mean); Erickson *et al.*, 1985; Means *et al.*, 1985; Edmonds *et al.*, 1986 (mean surface samples); Sollins *et al.*, 1987; Spies *et al.*, 1988; Stone *et al.*, 1998.

Erickson et al. (1985) and Edmonds et al. (1986) studied the impact of log position on decomposition rate for P. menziesii. Soil contact is important for the acceleration of decomposition processes in CWD. Soil contact often improves the moisture content of the log and enables direct access to decomposing organisms. It may also improve the availability of water and nutrients for wood-colonising fungi, if they extend their hyphae into the soil. Erickson et al. (1985) found that decomposition of CWD with soil contact was more than twice as fast as that of elevated logs (Appendix 1; see also Christensen, 1984). Edmonds et al. (1986) reported a faster decomposition rate for logs buried in soil than for logs on the soil surface and elevated logs. Decomposition rates of logs on the soil surface tended to be higher than those for elevated logs, however, differences were not significant. Similar results were found for other species (Barber & VanLear, 1984; Rice et al., 1997).

A study by Harmon *et al.* (1995) in the dry tropical forests of Quitana Roo, Mexico is of interest to this review because of the variety of parameters studied, and because the climatic conditions (mean annual temperature 25° C and 1100 mm precipitation) may be comparable to regions in northern Australia. For most of the species Harmon *et al.* found a negative correlation between log diameter and decomposition rate (see also above). Furthermore, it was shown that species with low wood-densities decayed considerably faster than high density species. Species such as *Beaucarnea pliabilis* and *Bursera simaruba*, with a wood density of approximately 0.25 g cm<sup>-3</sup> and 0.33 g cm<sup>-3</sup>, respectively, had a

calculated turnover time  $(t_{0.95})$  of 6 to 8 years. High density species such as *Manilkara zapota*, *Blomia cupanoides* and *Talisia olivaeformis*, with wood densities of approximately 0.8 g cm<sup>-3</sup>, had calculated turnover times  $(t_{0.95})$  of between 100 and 375 years (Appendix 1). However, as discussed earlier, decomposition rate is not merely a function of wood density (see Schowalter, 1992), but is also dependent on factors such as content of extractives.

Only few studies were conducted in the tropics. Lang & Knight (1979) reported one of the fastest turnover-times of CWD (7 years; t<sub>0.95</sub>). However, it is difficult to put these results into context since necessary information on climate, species and initial CWD-condition are not available. Possibly the surveyed species had a low wood density and were thus highly susceptible to decay (see Harmon *et al.*, 1995) or suffered from severe termite attack. Lieberman *et al.* (1985) also reported fast decomposition of more than 60 trees and palms (median dbh: 22 cm) within 13 years in a perhumid old-growth forest in Costa Rica. But again, data on species and initial density are not available.

Studies on the decomposition rate of large roots are scarce (Yavitt & Fahey, 1982; Fahey et al., 1988; Fahey & Arthur, 1994, Scheu & Schauermann 1994). However, data seem to indicate that roots decompose at a much lower rate than comparable above-ground material. Scheu and Schauermann (1994) compared C loss in branches and roots of Fagus sylvatica of similar diameter (>1 cm). Although these root diameters are relatively small, the comparison of below ground decomposition of roots and surface decomposition of branches may be indicative of the relative differences in larger diameter material. The decay rate constants for root material calculated from their study are only ca. 60% of those for branch material. Fahey et al. (1988) compared the decomposition rate of roots of Acer saccharum, Fagus grandifolia and Betula alleghaniensis to unpublished results by Hughes and Fahey for above-ground material of the same species with comparable sizes (4-8 cm). Whereas decomposition rate constants for above-ground material were 0.131, 0.157 and 0.151, respectively, which equals turnover times  $(t_{0.95})$  of 19 to 23 years, calculated turnover time for roots ranged from 32 to 54 years (Appendix 1). Results from Yavitt and Fahey (1982) on root decomposition of *Pinus contorta* indicate turnover times  $(t_{0.95})$  of 100-125 years for roots with a diameter of 2.5 to 5 cm. Unfortunately, a comparison with results for P. contorta logs by Busse (1994, Appendix 1) cannot be done due to pronounced differences in sample diameter sizes (15-41 cm vs. 2.5-5 cm) and plot altitudes (1700 vs. 2800 m) and a comparison with Fahey (1983) is also problematic. Another study by Fahey and Arthur (1994) found much faster decomposition rates for roots (mass loss of 45-63% over 4 years) compared to their first study (Fahey et al., 1988), but these are difficult to interpret because of differences in experimental design.

Various factors may cause a slower decay of roots. Chemical and physical differences between the wood of roots and stems or branches are likely influences. Biochemical components in root bark are known to protect roots from soil micro-organisms and slower growth of roots should result in a relatively high wood density. Yavitt & Fahey (1982) observed that roots do not die immediately after a tree is cut. The root systems of tree species with coppicing ability can survive a reasonably long time, even if the stump eventually dies (Bauhus & Bartsch, 1996). Grafting of lateral roots of *P. radiata* is known to keep roots alive for up to 9 years following cutting of the above-ground part (Will, 1966, *fide* Yavitt & Fahey, 1982). Because root grafting and coppicing cannot be ruled out, chronosequence studies on root decay must be regarded as unreliable.

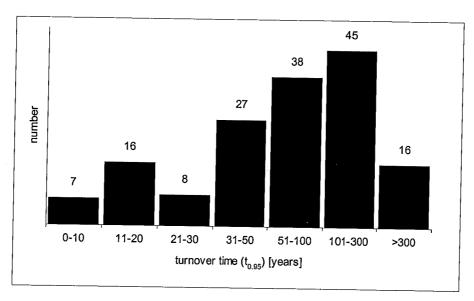


Figure 2. Number of calculated CWD-turnover times  $(t_{0.95})$  according to the results listed in Appendix 1. The study by O'Connell (1987) was excluded since it referred to fine litter only and while the 5-year study by Schowalter *et al.* (1998) was considered, the previous 2-year study by Schowalter (1992) was not. If available, minimum and maximum values were included.

In total, 157 values for turnover times  $(t_{0.95})$  of CWD were calculated from available literature studies. Two-thirds of all results had a calculated turnover time  $(t_{0.95})$  of more than 50 years (Fig. 2). Although the above presentation does not allow estimates for CWD-turnover times of Australian species, the decomposition periods clearly indicate that the IPCC default value of 10 yrs across all species is unrealistic. Clearly, turnover times of 10 yrs and less are the exception rather than the rule.

# 3.7 Durability studies of Australian timbers

Wood durability studies aim to identify the lifetime of timber products for different purposes, such as service time for poles. A typical component of these studies is the classification of decay resistance of

untreated timber, especially for heavy outdoor construction. Extensive durability studies of Australian timbers have been conducted, covering more than 40 years (see Da Costa *et al.*, 1957). However, mass loss of wood was usually not recorded, and hence the results of these studies can not readily be translated into decomposition rates and turnover times of woody litter from native species. Despite these shortcomings durability studies provide some useful information regarding the longevity of timber under certain environmental conditions. In the following section, published durability studies have been reviewed for their information on decay resistance, the wood properties influencing decay resistance, and durability classifications of Australian timbers.

# Evaluation of decay resistance

Generally, decay resistance is evaluated by the loss of weight of untreated wood specimen (Da Costa, 1973). Other classification approaches include tentative ratings based on experts consensus (Standards Association of Australia, 1979, 1980, *fide* Thornton *et al.*, 1983) or visual rating systems (Thornton *et al.*, 1983; Bultmann & Southwell, 1976). In general, wood specimens consist of small-sized sapwood or outer heartwood samples, which are half-buried in soil or, not so commonly, fixed without soil contact. Sample sizes vary between 1.2 to 5 cm in width and 5 to 45 cm in length (e.g. Bultmann & Southwell, 1976; Da Costa, 1979; Thornton *et al.*, 1983). Samples are generally taken from the most durable wood of a tree, that is, the outer heartwood from the butt section. Durability studies have been carried out in the field under natural conditions and in the laboratory under controlled conditions. In field studies, which can cover different climatic regions, specimens have been left for periods of up to 25 years during which the decay status was frequently monitored (Thornton *et al.*, 1991). To identify the importance of individual factors for wood durability, various studies have used field simulation techniques (soil block technique) which provide stable and controlled conditions for the studied specimens (Da Costa, 1975, 1979; Johnson *et al.*, 1988; Thornton *et al.*, 1995a, b).

Many field-based studies on wood decay resistance have not expressed the results in mass loss of sample, but by using a relative grading system or comparison between sample species (e.g. Wong *et al.*, 1983, 1984; Chafe, 1987; Wong & Wilkes, 1988). While these studies are useful for identifying decay-controlling factors for various species, they do not allow the quantitative estimation of decay rates.

A detailed durability study carried out by the CSIRO Division of Forest Products (now CSIRO Forestry and Forest Products) provided a range for expected service life of timbers (Thornton *et al.*, 1983, 1991). The study included 77 species at five sites in different climatic zones. Most of the species studied were native to Australia. They included 53 eucalypt species and 8 exotic species such as *Tectona grandis*, *T*.

plicata and P. menziesii. Sites were located in Innisfail (17°30' South, 3600 mm precipitation, 16-30°C) and Brisbane (27°30' South, 1500 mm, 9-25°C), Queensland, Pennant Hills (33° 42' South, 940 mm, 7-28°C), New South Wales, and in Walpeup (35°07' South, 340 mm, 5-32°C) and Mulgrave (38°00' South, 920 mm, 5-26°C), Victoria.

Thornton *et al.* (1983) used a scale of 0 to 8 to rate decay resistance of wood samples. The initial rating system was later revised. Initially, a score of 8 described completely sound wood, while a score of 0 was defined as the whole cross-section seriously affected by biological agents (fungi or termites). The rating system distinguished between fungi- or termite-caused decay. A specimen was considered unserviceable with a score of 3 or less. A score of 3 was given to cross-sections in which half the area was seriously affected by biological agents. However, no further definition of the term "seriously affected" was provided. The classification system was changed from the 15th year of wood exposure onwards (Thornton *et al.*, 1991). In the revised system, a score of 0 represented a total loss of cross-section, while a score of 8 indicated no cross-section loss. A rating of 3 was defined as 60 to 75% loss of cross-sectional area, which was considered to be equivalent to an unserviceable condition.

Thornton *et al.* (1983) used these data to calculate species-specific average specimen lifetime (ASL). The ASL was determined as halfway between an inspection at which a specimen score was 4 or higher and the next inspection at which the same specimen scored 3 or less. At least 3 specimens per site and biological hazard (fungi or termites) were used to calculate the ASL. Thornton *et al.* (1991) replaced ASL with the median of specimen life (MEDSL), which is calculated as the median of specimen life values for the replicates of that species.

### Causes of decay resistance

In addition to environmental factors, such as moisture, temperature and the presence/absence of fungal species, the content and composition of fungitoxic extractives and wood density are considered to be the most important properties influencing decay resistance (Da Costa *et al.*, 1962; Rudman, 1964, 1966; Gay & Evans, 1968; Edwards, 1982; Wong *et al.*, 1983; Wilkes, 1985a,b,c; Chafe, 1989). Extractives and density vary with age, within a tree, and within and between tree species (e.g. Wilkes, 1984), hence decay resistance can be expected to vary widely.

Experiments have failed to relate decay resistance to the colour of wood (Da Costa et al., 1962; Eaton & Hale, 1993). Da Costa (1975) pointed out that the variety of different factors, and wide range of possible

combinations of these factors, complicate a quantitative evaluation of the causes of decay resistance and thus the term 'decay resistance' has to be specified more precisely.

# Classification of decay resistance in wood of Australian species.

The in-ground durability of outer heartwood specimens from several species are summarised in Table 2. These generalised ratings are based on the median specimen life values obtained in field decay studies by Thornton *et al.* (1995b, 1997). However, Thornton *et al.* (1997) caution that it is not possible to transform the given durability studies into an accurate prediction of service life for wood products in particular places. Thus the service life values below must be regarded as a guide to what may be expected.

Table 2. Expected life time (median specimen life, MEDSL) and durability class of 76, mostly Australian, timber species according to long-term durability studies (Thornton *et al.* 1997).

E. amygdalina	E. rubida	Nothofagus cunninghamii	
E. elata	E. viminalis	P. radiata	
E. obliqua	Agathis robusta	Prumnopitys amara	
E. radiata	Litsea reticula	P. menziesii	
E. regnans	Lophostemon confertus	Quercus alba	
Expected lifetime between 1 and	15 years (1-3 years north of 30° latitude)	_	
E. calopylla	E. fastigata (T: 1-9)	Ansioptera thyrifera (T: 1-9)	
E. eugeniodes	E. jacksonii (T: 1-9)	Phyllocladus asplenifolius	
Expected lifetime of 8.5-15 years	(2-7 years north of 30° latitude). Durabi		
E. capitella (T: 1-9)	E. globulus (T: 1-9)	Lagorostrobos franklinii (T: 1-9	
E. cypellocarpa (T: 1-9)	E. grandis	Pterocarpus indicuss	
E. dives	E. muelleriana (T: 1-9)	Sequoia sempervirens T. plicata	
E. eugenoides	Athrotaxis selaginoides		
Expected lifetime between 8.5 and	d 24.5 yrs (2-14 yrs north of 30° latitude)	Durability class 2-3	
E. botryoides	E. marginata	E. sieberi (T: 1-9)	
E. diversicolor (T: 1-9)	E. megacarpa (T: 1-9)	Intsia bijuga	
E. goniocalyx (T: 8.5-15)	E. pilularis (T: 8.5-15)	Syncarpia hillii	
E. haemastoma (T: 8.5-15)	E. saligna (T: 8.5-15)		
expected lifetime of 12-24.5 years	s (5-14 years north of 30° latitude). Dural	bility class 2	
. camaldulensis	E. maculata	Lophostemon suaveolens Syncarpia glomulifera Tectona grandis	
. consideniana (T: 8.5-15)	E. patens (T: 1-9)		
'. guilfoylei (T: 8.5-15)	E. resinifera		
. guisoyiei (1. 8.3-13)	y	reciona granais	

E. astringens E (T: 12-24.5)

E. leucoxylon

E. tereticornis

E. cornuta (T: 8.5-15)

E. salmonophloia (T: 8.5-15)

Expected lifetime of 21	
Expected methic of >21 years (>14 years north of 30° lat-	ituda) Durohility alega 1
Expected lifetime of >21 years (>14 years north of 30° lat.	reduct. Durability class I

E. bosistoana (T: 12-24.5)

E. moluccana (T: 12-24.5)

E. wandoo

E. cloeziana

E. paniculata

Acacia acuminata

E. gomphocephala (T: 8.5-15)

E. polyanthemos

A. harpophylla (T: 12-24.5)

E. longifolia (T: 12-24.5)

E. sideroxylon

Allocasuarina luehmannii (T:12-24)

E. melliodora

Expected lifetime refers to resistance against decay and decay plus termites. In cases where a lower durability due to termites occurred, expected lifetime is given in parenthesis.

Thornton et al.'s (1997) results for Callitris glaucophylla and P. menziesii compare well with those by Bultman and Southwell (1976) for a 13-year durability field study at three tropical sites in Panama. The latter authors found that small-sized heartwood specimens of P. menziesii lasted less then 7.5 years if exposed to subterranean termites, in both above- and below-ground conditions. By contrast, specimens of C. glaucophylla showed only traces of damage or light damage after 13 years when located on the soil surface with or without subterranean termites. However, C. glaucophylla samples located below ground exhibited heavy damage (comparable to a loss of 50-75%). This performance of Callitris is, however, at the lower end of decay resistance. Thornton et al. (1983) found that Callitris spp. are considerably more decay resistant at the drier sites of their natural habitat than at any tropical site.

Thornton et al.'s (1983) findings on the durability of E. diversicolor, E. pilularis and S. glomulifera clearly differ from those of Purslow in Europe (1976, fide Thornton et al., 1983), who found average lifetimes of more then 30 years for these species.

As outlined above, median service life values obtained from durability studies must not be interpreted as turnover times for particular CWD. The turnover times for CWD from Australian species can be expected to be different for the following reasons:

- Median specimen life is determined as a loss of 60-75% of cross-section (Thornton et al., 1991), while turnover time is defined as a 100% mass loss (approximated by t<sub>0.95</sub>) of wood samples.
   Assuming that the widely used exponential decay model applies equally well to wood from Australian species (see Appendix 1) total turnover time (e.g. t<sub>0.95</sub>) can be expected to be much longer than median specimen life (see below);
- Since durability studies aim to identify weaknesses in the function of timber, only the most deteriorated wood cross-sections below the soil surface or at the soil surface level (ground-line) were

rated for durability (Thornton et al., 1991). The above-ground part of specimens that have no soil contact would exhibit a smaller degree of decay;

- Specimens are small-sized samples of outer heartwood (5 cm edge length). Based on the often observed diameter-effect (see section: Overseas studies on CWD decomposition) the decomposition rate of CWD can be expected to be much slower;
- Sapwood and bark components were not included in the study. While decomposition rate for sapwood is faster than for outer heartwood, no assumptions can be made for bark components.

It is therefore difficult to compare results of decomposition studies (Appendix 1) to those of durability studies (Table 2). However, one way to compare the data from durability studies with those for turnover times of CWD, is to assume that 60-75% loss of cross-sectional area (Thornton *et al.*, 1991) is equivalent to 75% mass loss. Using the decay constant (*k*) provided by the exponential decay model (Olson, 1963), the time required to loose 75% mass can be calculated, which can then be compared to the median specimen life:

$$t_{0.75} = -\ln(0.25) / k = 1.4 / k$$
 (equation 6)

Long-term decomposition studies by O'Connell (1997) and Brown *et al.* (1996) on *E. diversicolor* and *E. marginata* indicate  $t_{0.75}$ -values of 8 to 67 years (Appendix 1) and are thus only roughly comparable to results by Thornton *et al.* (1997) indicating median specimen life values of 9-25 years. In any case, turnover times (e.g.  $t_{0.95}$ ) for these species are expected to be longer (see Appendix 1). Studies on the decomposition rate of buried logs of *P. menziesii* showed the lowest calculated  $t_{0.75}$ -values ranged from 7 to 18 years (Edmonds *et al.*, 1986; cf. Appendix 1). Again this did not agree closely with the results of Bultman and Southwell (1976) and Thornton *et al.* (1997). Indeed, the majority of  $t_{0.75}$ -values for CWD of *P. menziesii* ranged from 50 to 200 years (cf. Appendix 1). These discrepancies between data from durability and decomposition studies can be expected for the reasons outlined above. In addition, the comparison made here does not take into account differences in climate and soil biota.

Despite the conceptual difficulties in comparing results from durability studies to those from CWD decomposition studies, the turnover time for 95% mass loss  $(t_{0.95})$  was calculated by deriving an estimated k-value for the MEDSL-values given by Thornton *et al.* (1997; equations 5, 7 and 8):

$$1.4 / k = MEDSL = t_{0.75}$$
 (equation 7)  
 $t_{0.95} = 3 * (MEDSL / 1.4)$  (equation 8)

where MEDSL = median specimen life according to Thornton et al. (1997; see Table 2).

This approach assumes an exponential decay model. For an assumed median specimen life of 5 years (see first group in Table 2) the calculated  $t_{0.95}$ -value was 11 years. Average MEDSL-values of 12, 18 and 25 years (see third, fifth and seventh group in Table 2) translate into  $t_{0.95}$ -values of 26, 39 and 54 years, respectively. According to Thornton *et al.*, durability decreases substantially north of 30° latitude, which is largely due to the increasing importance of wood destroying agents such as termites. Assuming average MEDSL values of >14, 9.5, 5, and 2 years, the adjusted turnover times for these conditions are >30, 20, 11, and 4 years for the durability classes 1, 2, 3, and 4.

These time spans can be regarded as 'worst case scenarios' for decomposition, which may be applicable only to small pieces of wood in intimate contact with the soil. Results on turn-over times from long-term decomposition studies are likely to provide higher values.

Thornton et al.'s (1997) results can also be compared to those of Da Costa (1979), who studied the decay resistance of various, mostly Australian, timbers to different fungi in specially designed, so-called Accelerated Laboratory Tests. In these tests, Da Costa (1979) incubated small timber specimens of outer heartwood with fungi in an environment (25°C and high relative humidity) ideal for fungal growth for 22 weeks. Results for selected species are summarised in Table 3.

Da Costa (1979) performed four different tests covering various species and two specimen positions. Species, such as *E. diversicolor* and *E. grandis*, which were examined in similar tests exhibited large differences in decay resistance. These variations were not further discussed by Da Costa (1979). However, the observed variations might very well represent a natural variability in the decay resistance of the various, especially durable, timber species. Interestingly, it appeared that specimens with soil contact had a lower decay resistance than specimens which were buried in soil. This is contrary to findings from field studies on decomposition rates (Appendix 1; Edmonds *et al.*, 1986), but may be explained by suboptimal oxygen supply under buried conditions, where fungi growing under favourable conditions may induce locally anaerobic conditions.

Table 3. Results of decay resistance of Australian timbers in Accelerated Laboratory Tests by Da Costa (1979), and calculated turnover times. Decay resistance is expressed as relative weight loss of sample.

		Range	Mean	t <sub>0.75</sub>	t <sub>0.95</sub>
E. acmenoides	test A	0.6-1.9	1.5	93	200
E. camaldulensis	test B-1/2	0-7.1	0.8	175	375
E. diversicolor	test B-1	2.8-30	16.5	8	18
	test B-2	0.3-9.4	4.2	33	71
•	test C	0.1-8.1	1.5	93	200
	test D	11-47	21.5	7	14
E. grandis	test A	3.4-18.1	8.5	16	35
	test B-1/2	0-24.8	8.7	16	34
	test D	13-40	25.0	6	12
E. maculata	test A	8.1-14.7	10.6	13	28
	test B-1	1.9-13	7.9	18	38
	test B-2	0.6-7.6	3.8	37	79
E. marginata	test B-1/2	0-12.0	2.5	56	120
	test C	0.6-13.5	6.3	22	48
E. microcorys	test A	2.6-4.2	3.3	42	91
E. obliqua	test B-1/2	0-30.4	12.0	12	25
	test D	16-40	30.0	5	10
E. paniculata	test A	2.5-7	4.4	32	68
E. pilularis	test A	3.6-7.7	7.0	20	43
	test B-1/2	0-10.9	4.8	29	63
E. regnans	test D	22-56	44.0	3	7
E. saligna	test D	6-36	18.0	8	17
E. sieberi	test B-1/2	0-17.6	5.9	24	51
	test D	4-45	23.0	6	13
E. tereticornis	test B-1/2	0-6.3	0.8	175	375
P. radiata (sapwood)	test D	24-68	52.5	3	6
P. radiata	test D	28-67	52.5	3	6
P. menziesii	test B-1/2	1.9-57.1	24.5	6	12
	test D	3-57	33.0	4	9

Test A: 8 timbers incubated (buried) for 22 weeks with 7 brown rot and 5 white rot fungi species in loamy soil. Specimen cut from outer heartwood, 5x1.25x1.25 cm, 25°C, 95% relative humidity.

Test B: General design similar to test A. B-1 refers to samples with soil contact and B-2 refers to buried samples. In total 25 timbers were tested (only few selected here).

Test C: Technique as in test B. Results include samples with soil contact and buried samples. In total 15 timbers from Western Australia were tested (only few selected here).

Test D: Design similar to test B for 29 non- and moderately-durable timbers (only few selected here). Soil contact samples were incubated with brown rot fungi, soil buried samples with white rot fungi.

Da Costa (1979) expressed decay resistance as weight loss of specimens, which we used for a calculation of turnover time ( $t_{0.75}$  and  $t_{0.95}$ ; Olson, 1963) by assuming exponential decay and transferring relative weight loss value into the decomposition value k (equation 9):

relative weight loss (%) / 100 = decomposition value k (equation 9)

Despite the different approaches, median specimen life values (MEDSL) developed by Thornton *et al.* (1997; Table 2) compare very well with  $t_{0.75}$ -values as calculated from data given in Da Costa (1979, Table 3). Major differences occurred for *E. camaldulensis* and *E. tereticornis*, both of which had a much higher decay resistance according to Da Costa (1979;  $t_{0.75} = 175$  yrs) than that estimated by Thornton *et al.* (1997; 8.5-24.5 yrs).

The turnover time at which 95% of mass is lost was estimated for most specimens to be above 30 years (Table 3). For *E. acmenoides*, *E. camaldulensis* and *E. tereticornis*, as well as partly for *E. diversicolor* and *E. marginata*, turnover times can be expected to be more than 100 years (Table 3). Turnover times  $(t_{0.95})$  between 10 to 30 years were calculated for *E. obliqua*, *E. saligna* and *P. menziesii*. Only *P. radiata* and *E. regnans* had turnovers of less than 10 years (Table 3).

Comparing the turnover times  $(t_{0.95})$  as calculated from data by Da Costa (1979; Table 3) with field studies on decomposition rates (Appendix 1), we found that results for *E. diversicolor* and *E. marginata* were within the same order of magnitude.

Results from field studies on *P. menziesii* (see Appendix 1) are in all cases very different from the findings of Da Costa (1979). This reflects the different climatic conditions in the studies as well as different methodologies. Again it must be stated that because of the methodological approach used in durability studies, they can only be regarded as a first indicator for the turnover time of CWD under natural conditions. We assume that service life and extrapolated turnover times of durability studies only indicate potential minimum values for the turnover of CWD (if termites are not a factor). The results of

our experimental studies show that turnover times for CWD of selected species can be expected to be much longer.

## 4. Experimental study

#### 4.1 Methods

Decomposition rates of CWD were measured using two complementary methods. Method A included sampling of cross-sections of CWD of known age since clearing and determination of their wood density. This established a chronosequence of sites since disturbance, which spanned from ca. 1 to 10 years. To estimate decomposition rates, the decrease in wood density or weight loss was compared to the initial density Although this method neglects decomposition due to fragmentation and biological transformation (see below), it is considered a standard method for estimation of decomposition rates (Healey & Swift, 1971; Christensen, 1984). In Method B the rate of CO<sub>2</sub> emission was used to calculate the current decay rates of the different wood samples. This entailed the measurement of respiration (CO<sub>2</sub>-release) of large CWD samples, which were incubated under constant environmental conditions for a certain period of time. To measure emission rates during various stages of wood decay, samples were also taken from the chronosequences..

Both methods were applied to samples of three tree species: *P. radiata*, *E. regnans*, and *E. maculata*. All species represent important forest management systems and ecosystems. They also represent low-, medium- and high-density wood species and thus may allow an extrapolation of decomposition patterns to other similar hard- and softwood timbers. Details of sample areas, their climate and management system are given in Appendix 2.

#### Method A (wood density decrease)

Woody debris left on site following clearing or harvesting occurs in different situations: suspended; on the soil surface; or pushed into the soil to various degrees. The specific location influences decomposition rates because it affects the water content of the wood, and the susceptibility to fungal and termite attack. To reduce this variability samples were only collected from logs positioned on the soil surface.

From each log, two cross sections of ca. 5 cm width were sampled within a distance of 0.3 to 1 m of each other with a chainsaw. Between 16 to 24 logs of 10 to 30 cm diameter were sampled from each species and age class (see Appendix 2). *P. radiata* samples from the two oldest age classes were often fragile. To avoid disintegration, one block 25 cm in length was sampled and this was wrapped with adhesive tape prior to cutting. The cylindrical volume of these older samples was calculated from the diameter at both ends and the length.

Samples were labelled and stored in plastic bags for up to 5 days during fieldwork and later stored cool until further processing. Prior to measurement, bark, mosses, fungal fruiting bodies and soil were removed from each disc. Fresh weight and diameter were measured, and volume determined gravimetrically by water displacement. Samples were then oven-dried at 105°C until a constant weight was achieved Subsequently, water content and wood density were calculated.

# Method B (CO<sub>2</sub> emission rate)

For calculation of CO<sub>2</sub> emission rates, five log samples per age class and species were collected. These were log sections with an average length of 30 cm and diameters between 10 and 30 cm, cut between the discs collected for method A. Their water content and wood density were derived from the accompanying cross-section samples. Storage was the same as for the wood density samples.

CO<sub>2</sub> emissions were determined using soda lime. This method is well established for soil respiration measurements (Edwards, 1982). Samples were kept moist in airtight plastic bags (REXAM product code BAO30FB, one side metallised, biaxially orientated polypropylene film) and incubated in climate chambers for three days at constant temperature (25°C). Twenty grams of dried soda lime was placed into the incubation bag with the sample. Before and after incubation soda lime was dried at 105°C and weighed. The gain in weight after incubation equalled the adsorbed amount of CO<sub>2</sub>, corrected for chemically released water using a factor of 1.69.

To express the current decay rates in terms of  $\mathrm{CO_2}\text{-}\mathrm{C}$  evolved per unit of C remaining, the C concentrations in the wood were determined. For this purpose, a wedge from the outer sapwood to the pith, representing approximately 1/8 of the cross-sectional area, was cut from a disc belonging to the incubated log sections. The wedge was shredded and the shredded material ground to be analysed for C and N in an automatic C/N analyser using the combustion method (LECO CHN-1000, St. Joseph, Michigan).

#### 4.2 Results

#### Pinus radiata

The chronosequence samples, were collected at sites representing 1, 2.5, 6, and 9 years after harvesting from similar sites within the ACT. The external cylindrical shape of log sections sampled was intact. This was not representative for the sites from which they were sampled, because it is a standard practice in the ACT to crush the slash to facilitate site preparation and planting. However, this mechanical fragmentation was not specifically addressed in our study. Figure 3 shows the density decline between one and nine years following harvesting.

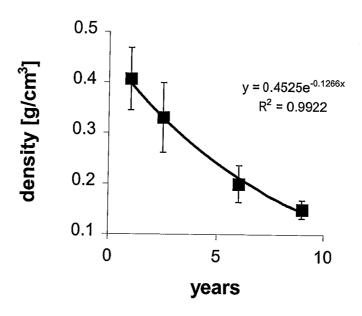


Figure 3. Development of wood density in *P. radiata* logs decomposing *in situ* for 1, 2.5, 6, and 9 years following clear-cut harvesting. The decline in density was fitted to a negative exponential decay model. Bars represent standard deviation.

In the case of P. radiata the wood density method appeared to provide meaningful results. The decomposition constant of k = 0.1266 indicates that the turnover time  $(t_{0.95})$  for this wood is 24 years. This is several times greater than was suggested by the calculations based on Da Costa's data derived from laboratory studies (Table 3). However, this turnover time is shorter than for the other pines used in decomposition studies listed in Appendix 1. At this decomposition rate, 29% of the original mass will be left after 10 years.

We found no relationship between log diameter and density within age groups, which suggests that size does not influence decomposition. However, this is difficult to confirm without also sampling larger

diameter classes and following individual pieces of wood of different diameter throughout the decomposition process.

It is interesting to note that the variability in density, as expressed by the standard deviation bars, decreases with age. This may indicate that the initial density variation is caused largely by more easily decomposable wood components, and that there is less variation in the content of more resistant wood fractions. We did not determine the density of undecomposed *P. radiata* wood, since this might not have been very meaningful given its high natural variability in wood density (Wilkes, 1989).

As decomposition proceeds, the moisture content of the pine wood increases (Table 4), and the C/N ratio decreases (Fig. 4). Nitrogen is limiting to wood decomposing micro-organisms (Cowling, 1970), therefore, nitrogen is immobilised by microbes while C is released through respiration (Harmon *et al.*, 1986). As a consequence, the C/N ratio declines and can thus be used as an indicator of the decomposition stage within a given wood type.

Table 4. Density, water content, carbon-to-nitrogen ratio and respiration in wood samples of P. radiata, E. regnans, and E. maculata at different stages of decomposition. Mean  $\pm$  standard deviation shown. Number of samples given in Appendix 2.

	Age	Density	Water content	C/N	Respiration
	(yrs)	(g cm <sup>-3</sup> )	(% dry weight)		$(mg CO_2-C g C^{-1}d^{-1})$
P. radiata	1	$0.41 \pm 0.06$	$61.1 \pm 30.5$	306.1 ±150.1	$0.672 \pm 0.407$
	2.5	$0.33 \pm 0.07$	$111.0 \pm 47.1$	$226.6 \pm 57.5$	$0.746 \pm 0.482$
	6	$0.20 \pm 0.04$	$173.9 \pm 50.0$	$234.5 \pm 90.0$	$0.405 \pm 0.174$
	9	$0.15\pm0.02$	$256.1 \pm 43.7$	$138.4 \pm 32.5$	$0.585 \pm 0.248$
E. regnans	1	$0.56 \pm 0.08$	$49.6 \pm 12.5$	$403.0 \pm 77.9$	$0.117 \pm 0.075$
	3.5	$0.45 \pm 0.09$	$84.0 \pm 38.5$	$350.8 \pm 109.3$	$0.232 \pm 0.031$
	6.5	$0.38 \pm 0.09$	$151.7 \pm 71.6$	$145.2 \pm 61.6$	$0.510 \pm 0.285$
	12	$0.35 \pm 0.11$	$183.8 \pm 96.0$	$236.9 \pm 122.7$	$0.331 \pm 0.208$
E. maculata	1.5	$0.65 \pm 0.11$	$47.3 \pm 9.3$	$424.2 \pm 96.6$	$0.560 \pm 0.369$
	6.5	$0.55 \pm 0.07$	$61.6 \pm 21.2$	$406.3 \pm 104.7$	$0.346 \pm 0.129$
	11.5	$0.69 \pm 0.09$	$58.8 \pm 29.9$	$673.7 \pm 207.$	$0.169 \pm 0.128$

If we assume that the constant loss in density, as presented in Figure 3, was a result of respiration, then the respiration rates measured for the different age classes under laboratory conditions should also have been constant; this was not the case (Fig. 4). Instead, respiration rates fluctuated without any recognisable trend. A general linear model analysis showed that neither age, nor wood density, moisture content, or C/N ratio could explain the variation in respiration rates. The average respiration rate across all age classes was  $0.62 \text{ mg CO}_2$ -C g C<sup>-1</sup> d<sup>-1</sup>. This value is 18 times higher than the decomposition constant derived from the density loss. If we correct for the differences in temperature between the incubation and the field (using the equation provided by Burger and Pritchett (1984) and assuming a  $Q_{10}$  of 2) the decomposition constant is still 8 times higher than the one derived form the density loss over time. Even using this lower value 74% of the C in wood would be lost during the first year. This points to strong limitations on decomposition in the field, which may be the result of harsh moisture and extreme temperatures. The results may also indicate that the true  $Q_{10}$  is higher than 2.

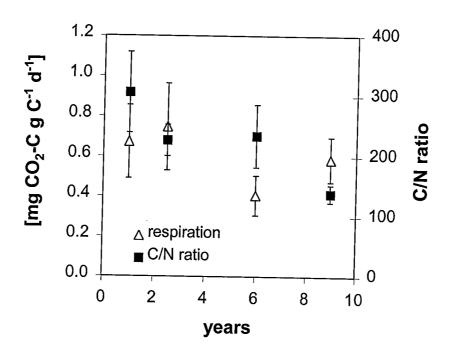


Figure 4. Respiration rates and carbon-to-nitrogen ratios in *P. radiata* logs decomposing *in situ* for 1, 2.5, 6, and 9 yrs following clear cut harvesting. Respiration was determined using the soda-lime technique during three days of incubation at 25°C. Bars represent standard errors.

### Eucalyptus regnans

Mountain Ash samples were collected from sites in the Toolangi district, Victoria, harvested 1, 3.5, 6.5, and 12 years before. The stand regeneration practice in these forests is clearfelling, followed by a hot slash burn. Care was taken to avoid sampling of charred material. This could not be avoided in all cases. However, the density of charred samples was not significantly different from unburned samples. Field observation showed that charring did not stop the decomposition of wood beneath the charred layer.

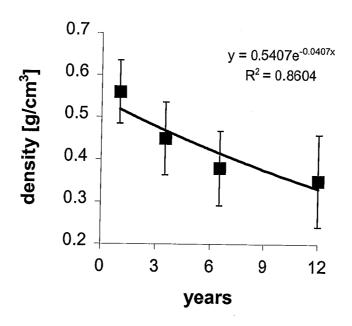


Figure 5. Wood density in *E. regnans* logs decomposing *in situ* for 1, 3.5, 6.5, and 12 yrs following clear-cut harvesting. A negative exponential decay model was fitted. Bars represent standard deviations.

The single exponential model fitted the *E. regnans* data less well than for *P. radiata*. It appears that very little density loss occurred in logs between years 6.5 to 12. The decomposition constant derived from the model is k = 0.0407. This would equal a turnover time  $(t_{0.95})$  of 74 years. Again this time is much longer than was indicated by the durability studies. However, the value lies between the turnover times determined by O'Connell (1997) and Brown *et al.* (1996) for *E. diversicolor*, a timber of medium to low durability.

The density loss pattern depicted in Figure 5 points to a potential problem associated with the methodology used. Using the water replacement technique to determine the volume of wood samples takes into account the loss of density associated with a loss of substance within otherwise solid wood. However, as decomposition proceeds some of the original volume is also lost. Therefore, using the water replacement technique does not relate the current weight to the original volume of the sample, but to the current volume and may lead to an underestimation of the density loss. This is a particular problem in samples where the sapwood decays faster than the heartwood, which makes it difficult to establish the original sample diameter once the sapwood has disappeared. Whereas in *E. maculata* it was possible to correct the volume for sapwood loss, this was not possible in *E. regnans*, where it is difficult to discern the sapwood from the heartwood. The problem was overcome in *P. radiata*, where case-hardening

preserved the outer wood surface and thus the volume of even the older samples (6.5 and 9 yrs) was determined through length and diameter measurements.

The assumption that the small density loss between years 6.5 to 12 was caused by a loss of sapwood volume is supported by the C/N ratios in the wood (Fig. 6). Up to age 6.5, the C/N ratio declines steeply as decomposition and concomitant N immobilisation increases. The subsequent increase in the C/N ratio shows that the material at age 12 is less decomposed than that at age 6.5, which indicates a higher proportion of heartwood.

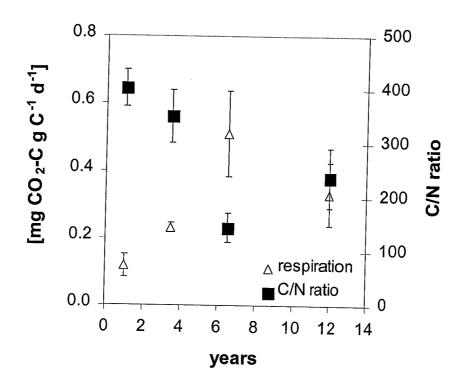


Figure 6. Respiration rates and carbon-to-nitrogen ratios in *E. regnans* logs decomposing *in situ* for 1, 3.5, 6.5, and 12 yrs following clear cut harvesting. Respiration was determined using the soda-lime technique during three days of incubation at 25°C. Bars represent standard errors.

If we base the determination of the decomposition constant on the first three data points in Figure 6, we obtain a value of k = 0.07, which provides a turnover time  $(t_{0.95})$  of 43 yrs. This value seems to be more realistic, since durability (Table 2) and decay resistance (Table 3) of *E. regnans* was similar to that of *P. radiata*.

The laboratory respiration rates in decaying wood of *E. regnans* were highly variable. They also defy the notion of a constant decomposition rate as assumed in the negative exponential decay model. Respiration rates were lowest in the youngest wood, and peaked in the 6.5 yr old material, which may indicate that

the wood is gradually colonised by microbes. The average respiration rate was 0.2983 mg CO<sub>2</sub>-C g C<sup>-1</sup> d<sup>-1</sup>. When corrected for temperature differences between laboratory and the field (see above, under *P. radiata*), this is 7.5 times faster than decomposition in the field. At his rate, 40% of the original mass would be lost in the first year. The discrepancy between increasing respiration rates up to year 6.5 and fairly constant density loss rates over that period in wood from *E. regnans* may indicate the importance of fragmentation and leaching in the initial stages of decomposition.

# Eucalyptus maculata

Spotted Gum samples were collected from North Brooman State Forest, on the south coast of NSW. The sites were harvested 1.5, 6.5, and 11.5 years previously. These stands are harvested on a group selection basis.

Sampling was concentrated on pure patches of *E. maculata* in otherwise mixed forests. Initially it was intended to sample older age classes as well, but it was not possible to identify the species without doubt in the field once the bark had fallen off. At younger ages, the logs could be linked to stumps that were either still carrying the bark or coppiced, which allowed species identification.

Figure 7 shows, that the approach used to derive decay from changes in density is not suitable for this species. Following a decline in density during the first 6.5 years, which results largely from the decomposition of sapwood, the density increases in 11.5 year old samples. The problem has already been addressed in the discussion of results for *E. regnans*. Whereas, in 6.5 year old samples the original volume is still measurable, this is not the case in 11.5 yr old samples, which have lost all sapwood. Thus, the latter samples consist almost entirely of heartwood, which has a higher density than the combined sapwood and heartwood samples at 1.5 years of age. This assumption is supported by the high C/N ratios and low respiration rates in 11.5 yr old *E. maculata* samples (Fig. 8). Heartwood has a higher C/N ratio than sapwood, and the increase in the C/N ratio in older samples can therefore be explained by the loss of sapwood.

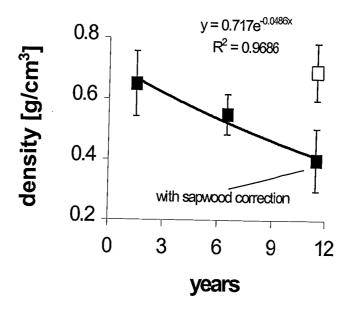


Figure 7. Wood density in *E. maculata* logs decomposing *in situ* for 1.5, 6.5, and 11.5 yrs following selective harvesting. Bars represent standard deviations. The empty square at year 11.5 represents the measured value, whereas the filled square used in the regression has been corrected for the loss of sapwood.

These findings point to the need to combine the density loss method with other approaches. In this case we corrected for the missing sapwood. According to Hillis (1987) the width of sapwood in eucalypts over 15 years old remains largely unchanged. Therefore, to determine a more realistic density, we measured the average sapwood width of younger samples  $(2.54 \pm 0.55 \text{ cm})$  and calculated the 'original' volume of 11.5 year old *E. maculata* discs. This estimated density has been included in Figure 7, and is the basis for the calculation of the negative exponential regression. Based on the correction for sapwood loss the estimated decay constant is k = 0.0486 and the turnover time  $(t_{0.95})$  is 62 yrs. This value falls within the range of turnover times derived from Da Costa's laboratory decay resistance tests (Table 3).

The laboratory respiration rates of *E. maculata* followed a completely different pattern than those in *E. regnans* (Fig. 6 & 8). Carbon loss through respiration in *E. maculata* was highest in the youngest samples, supporting field observation of intensive fungal colonisation of the sapwood. The decline of respiration from youngest to oldest samples could not be explained by the variation in wood density, moisture content, and C/N ratio in Spotted Gum. This may indicate the importance of other factors such as the content of extractives, which we did not determine in this study.

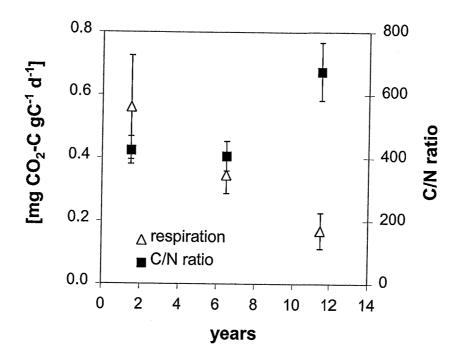


Figure 8. Respiration rates and carbon-to-nitrogen ratios in *E. maculata* logs decomposing *in situ* for 1.5, 6.5, and 11.5 yrs following selective logging. Respiration was determined using the soda-lime technique during three days of incubation at 25°C. Bars represent standard errors.

#### 4.3 Discussion

Estimation of decomposition rates through measurement of the wood density of chronosequence samples has been used widely (see Appendix 1). However, this approach suffers from some methodological shortcomings. As mentioned above, chronosequence studies generally can not take into account mass or volume losses due to fragmentation. This problem is apparent in older samples from *E. regnans*, and more so in older *E. maculata* samples, where parts of the highly decomposed sapwood had often disappeared, while the apparently unchanged heartwood remained. The visual estimation of losses due to fragmentation, as done in this study, is helpful but they are only provisional. If the loss of decomposing wood fragments from the sample cannot be accounted for, decomposition rates based on density loss will be underestimated. Our study has demonstrated that a combination of different methods, including current respiration rates and chemical characterisation of the decomposition stage (C/N ratio), can assist the development of a realistic picture of wood decay.

Decomposition rates based on respiration loss during incubation were 7.5 - 14.6 times higher than those measured in the field. These values were corrected for temperature differences assuming that the

biochemical activity will double with a temperature increase of  $10^{\circ}$ C ( $Q_{10} = 2$ ). The  $Q_{10}$  used has a strong influence on the difference between field and laboratory decay rates; in the absence of data we assumed a factor of 2. However, for modelling purposes it will be important to determine the influence of temperature on decomposition.

Although laboratory respiration rates cannot be directly converted into field decay rates, they are helpful in establishing decay patterns and differences between the different types of wood. The discrepancy between laboratory and field decay rates may be explained by the near optimal temperature and moisture conditions for fungi during incubation. The differences also point to strong limitations on decomposition in the field. However, it needs to be kept in mind that respiration rates were based on relatively short incubations. Thus, the carbon released may not only stem from the remaining wood, but also from the turnover of part of the microbial biomass in the wood.

We applied a single-component negative exponential decay model to derive decay rates for different woods from density loss. However, the results for *E. regnans* and *E. maculata* indicate that a two-component decay model, accounting for the differences in decay resistance between the sapwood and the heartwood, may be more appropriate. In the case of this study, the data base was not big enough to apply a two-component decay model.

Further problems arise from the modification of decay through charring of logs, which may be a result of slash burning after logging, or prescribed fires and wildfires. As charcoal is highly resistant to decay, it is usually assumed that decay of charred logs is reduced. However, our observations in the field do not confirm this. The surface of logs is never entirely charred, and the cracks in the charcoal allow entry of fungal spores (if not already present before the logs were charred). Thus we found that decomposition processes had continued beneath the charred surface. This aspect deserves further study.

Our sampling was concentrated on logs that were positioned on the surface. However, it cannot be ruled out that some of these logs may have been initially suspended and only later fell to the ground, and thus would not have undergone decomposition on the surface for the entire period following logging. Sampling of wood was also from log sections that belonged to a stem or crown, which had clearly been cut, and thus was not a result of natural stand disintegration processes. However, in some rare cases, felled trees might have already been dead, or, in the selection logging system, the logs on the ground might have originated from previous operations such as pole thinning.

With the hardwoods, samples were collected from both stems and large branches, for which differences in initial density might be expected. This may have caused some of the variation in density detected in E. regnans and E maculata.

The above considerations point to the limitations of the chronosequence approach. They also indicate the necessity to establish long-term CWD decomposition experiments that allow a controlled investigation of the different factors that may influence decay.

# 5. The significance of decay rates for estimating ${\rm CO_2}$ release from coarse woody debris in the reference year

To determine CO<sub>2</sub> release from the decay of coarse woody debris as a result of land use change and forestry activities in the reference year (1990), it is important to know how far back in time to take estimates of the input of CWD into the decaying pool. To address this question we have carried out a simple simulation based on some assumptions.

For this simulation we assumed that clearing started in year 0, and the amount of CWD put into the decaying pool was equal to 100 units. This pool underwent decomposition at three different rates, k = 0.3, 0.1, and 0.05, which represent turnover times  $(t_{0.95})$  of 10, 30, and 60 years, respectively. It was further assumed that the same amount was entered into the pool of decaying wood every year and underwent decay at the same rate.

As the simulation in Figure 9 illustrates, the higher the decay rates and the shorter the turnover times, the sooner an equilibrium between input and decay is reached. The point in time at which the  $CO_2$  release is 95 units is equivalent to the turnover time  $(t_{0.95})$ . That means that for the currently used IPCC default turnover time, it would be necessary to have input estimates of CWD entering the decaying pool for 10 yrs prior to 1990. For lower decay rates, which appear to be more realistic, it will be necessary to derive estimates of CWD entering the decaying pool for much longer periods prior to 1990. However, the importance of longer periods will depend on the required level of accuracy, and the actual clearing rates in those years. Based on the decay rates calculated in this study, to develop the 1990 baseline, it is recommended that the amounts of CWD entering decay should be estimated for the period 1960-1990.

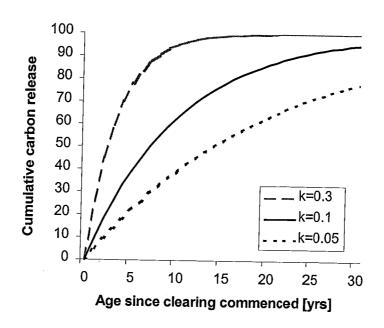


Figure 9.The effect of different decay rate constants on the cumulative release of  $CO_2$  from the pool of coarse woody debris. The simulations assume constant input of 100 units of carbon every year. The decay rate constants k = 0.3, 0.1, and 0.05 represent turnover times  $(t_{0.95})$  of 10, 30, and 60 yrs respectively.

## 6. How to scale up?

For the National Carbon Accounting System it will be necessary to provide regionally and nationally aggregated figures for CO<sub>2</sub> release from decay of fine litter and coarse woody debris as a result of land use change and forestry activities in the reference year (1990). This report has so far considered only decay rates of CWD. However, the question arises as to how the decay of CWD and other litter may be modelled to provide the required figures.

This report provides estimates of turnover times and decomposition rates for tree species of different durability. Thus, as a first step to refine CO<sub>2</sub> release estimates, tree species or forest and woodland types could be stratified into decay classes. Further information required to estimate CO<sub>2</sub> release from decaying CWD on a regional basis is summarised below:

• The quantity of CWD and smaller litter fractions entering the decay process. Currently only very limited information is available on the initial carbon density of different vegetation types (in biomass and litter), the proportion of biomass left as slash following clearing or harvesting, and the proportion of the different litter fractions consumed by fire, if burning is used. This essential information needs

to be broken down further into tree species or guilds, to account for the different decay resistance of coarse woody debris.

- <u>Clearing method</u>. The decomposition of CWD will depend on the position in which the wood is decaying, for example, it is accelerated when the debris is in contact with soil and decelerated when suspended.
- The influence of moisture and temperature on CWD decay. From the review of the literature no clear recommendation can be given on how these two important and interacting factors should be included into models. Durability studies indicate that decay is faster in tropical climates, but these studies were carried out in tropical areas of high rainfall. It is not clear whether the same can be said about drier regions in the tropics and subtropics, where most of the clearing activity currently occurs. It is also not clear whether the high decay rates at tropical sites were a result of the climate or a higher abundance of termites, or a combination of both factors.

For a given moisture content, the effect of temperature can be modelled according to van Hoof's rule, by applying a  $Q_{10}$  factor, which can be derived form laboratory incubations. Thus, it will be most critical to establish the effect of precipitation regimes on decay of CWD, and collect information on the interaction between moisture and temperature.

- <u>Substrate quality</u>. For better predictions of decay rates, refined information on the influence of wood properties (density, content of extractives, nutrient status, dimension) on the decomposition process is required. Also, information on the decay of below-ground woody litter relative to that of aboveground debris is urgently needed.
- <u>Influence of termites</u>. The influence of termites may override all other factors. Estimates are required of the acceleration of decay under the influence of termites and the proportion of the CWD pool that is affected by termites in different regions.
- <u>Influence of fire</u>. Managed forests and cleared land used for grazing are subject to wildfires and prescribed burning. In many systems the frequency of fires may be higher than the turnover rates suggested by this study. Thus, fires will consume a proportion of the carbon that would otherwise decay. The influence of fire on the decay process of CWD is not known and requires investigation.

This may be carried out at some of the fire frequency trials that have been established in different parts of Australia.

## 7. Conclusions

The results of the literature review demonstrate that the number of studies on decomposition rates of CWD in Australia is insufficient to derive reliable data at a regional or national scale. Nevertheless, by referring to international studies on decomposition rates, and to durability studies on Australian timbers, it can be concluded that an assumed turnover time of 10 years (IPCC default) is a considerable overestimation of the rate of CWD decomposition. Despite the variety of parameters influencing the rate of decay, we estimate that CWD turnover time exceeds 25-30 years in most cases.

As a first approach towards improved assessment of turnover times for Australian timber species it is recommended that  $t_{0.95}$ -values are calculated for the durability classes of Thornton *et al.* (1997). The durability classes 1, 2, 3 and 4 (Thornton *et al.*, 1997) are expected to have minimum turnover times  $(t_{0.95})$  of 54, 39, 26 and 11 years. These turnover times may be reduced to >30, 20, 11, and 4 years north of 30° latitude. However, results on turn-over times according to long-term decomposition studies are expected to provide higher values.

Quantitative information on the relative importance of key drivers for decomposition is lacking. Abiotic factors such as the moisture and temperature regimes determine general conditions for decomposition, whereas factors such as the substrate quality influence these abiotic conditions as well as regulate specific conditions for decomposition. Because of the impact of temperature and moisture regimes, and the presence/absence of wood-destroying invertebrates such as termites, turnover rates of species have to be considered in a regional context. Decomposition drivers such as wood quality, charred surfaces, positioning of wood and wood diameter have to be evaluated at a local scale before they can be incorporated into future decomposition models.

# 8. Recommendations

• The current IPCC default for decay rates of coarse woody debris should be replaced. Instead of assuming a linear decay of all material within 10 yrs, an exponential decay function, with rate

constants estimated according to the durability class of species, should be used. The proposed minimum turnover times for wood grouped in durability classes 1-4 are 54, 39, 26 and 11 years, respectively. In the absence of better information these turnover times should be reduced to >30, 20, 11, and 4 years north of 30° latitude to account for the influence of termites and different climatic conditions. However, for most Australian hardwoods a turnover time of at least 25-30 years can be expected. For many durable species a turnover time of more than 100 years is realistic. Species-specific turnover values can be derived from results of durability studies. However, these estimates should be regarded as minimum turnover times.

- To gain data on the decomposition rate of Australian timbers, a detailed long-term study is strongly recommended. Long-term studies, rather than chronosequence studies, will allow for continued and standardised research on CWD decomposition. The study design must incorporate the various drivers of CWD decomposition, such as climatic factors, substrate quality, size and position of logs. This experiment should be set up soon, involve species of a range of natural durabilities, and include species from forest and woodland types most strongly affected by clearing.
- The application of decomposition models is limited by the lack of detailed and reliable data on the
  fractions of fine litter and CWD in major managed and unmanaged forest and woodland ecosystems
  of Australia. It is therefore recommended that methods to quantify these pools be further developed.
- The methodology to more accurately assess the decomposition of CWD and other litter requires further development and standardisation.

### Acknowledgments

We thank Mick Morley (DNRE Victoria, Toolangi), Aidan Flanagan (ACT Forests, Canberra) and Ian Barnes (State Forests of NSW, Batemans Bay) for their co-operation and assistance with the selection of suitable sampling sites. We thank John Kayne, Sanjiva de Silva, and Scobie Mackay for their enthusiastic help with sampling, analysis and data processing as well as Nina Stahl and Emily Backen for collecting and managing the references. Phil Evans and Gary Richards provided helpful comments on an earlier draft. Rodney Keenan contributed some good ideas in the development phase of this project. We also acknowledge the support of Gregor Christie and Paul Smart (CSIRO, Division of Material Science and Technology), who generously donated the foil used for incubation experiments.

#### References

Abbott, DT & Crossley, DA, 1982. Woody litter decomposing following clear-cutting. Ecology 63(1): 35-42.

Alban, DH & Pastor, J, 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Canadian Journal of Forest Research 23: 1744-1749.

Arthur, MA, Tritton, LM & Fahey, TJ, 1993. Dead bole mass and nutrient remaining 23 years after clear-felling of a northern hardwood forest. Canadian Journal of Forest Research 23: 1298-1305.

Barber, BL & VanLear, DH, 1984. Weight loss and nutrient dynamics in decomposing woody Loblolly Pine logging slash. Soil Science Society of America Journal 48: 906-910.

Bauhus, J & Bartsch, N, 1996 Fine root growth in beech (Fagus sylvatica L.) forest gaps. Canadian Journal of Forest Research 26: 2153-2160.

Berg, B, 1984. Decomposition of root litter and some factors regulating the process: Long-term root litter decomposition in Scots Pine forest. Soil Biology & Biochemistry 16: 609-617.

Blanchette, RA, 1995. Degradation of the lignocellulose complex in wood. Canadian Journal of Botany 73 (Suppl. 1): 999-1010.

Boddy, L, 1983. Carbon dioxide release from decomposing wood: Effect of water content and temperature. Soil Biology & Biochemistry 15: 501-510.

Boddy, L & Swift, MJ, 1984. Wood decomposition in an abandoned beech and oak coppice woodland in SE England. III. Decomposition and turnover of twigs and branches. Holarctic Ecology 7: 229-238.

Brackebusch, AP, 1975. Gain and loss of moisture in large forest fuels. USDA Forest Service Research Paper INT-173. Intermt. Forest and Range Experimental Station, Ogden, Utah.

Brown, PM, Shepperd, WD, Mata, SA & McClain, DL, 1998. Longevity of windthrown logs in a subalpine forest of central Colorado. Canadian Journal of Forest Research 28: 932-936.

- Brown, S, Mo, J, McPherson, JK & Bell, DT, 1996. Decomposition of woody debris in Western Australian forests. Canadian Journal of Forest Research 26: 954-966.
- Bultman, JD, & Southwell, CR, 1976. Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica 8(2): 71-95.
- Bunnell, FL, Tait, DEN, Flanagan, PW & van Cleve, K, 1977. Microbial respiration and substrate weight loss. II. A model of the influence of chemical composition. Soil Biology & Biochemistry 9: 41-47.
- Burger, JA & Pritchett, WL, 1984. Effects of clearfelling and site preparation on nitrogen mineralization in a Southern pine stand. Soil Science Society of America Journal 48: 1432-1437.
- Busse, MD, 1994. Downed bole-wood decomposition in lodgepole pine forests of Central Oregon. Soil Science Society of America Journal 58(1): 221-227.
- Chafe, SC, 1986. Collapse, volumetric shrinkage, specific gravity and extractives in *Eucalyptus* and other species. Part 1: The shrinkage/specific gravity ratio. Wood Science and Technology 20: 293-307.
- Chafe, SC, 1989. Observations on the relationship between wood durability and density. Journal of the Institute of Wood Science 11(5): 182-185.
- Cheney, NP, Raison, RJ & Khanna, PK, 1980. Release of carbon to the atmosphere in Australian vegetation fires. In: Pearman, GI. (Ed.) Carbon dioxide and climate: Australian Research, Australian Academy of Science, Canberra: 153-158.
- Christensen, O, 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. Oikos 28: 177-186.
- Christensen, O, 1984. The states of decay of woody litter by relative density. Oikos 42: 211-219.
- Cowling, EB, 1972. Nitrogen in forest trees and its role in wood deterioration. Abstracts of Uppsala Dissertations in Science.
- Crawford, RL, 1981. Lignin Biodegradation and Transformation. Wiley, New York.

- Da Costa, EWB, 1973. Natural decay resistance of wood. Biological Transformation of Wood by Microorganisms, Minneapolis USA, Springer-Verlag.
- Da Costa, EWB, 1975. Natural decay resistance of wood. In: Biological Transformation of Wood by Microorganisms, Proceedings of the Session on Wood Products Pathology at the 2nd International Congress of Plant Pathology September 10-12, 1973, Minneapolis USA, W. Liese (Ed.): 103-117.
- Da Costa, EWB, 1979. Comparative decay resistance of Australian timbers in accelerated laboratory tests. Australian Forest Research 9: 119-135.
- Da Costa, EWB, Aplin, TEH. & Tamblyn, N, 1957. The comparative resistance to decay of eight Australian timbers under different conditions of testing. Divn. For. Prod. CSIRO Melbourne, Project P13-5; Project Report No. 1.
- Da Costa, EWB, Rudman, P & Deverall, FJ, 1962. Inter-tree variation in decay resistance of Karri (*E. diversicolor*) as related to colour, density and extractive density. Journal of the Institute of Wood Science 2: 48-55.
- Deverall, BJ, 1965. The physical environment for fungal growth. 1. Temperature. In: The Fungi. I. The Fungal Cell. Ainsworth, GC & Sussman, AS (eds.), pp. 543-550. Academic Press, New York.
- Eaton, RA & Hale, MDC, 1993. Wood: Decay, Pests, and Protection. London, Chapman & Hall.
- Edmonds, RL, Vogt, DJ, Sandberg, DH & Driver, CH, 1986. Decomposition of Douglas-fir and red alder wood in clear-cutting. Canadian Journal of Forest Research 16: 822-831.
- Edwards, NT, 1982. The use of soda-lime for measuring respiration rates in terrestrial systems. Pedobiologia 23: 321-330.
- Erickson, HE, Edmonds, RL & Peterson, CE, 1985. Decomposition of logging residues in Douglas-fir, Western Hemlock, Pacific Silver Fir and Ponderosa Pine ecosystems. Canadian Journal of Forest Research 15: 914-921.

- Eslyn, WE & Highley, TL, 1976. Decay resistance and susceptibility of sapwood of fifteen tree species. Phytopathology 66: 1010-1017.
- Fahey, TJ, 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta ssp. latifolia*) ecosystems, south-eastern Wyoming. Ecological Monographs 53(1): 51-72.
- Fahey, TJ & Arthur, MA, 1994. Further studies of root decomposition following harvest of a northern hardwoods forest. Forest Science: 618-629.
- Fahey, TJ, Hughes, JW, Pu, M & Arthur, MA, 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. Forest Science 34: 744-768.
- Foster, JR & Lang, GE, 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hamshire. Canadian Journal of Forest Research 12: 617-626.
- Frangi, JL, Richter, LL, Barrera, MD & Aloggia, M, 1997. Decomposition of *Nothofagus* fallen woody debris in forests of Tierra Del Fuego, Argentina. Canadian Journal of Forest Research 27: 1905-1102.
- Gay, FJ & Evans, RW, 1968. The status and termite durability of Northern Cypress Pine. Australian Forestry: 80-91.
- Good, HM & Darrah, JA, 1967. Rates of decay in wood measured by carbon dioxide production. Annals of Applied Biology 59: 463-472.
- Graham, RL & Cromack Jr., KC, 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research 12: 511-521.
- Graham, SA, 1925. The felled tree trunk as an ecological unit. Ecology 6: 397-416.
- Grier, CC, 1978. A *Tsuga heterophylla Picea sitchensis* ecosystem of coastal Oregon: Decomposition and nutrient balances of fallen logs. Canadian Journal of Forest Research 8: 198-206.
- Harmon, ME, 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. Oecologia 52: 214-215.

Harmon, ME & Hua, C, 1991. Coarse woody debris dynamics in two old-growth ecosystems. Comparing a deciduous forest in China and a conifer forest in Oregon. Bioscience 41: 604-610.

Harmon, ME, Franklin, JF, Swanson, FJ, Sollins, P, Gregory, SV, Lattin, JD, Anderson, NH, Cline, SP, Aumen, NG, Sedell, JR, Lienkaemper, GW, Cromack, JR & Cummins, KW, 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Harmon, ME, K. Cromack, J & Smith, BG, 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Canadian Journal of Forest Research 17: 1265-1272.

Harmon, ME, Whigham, DF, Sexton, J & Olmsted, I, 1995. Decomposition and mass of woody detritus in the dry tropical forests of the north-eastern Yucatan Peninsula, Mexico. Biotropica 27: 305-316.

Hayes, GL, 1940. The moisture content of large sized fuels as an index of intraseasonal and seasonal fire danger severity. M.Sc. Thesis, Yale Univ, New Haven, Connecticut.

Healey, IN & Swift, MJ, 1971. Aspects of the accumulation and decomposition of wood in the litter layer of a coppiced beech-oak woodland. Ann. Zool. Ecol. Anim./hors serie: 417-430.

Hillis, WE, 1977. Secondary changes in wood. Recent Adv. Phytochemistry 11: 247-309.

Hillis, WE, 1987. Heartwood and tree exudates. Springer Series in Wood Science. Springer Verlag, Berlin, 268p.

Jemison, GM, 1937. Loss of weight of wood due to weathering. Journal of Forestry: 460-462.

Jenny, H, Gessel, SP & Bingham, FT, 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. Soil Science 68: 419-432.

Johnson, GC, Thornton, JD, Creffield, JW & Howick, CD, 1988. Assessing timber durability using an accelerated field simulator I. Initiation of decay and termite studies. Material und Organismen 23: 97-114.

- Johnson, EA & Greene, DF, 1991. A method for studying dead bole dynamics in *Pinus contorta var. latifolia Picea engelmannii* forests. Journal of Vegetation Science 2: 523-530.
- Käärik, AA, 1974. Decomposition of wood. In: Biology of Plant Litter Decomposition. Dickson, CH & Pugh, GJE (eds.), Vol. 1, pp. 129-174. Academic Press, London.
- Keenan, RJ, Prescott, CE & Kimmins, JP, 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island. Canadian Journal of Forest Research 23: 1052-1059.
- Krankina, ON & Harmon, ME, 1995. Dynamics of the dead wood carbon pool in north-western Russian boreal forests. Water, Air and Soil Pollution 82: 227-238.
- Lambert, RL, Lang, GE & Reiners, WA, 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473.
- Lang, GE & Knight, DH, 1979. Decay rates for boles of tropical trees in Panama. Biotropica 11: 316-317.
- Lieberman, D, Lieberman, M, Peralta, R & Hartshorn, GS, 1985. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. Journal of Ecology 73: 915-924.
- MacMillan, PC, 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Canadian Journal of Forest Research 18: 1353-1362.
- Marra, JL & Edmonds, RL, 1994. Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, U.S.A. Canadian Journal of Forest Research 24: 1811-1817.
- Marra, JL & Edmonds, RL, 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A. Canadian Journal of Forest Research 26: 1337-1345.
- Mattson, KG & Swank, WT, 1984. Carbon dioxide fluxes from conventional and whole tree harvested watersheds effects of wood residue. Bulletin of the Ecological Society of America 65: 123.

- Mattson, KG, Swank, WT & Waide, JB, 1987. Decomposition of woody debris in a regenerating, clearcut forest in the Southern Appalachians. Canadian Journal for Forest Research 17: 712-720.
- McCarthy, BC & Bailey, RR, 1994. Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Canadian Journal of Forest Research 24: 1317-1329.
- McFee, WW & Stone, EL, 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Science Society of America Proceedings 30: 513-516.
- Means, JE, Cromack, J & MacMillan, PC, 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Canadian Journal of Forest Research 15: 1092-1098.
- Melillo, JM, Naiman, RJ, Aber, JD & Eshleman, KN, 1983. The influence of substrate quality and stream size on wood decomposition dynamics. Oecologia 58: 281-285.
- Mikola, P, 1960. Comparative experiments in decomposition rates of forest litter in southern and northern Finland. Oikos 11: 161-166.
- Miller, WE, 1983. Decomposition rates of Aspen bole and branch litter. Forest Science 29: 351-356.
- Minderman, G, 1968. Addition, decomposition and accumulation of organic matter in forests. Journal of Ecology 56: 355-362.
- NGGIC 1997a. Land Use Change & Forestry. Workbook for Carbon Dioxide from the Biosphere. Workbook 4.2, Revision 2.
- NGGIC 1997b. National Greenhouse Gas Inventory. Land Use Change and Forestry Sector 1988-1995, based on Workbook 4.2.
- O'Connell, AM, 1987. Litter dynamics in Karri (*Eucalyptus diversicolor*) forests of south-western Australia. Journal of Ecology 75: 781-796.
- O'Connell, AM, 1997. Decomposition of slash residues in thinned regrowth eucalypt forest in Western Australia. Journal of Applied Ecology 34: 111-122.

Olson, JS, 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322-331.

Purslow, DF, 1976. Results of field tests on the natural durability of timber (1932-1975). BRE Current Paper CP6/76. Build. Res. Establ., UK.

Raphael, MG & Morrison, ML, 1987. Decay and dynamics of snags in the Sierra Nevada, California. Forest Science 33: 774-783.

Rayner, ADM & Boddy, L, 1988. Fungal Decomposition of Wood – Its Biology and Ecology. Wiley & Sons, UK.

Rice, MD, Lockaby, BG, Stanturf, JA & Keeland, BD, 1997. Woody debris decomposition in the Atchafalaya River Basin of Louisiana following hurricane disturbance. Soil Science Society of America Journal 61: 1264-1274.

Rudman, P, 1964. Durability in the genus Eucalyptus. Australian Forestry 28: 242-257.

Rudman, P, 1966. Decay resistance in the Cypress pines. Australian Forestry 30: 279-282.

Savely, HE, 1939. Ecological relations of certain animals in dead pine and oak logs. Ecological Monographs 9: 322-385.

Scheffer, TC & Cowling, EB, 1966. Natural resistance of wood to deterioration. Annual Review of Phytopathology 4: 147-170.

Scheu, S & Schauermann, J, 1994. Decomposition of roots and twigs: Effects of wood type (beech and ash) diameter, site of exposure and macrofauna exclusion. Plant and Soil 163: 13-24.

Schowalter, RD, 1992. Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition. Canadian Journal of Forest Research 22: 161-166.

- Schowalter, TD, Zhang, YT & Sabin, Te, 1998. Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition. Ecography 21: 3-10.
- Simpson, JA, 1996. Wood decay fungi. Canberra, CSIRO. 1B Introduction Fungi in the Environment: 95-128.
- Sinsabaugh, RL, Antibus, RK, Linkins, AE, MacClaugherty, CA, Rayburn, L, Rupert, D & Weiland, T, 1992. Wood decomposition over a first-order watershed: Mass loss as a function of lignocellulose activity. Soil Biology & Biochemistry 24: 743-749.
- Skaar, C, 1972. Water in Wood. Syracuse Wood Science Series 4, Syracuse Univ. Press.
- Smith, LV & Zavarin, E, 1960. Free mono- and oligosaccharides of some California conifers. Tappi 43: 218-221.
- Sollins, P, 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research 12: 18-28.
- Sollins, P, Cline, SP, Verhoeven, T, Sachs, D & Spycher, G, 1987. Patterns of log decay in old-growth Douglas-fir forests. Canadian Journal of Forest Research 17: 1585-1595.
- Spies, TA, Franklin, JF & Thomas, TB, 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69: 1689-1702.
- Standards Association of Australia, 1979. Timber poles for overhead limes. Standards Association of Australia, Sydney, NSW, AS 2209.
- Standards Association of Australia, 1980. Preservative-treated sawn timber, veneer and plywood. Standards Association of Australia, Sydney, NSW, AS 1604.
- Stewart, GH & Burrows, LE, 1994. Coarse woody debris in old-growth temperate beech (*Nothofagus*) forests of New Zealand. Canadian Journal of Forest Research 24: 1989-1996.

- Stewart, HTL & Flinn, DW, 1985. Nutrient losses from broadcast burning of *Eucalyptus* debris in northeast Victoria. Australian Forest Research 15: 321-332.
- Stone, JN, MacKinnon, A, Parminter, JV & Lertzman, KP, 1998. Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. Canadian Journal of Forest Research 28: 788-793.
- Sturtevant, BR, Bissonette, JA, Long, JN & Roberts, DW, 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7: 702-712.
- Swift, MJ, 1973. The estimation of mycelial biomass by determination of the hexoamine content of wood tissue decayed by fungi. Soil Biology & Biochemistry 5: 321-332.
- Swift, MJ, 1977. The ecology of wood decomposition. Science Progress 64: 175-199.
- Swift, MJ, Healey, IN, Hibberd, JK, Sykes, JM, Bampoe, V & Nesbitt, ME, 1976. The decomposition of branch-wood in the canopy and floor of a mixed deciduous woodland. Oecologia 26: 139-149.
- Swift, MJ, Heal, OW & Anderson, JM, 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley.
- Temnuhin, VB, 1996. Preliminary quantitative estimation of wood decomposition by fungi in a Russian temperate pine forest. Forest Ecology and Management 81: 249-257.
- Thornton, JD, Walters, NEM & Saunders, IW, 1983. An in-ground natural durability field test of Australian timbers and exotic reference species I. Progress report after more than 10 years' exposure. Material und Organismen 18: 27-49.
- Thornton, JD, Johnson, GC & Nguyen, N, 1991. An in-ground natural durability field test of Autralian timbers and exotic reference species. Material und Organismen: 1-17.
- Thornton, JD, Johnson, GC & Creffield, JW, 1995a. Hazard-based natural durability ratings and mean rates of biodeterioration proposed for use in the reliability-based durability design method. 25th Forest Products Research Conference, Melbourne, 18-21 November 1996.

Thornton, JD, Johnson, GC & Nguyen, N, 1995b. Revised natural durability ratings for the outer heartwood of mature Australian timbers in ground contact. Proceedings of the 25th Forest-Products Research Conference, Melbourne, 18-21 November 1996, Paper 1/18.

Thornton, JD, Johnson, GC & Nguyen, N, 1997. Revised CSIRO natural durability classification - Inground durability ratings for mature outer heartwood. CSIRO Forestry & Forest Products, Melbourne, 1-2.

Torres, JA, 1994. Wood decomposition of *Cyrilla racemiflora* in a tropical montane forest. Biotropica 26: 124-140.

Tyrell, LE & Crow, TR, 1994. Dynamics of dead wood in old-growth hemlock-hardwood forests of northern Wisconsin and northern Michigan. Canadian Journal of Forest Research 24: 1672-1683.

Wei, X, Kimmins, JP, Peel, K & Steen, O, 1997. Mass and nutrients in woody debris in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. Canadian Journal of Forest Research 27: 148-155.

Wengert, EM, 1966. Parameters for predicting maximum surface temperatures of wood in exterior exposures. U.S. Forest Service Research Paper FPL 62.

Wieder, RK & Lang, GE, 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63: 1636-1642.

Wilkes, J, 1984. The influence of rate of growth on the density and heartwood extractives content of Eucalypt species. Wood Science and Technology 18: 113-120.

Wilkes, J, 1985a. Host attributes affecting patterns of decay in a regrowth Eucalypt forest. I. Patterns of natural decay. Holzforschung 39: 17-22.

Wilkes, J, 1985b. Host attributes affecting patterns of decay in a regrowth Eucalypt forest. II. The resistance of heartwood to decay *in vitro*. Holzforschung 39: 137-141.

Wilkes, J, 1985c. Host attributes affecting patterns of decay in a regrowth Eucalypt forest. III. The responses of heartwood to injury and infection. Holzforschung 39: 253-257.

Will, GM, 1966. Root growth and dry-matter production in a high-producing stand of *Pinus radiata*. New Zealand Forest Research Note No. 44.

Wong, AHH & Wilkes, J, 1988. Association of tissue characteristics with susceptibility to decay in the sapwood of *Pinus radiata*. Holzforschung 42: 399-402.

Wong, AHH, Wilkes, J & Heather, WA, 1983. Influence of wood density and extractives content on the decay resistance of the heartwood of *Eucalyptys delegatensis* RT Baker. Journal of the Institute of Wood Science 54: 261-263.

Wong, AHH, Wilkes, J & Heather, WA, 1984. Inter- and intra-incremental variation in basic density, extractives content, and decay resistance in *Eucalyptus delegatensis*. Material und Organismen 19: 141-148.

Yavitt, JB & Fahey, TJ, 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, south-eastern Wyoming. Canadian Journal of Forest Research 12: 745-752.

# Appendix 2: Sampling specifications for experimental study

Pinus radiata

Sample region:

ACT Forestry, ACT, Australia

Sample area:

Pierces Creek - Tidbinbilla

Climate:

median precipitation 791 mm yr<sup>-1</sup>, mean daily min-max temp. 7.3°C /19.5°C

Sample plots:

Block 60 - Compartment 224 (felling in 1998/1999, age: 1)

Block 60 - Compartment 203 (felling in 1997, age: 2)

Block 60 - Compartment 202 (felling in 1993, age: 6)

Block Oakey Creek - Compartment 150 (felling in 1990, age: 9)

Sampling date:

21/6 - 24/6/1999

Number of samples:

Age-class 1:

20 logs @ 2 discs per log (n=40)

Age-class 2.5:

20 logs @ 2 discs per log (n=40)

Age-class 6:

20 logs @ 1 block (25cm) per log (n=20)

Age-class 9:

20 logs @ 1 block (25cm) per log (n=20)

Eucalyptus regnans

Sample region:

Central Highlands, Victoria, Australia

Sample area:

Toolangi Forest District, DNRE

Climate:

median precipitation 1300-1500mm yr<sup>-1</sup>, mean daily min-max temp. 4°C/23°C

Sample plots:

Ebbels (felling in 2/98 - 6/98, age: approx. 1 year)

Klondyke PT (felling in 10/95 – 12/95, age: approx. 3.5 years)

Vic Range TK (felling in 10/92 – 12/92, age: approx. 6.5 years)

Blowhard Rd. 82604 (felling in 1/87 - 6/87, age: 12 years)

Sampling date:

26/5 - 29/5/1999

Number of samples:

Age-class 1:

20 logs @ 2 discs per log (n=39)

Age-class 3.5:

20 logs @ 2 discs per log (n=33)

Age-class 6.5:

20 logs @ 1 block per  $\log (n=62)$ 

Age-class 12:

 $20 \log @ 1$  block per  $\log (n=37)$ 

Eucalyptus maculata

Sample region:

South Coast, New South Wales, Australia

Sample area:

North Brooman State Forest

Climate: dily median precipitation 1100 mm yr<sup>-1</sup>, mean daily min-max temp. 11.2°C/21.2°C

Sample plots: Compartment 46 (felling in 5/97 – 4/98, age: approx. 1.5 year)

Compartment 43 (felling in 5/92 - 4/93, age: approx. 6.5 years)

Compartment 45 (felling in 3/87 – 3/88, age: approx. 11.5 years)

Sampling date: 28/6 - 30/6/1999

Number of samples: Age-class 1.5: 22 logs @ discs per log (n=44)

Age-class 6.5: 16 logs @ discs per log (n=31)

Age-class 11.5: 18 logs @ discs per log (n=36)