DECOMPOSITION OF COARSE WOODY DEBRIS, AND METHODS FOR DETERMINING DECAY RATES

LORETTA GARRETT*, MURRAY DAVIS, and GRAEME OLIVER
Ensis, Private Bag 3020,
Rotorua, New Zealand.

(Received for publication 9 January 2006; revision 8 June 2006)

ABSTRACT

Understanding decay rates of above- and below-ground coarse woody debris pools is necessary for quantifying forest ecosystem carbon storage and cycling processes. Decay rates were determined from both time series and chronosequence studies. Time series studies, using measurements of wood samples of known initial mass and volume over time, provide more reliable data than chronosequence studies. However, the latter allow more rapid determination of decay rates which is an important factor since the decay of coarse woody debris is a slow process. Most studies indicate that, for both above- and below-ground material, between 30 and 200 years are required to achieve 95% decay. Roots generally take a longer time to decay than above-ground coarse woody debris of similar dimension. Factors controlling decay rate include temperature, precipitation, species, substrate quality and composition, moisture content and dimension of the material, whether the material is suspended or in contact with the soil, and characteristics of the decomposer community. Studies of above-ground coarse woody debris decay rates for *Pinus radiata* D. Don, New Zealand's dominant plantation species, have been limited to relatively low rainfall locations in New Zealand and Australia. No data are available on this species for below-ground coarse woody root decay rates.

Keywords: decomposition; decay rate; chronosequence; time series; coarse woody debris; roots.

INTRODUCTION

Above- and below-ground coarse woody debris is an important structural and functional component of managed and natural forest ecosystems (Harmon *et al*. 1986). For example, Allen *et al*. (1997) found above-ground coarse woody debris in forests of mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole) to vary from 20 to 170 mg/ha depending on the stage of stand development.

* Corresponding author: loretta.garrett@ensisjv.com

Coarse woody debris can be generated in the form of fallen logs, large branches, and standing dead trees, as well as associated root debris, by catastrophic disturbance of a forest by wind, fire, earthquake, or disease. In a plantation forest the main sources of woody debris are thinning and harvesting operations which generate root debris below-ground in addition to stems and branches above-ground (Erickson *et al*. 1985).

As a party to the United Nations Framework Convention on Climate Change and the Kyoto Protocol, New Zealand has an obligation to report on carbon emissions and removals arising from forestry activities, consistent with the Intergovernmental Panel on Climate Change Good Practice Guidance for Land Use, Land-Use Change, and Forestry (IPCC 2003). Coarse woody debris is an important component of these fluxes and therefore an understanding of the decay rates of coarse woody debris is necessary for quantifying forest ecosystem carbon storage and cycling processes (Beets *et al*. 1999). However, the decay of coarse woody debris generally, and roots especially, has often been neglected in the past due to difficulties in measurement. Internationally only a few studies have examined the decay rate of coarse woody roots in soil (Yavitt & Fahey 1982; Fahey *et al*. 1988, 1991; Fahey & Arthur 1994; Chen *et al*. 2001; Ludovici *et al*. 2002; Janisch *et al*. 2005). In New Zealand there has been only one study published on decay rates of stem and branch material in plantation forests (Ganjegunte *et al*. 2004) and research on coarse woody root decay has been limited to work on the rate of decay in root strength after timber harvesting (O'Loughlin & Watson 1979; Phillips & Watson 1994).

Because of the need for further information, this review was conducted to identify methods for measuring decay and calculating decay rates of both above- and below-ground coarse woody debris. Another aim was to identify important factors controlling decay as a basis for further studies for determining decay rates for *Pinus radiata*, New Zealand's dominant plantation forest species.

Defining Coarse Woody Debris

Coarse woody debris includes all non-living woody biomass, either standing, lying on the ground, or within the soil as dead roots and stumps. No standard minimum diameter for defining coarse woody debris has been published; however, above-ground coarse woody debris has typically been considered to be greater than 10 cm in diameter (Harmon & Sexton 1996; Payton et al. 2004) and coarse woody root debris to be greater than 1 cm diameter (Fahey *et al*. 1988; Harmon & Sexton 1996). We considered all pools of coarse woody debris and size classes, with particular emphasis on diameters greater than 1 cm.

Decomposition of woody material involves the processes of respiration, biological transformation, fragmentation, leaching, and weathering (Harmon *et al*. 1986).

Respiration by microbes with the evolution of carbon dioxide (CO_2) is the main process involved in the decomposition of woody material. Biological transformation is the metabolism of wood by microbial decomposers, and to a lesser extent by invertebrates, into new compounds. Fragmentation is the physical break-up of wood and bark, while leaching results from dissolution and loss of materials caused by percolating water. Weathering is the physical and chemical breakdown of wood due to climatic elements.

METHODS OF MEASURING DECOMPOSITION

The measurement of coarse woody debris decay can pose difficulties because of the slow decay rate and the heterogeneity of the material, the varying contact within and between sample units with the soil, and partial decay of the sample before death (Means *et al.* 1985). All of these factors must be taken into account when consideration is given to experimental design, sampling techniques, and measurements to be made to determine the decomposition rate of coarse woody debris.

Experimental Design

The two types of experiments used to measure decay rates of coarse woody debris are chronosequence studies and time series studies.

Chronosequence studies

The chronosequence approach has been used in a variety of experimental situations and is very useful and time efficient as it allows for long periods of decay and differing decay states to be assessed over relatively short time intervals. Chronosequence studies rely on the ability to age the woody debris accurately and to find sites that represent a range of time intervals, but are otherwise comparable (Sollins *et al.* 1987; Harmon & Sexton 1996). Reliable information for debris age determination and site selection can be gained from harvesting and management records (Chen *et al.* 2000; Ludovici *et al.* 2002; Ganjegunte *et al.* 2004), permanent sample plots or surveys (MacMillan 1988), or records of natural disturbances of an area (Boone *et al.* 1988). Where the age of coarse woody debris has to be estimated using indirect methods, the debris can be divided into decomposition classes, the mean ages of which are used as the measure of time (Harmon & Sexton 1996). Typically three to five decay classes are used and these are commonly based on physical rather than biological indicators (Lambert *et al.* 1980; Sollins *et al.* 1987). Samples of dead wood in each decomposition class can then be collected to determine their density. This method relies on the accurate classification of dead wood into correct decomposition classes and the adequate sampling of logs to represent each decay class.

Fragmentation of sample units is difficult to measure in a chronosequence as this requires an estimate of the initial weight or volume of the woody debris. Therefore fragmentation has generally been neglected, resulting in an under-estimation of total decay. Methods for estimating loss through fragmentation have been established and correction factors have been applied to include losses due to this process (Means *et al*. 1985; Harmon & Sexton 1996; Mackensen & Bauhus 2003). Another uncertainty with a chronosequence study is that the nature of the initial decaying environment may be difficult to define. For example, the position of a log may change from initially suspended to being in contact with the ground and this can exert considerable influence on the decay rate (Naesset 1999; Ganjegunte *et al*. 2004).

Determining coarse woody root decay using a chronosequence approach involves the excavation of part or all of the root system, which can be a major undertaking depending on the size and depth of root system. For example, in 25-year-old *P. radiata* Watson & O'Loughlin (1990) described a maximum root length extension from the stump of 10.4 m and depth from the soil surface of 3.1 m. Detailed methodology of large and small root system excavation has been outlined by Bohm (1979).

Time series

Time series studies provide the most reliable data for determining decomposition rates, by monitoring the change in volume, weight, and density of individual woody samples over long periods of time. This method allows for the assessment of decay as a result of respiration, leaching, and fragmentation but only a few studies have measured individual pieces over a long period. For example, Stone *et al*. (1998) studied decomposition of above-ground coarse woody debris of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) on Vancouver Island (Canada) over 65 years from permanent plots established in 1929 and 1930, and re-measured in 1995. In addition, Arthur *et al*. (1993) recorded decay rates of individual samples of four species over a 23-year period in New Hampshire, USA. The advantage a time series study has over a chronosequence is that the initial mass and volume of the individual samples are known. However, the disadvantage is that years or decades may be required before results can be obtained, especially for large-diameter material. Therefore small-diameter pieces have typically been used to ensure that the time series study is of a manageably short duration.

In a time series experimental design the position of woody debris — suspended, lying on the soil, or within the soil at different depths — can be controlled. Typically, above-ground studies have focused on samples placed on the forest floor to avoid the risk of suspended or standing dead stem samples falling to the ground

resulting in a changed decay environment (Abbott & Crossley 1982; Brown *et al.* 1996). Below-ground studies, in which fresh roots were buried and later recovered and re-measured, have considered only the upper layers at 5–15 cm depth in the mineral soil (Fahey & Arthur 1994; Scheu & Schauermann 1994; King *et al.* 1997) and humus layers (Berg 1984; Fahey *et al.* 1988). Relocating samples that have been incubated in the soil at a known depth and location can pose challenges (Fahey *et al.* 1988). To assist relocation, experimenters have used techniques such as attaching a nylon thread and tag to the sample (Fahey *et al.* 1988; Fahey & Arthur 1994), or placing roots, particularly smaller diameter roots, in a mesh litter bag (Berg 1984; Camire *et al.* 1991; Scheu & Schauermann 1994; King *et al.* 1997). Fahey & Arthur (1994) emphasised that exposed surfaces on cut samples appeared to increase decay rates by providing direct access for decay organisms. Harmon & Sexton (1996) recommended placing a sealer at both cut ends of the sample, or more simply making the sample length 10 times longer than the mean diameter, to avoid over-estimating decay rates from cut ends.

A hybrid approach of the time series method can be used where re-measurement of a chronosequence is undertaken, such as the study by Harmon *et al.* (2000) who re-sampled a chronosequence from north-western Russia. They observed that re-sampling after 3 years gave decomposition rates statistically similar to those of the one-time chronosequence method.

Measurement Parameters

The measurement parameters used to determine coarse woody debris decay depend largely on the objectives of the study; however, Harmon & Sexton (1996) recommended measuring a minimum of volume and density of individual components. Coarse woody debris is a heterogeneous substrate made up of bark, sapwood, and heartwood. The amounts of these components and their respective decay rates vary with size and species (Chen *et al.* 2001; Mackensen & Bauhus 2003), indicating that individual decay rates should be used to calculate an overall rate (Chen *et al.* 2001). However, individual components can be difficult to identify and measure, especially in highly decayed samples (Mattson *et al.* 1987; Yavitt & Fahey 1982; Fahey *et al.* 1988). Moreover, Ludovici *et al.* (2002) compared whole-sample decay rate with individual components used to calculate overall decay and observed no difference between the methods used when estimating long-term decomposition.

Volume can be calculated using diameter and length measurements or water immersion. Both of these methods, although standard, exclude measurement of volume loss in decayed samples due to fragmentation. The volume method used depends on the level of accuracy required, and the size of the sample (Abbott &

Crossley 1982; Harmon & Sexton 1996). With small samples measurement by displacement in water can be used, but this method is not practical with large samples. When samples are highly decayed and fragile, water immersion also requires care to prevent water from seeping into the sample, resulting in an under-estimate of volume (MacMillan 1988; Fahey *et al*. 1991; Stewart & Burrows 1994). Sealing samples with wax or in plastic film may prevent water absorption.

Calculation of volume directly through the measurement of diameter and length of individual pieces of coarse woody debris is a simple procedure easily applied to field situations and large pieces. As coarse woody debris can be of considerable size, volume can be obtained by dividing the sample length into a series of truncated cones (frustums) and measuring diameter at both ends of each cone. The volume of each truncated cone can be calculated using Equation 1, and the series is then summed to obtain total volume (Hodgman 1948).

$$V(m^3) = \frac{1}{3}\left[\frac{\pi}{4} \times L((d_1 \times d_1) + (d_1 \times d_2) + (d_2 \times d_2))\right] \quad (1)$$

where L is length of the sample (m),
and d_1 and d_2 are diameters of the frustum ends (m).

The volume of decomposing samples can be calculated with and without bark, and this allows bark to be determined. Similarly, volumes of heartwood and sapwood can be determined if diameters of these components are measured. As large pieces of coarse woody debris are often not round, especially when highly decayed (Lambert *et al*. 1980; Naesset 1999), a round diameter can be obtained from the mean of the minimum and maximum diameters in the ellipse shape, or more easily measured with a diameter-calibrated tape.

Density and mass of coarse woody debris are typically determined on disc sub-samples of the larger sample (volume known) and then applied to the larger sample to determine its density and mass. Density can be variable along the length of a sample, and so discs may be taken at intervals to obtain a mean density. For example, Ganjegunte *et al*. (2004) collected three discs from the bottom, middle, and top of decaying *Pinus radiata* stems. Mackensen & Bauhus (2003) collected two 5-cm discs from each log within 0.3–1 m of each other, and with fragile logs one disc 25 cm long was sampled per log. Where samples are highly decomposed, disc length and diameter can be recorded before cutting (Ganjegunte *et al*. 2004); placement of adhesive tape over the sub-sample before cutting can also assist in the accuracy of measurements (Mackensen & Bauhus 2003).

Decay Constant Estimates

Decomposition of coarse woody debris is generally expressed as a decay constant k which is made up of annual mass losses due to respiration, leaching, and

fragmentation. The constant is most commonly derived from a single exponential equation (Olson 1963):

$$X_t = X_0 e^{-kt} \quad (2)$$

where X_t = amount of substrate at time t,
X_0 = initial amount of substrate,
t = time.

The single exponential model treats the decayed wood as a homogeneous substrate and is based on the assumption that the decomposition rate is proportional to the amount of matter remaining (Olson 1963; Wieder & Lang 1982; Means *et al.* 1985). Less commonly used are double or multiple exponential models that consider coarse woody debris is not a homogeneous substrate and that different components can decay at different rates (Wieder & Lang 1982; Means *et al.* 1985; Chen *et al.* 2001). A linear model has also been used (Wieder & Lang 1982; Lambert *et al.* 1980). In a chronosequence study in Canterbury, New Zealand, Ganjegunte (2001) found that the linear and single exponential models were equally good at describing decay of *P. radiata* coarse woody debris, and both fitted the data better than the double exponential model.

The time taken for a coarse woody debris sample to decay can be estimated from the single exponential model; for example, the time to decay 50% ($t_{0.5}$) or 95% ($t_{0.95}$) of the original amount can be calculated from Equations 3 and 4 (Olson 1963):

$$t_{0.5} = -\ln_{(0.5)}/k \quad (3)$$

$$t_{0.95} = -\ln_{(0.95)}/k \quad (4)$$

Fragmentation of woody debris is the most difficult process to measure and a major source of error for estimating change in wood mass with time (Lambert *et al.* 1980; Sollins 1982). To separate out fragmentation from respiration and leaching, the decay rate constant can be divided into two parts so that:

$$k = k_m + k_f \quad (5)$$

where k = the overall rate constant,
k_m = the rate constant for losses due to respiration and leaching,
k_f = the decay rate constant for losses due to fragmentation (Lambert *et al.* 1980).

In reality the decay rate constants k_m and k_f may have a lag-time, which allows for slow decomposition during the very early stages under the assumption that there is a transition time until decomposers colonise the debris (Grier 1978; Harmon *et al.* 1986). Harmon *et al.* (2000) indicated three phases of decay — first when decomposers colonise the woody debris, a second period of rapid exponential mass loss, and a third period of slow decomposition. These distinct decay phases have also been observed in other studies (Mackensen & Bauhus 2003; Janisch *et al.* 2005).

DECAY RATES AND CONTROLLING FACTORS

Temperature, moisture, and position of the material in relation to the soil as well as size, substrate quality and composition, and the characteristics of the decomposer community all influence the decay rate of woody debris (Harmon *et al*. 1986). Studies that have estimated above- and below-ground decay rate of woody debris have used chronosequence or time series experimental design over a range of climates, tree species, diameters, positions in relation to the soil, and study durations. The differences among studies make comparisons of decay constants difficult. The estimated decay constants vary greatly among studies, and the time required to achieve 95% decay typically ranged between 30 and 200 years, although both shorter and longer decay times have been estimated.

Studies on the decomposition of coarse woody roots are limited and diameters are typically small (1–5 cm), although diameters up to 10 cm have been measured (Yavitt & Fahey 1982; Fahey *et al*. 1988, 1991; Fahey & Arthur 1994; Chen *et al*. 2001; Ludovici *et al*. 2002; Janisch *et al*. 2005). No studies have been undertaken on the decay of woody roots of *Pinus radiata*; however, O'Loughlin & Watson (1979) in a study of root strength of a *P. radiata* stand observed that 40 months after the stand was clearfelled most of the roots less than 3 cm diameter had disappeared and roots larger than 5 cm showed advanced decay, indicating fairly rapid decay for smaller diameter material. Only two studies have been published on decay of above-ground coarse woody debris of *P. radiata* (Mackensen & Bauhus 2003; Ganjegunte *et al*. 2004).

There is no general consensus on a single dominant controlling factor in decomposition and a range of factors are commonly used to describe decay (Means *et al*. 1985). The influence of these independent controlling factors on decay has been described only qualitatively in the field, with more detailed observations restricted to the laboratory. However, an analysis of decay studies by Mackensen *et al*. (2003) concluded that for coarse woody debris on the forest floor annual temperature was a main driver of decomposition, accounting for 34% of the variation in decay. Initial wood density and diameter were also important drivers.

Different environmental conditions influencing temperature and moisture have been observed to cause substantial variation in the rate of decay within a species. For example, Mackensen & Bauhus (2003) and Ganjegunte *et al*. (2004) reported decay rates of above-ground coarse woody debris of *P. radiata,* in Australia and New Zealand respectively. The annual decay rates were 0.127 and 0.074 (24 and 40 years $t_{0.95}$) respectively, for stems and branches in contact with the ground. As the annual rainfall for each site was similar (approx. 800 mm), differences in the decay rates may have been due to differences in factors such as temperature, decomposer communities, or soil drainage. On a local scale, temperature and

moisture regimes can change as a result of forest management practices such as thinning and harvesting changing the decaying environment and hence influencing the rate of woody debris decay (Erickson *et al.* 1985; Brown *et al.* 1996; Naesset 1999).

Decay rates generally decrease with increasing diameter in both above- and below-ground woody debris (Brown *et al.* 1996; Janisch *et al.* 2005). However, overriding factors working in succession may result in unclear relationships (MacMillan 1988; Fahey & Arthur 1994; Chen *et al.* 2001) or in fact have the opposite effect, observed only in above-ground debris, with smaller-diameter material decaying at slower rates than larger-diameter material (Erickson *et al.* 1985; Naesset 1999; Ganjegunte *et al.* 2004). For example, Naesset (1999) observed faster decay in larger-diameter logs that had side branches removed than in smaller-diameter logs where side branches had not been removed causing the log to be suspended, resulting in lower moisture contents in the initial period of decay. Ganjegunte *et al.* (2004) reported that *P. radiata* side branches decayed much more slowly ($k = 0.015$) than log-wood ($k = 0.074$) partly because not all side branches were in contact with the soil initially, resulting in moisture constraints and less contact with soil microbial flora. They also suggested that the higher lignin and lower carbohydrate concentrations of side branches compared to logs may have contributed to the slower decomposition of the side branches.

Decomposition rate has been observed to vary with species (Mattson *et al.* 1987; Arthur *et al.* 1993; Brown *et al.* 1996; Chen *et al.* 2001; Mackensen & Bauhus 2003; Yatskov *et al.* 2003; Janisch *et al.* 2005). Mattson *et al.* (1987) noted that tree species explained 61% of the variation in the decay constant, after measurements on coarse and fine woody debris of 17 species in a mixed hardwood forest in North Carolina. Janisch *et al.* (2005) reported above-ground stumps and logs of *Pseudotsuga menziesii* decomposed more slowly ($k = 0.016$ using accepted green-wood density) than western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) ($k = 0.036$). The same pattern was observed with below-ground roots, indicating that species effects are expressed in both above- and below-ground environments. Chen *et al.* (2001) suggested that the proportion of bark, wood, and resin cores, which decompose at different rates, plays a critical role in determining the decomposition rate of each species. Carbon components such as lignin and cellulose and their relative proportions influence the rate of decay, as lignin is more resistant to decay than cellulose; this results in higher lignin concentrations with increasing decay (Minderman 1968; Lambert *et al.* 1980; Means *et al.* 1985; MacMillan 1988; Camire *et al.* 1991).

Coarse roots have been observed to decay at a rate similar to or slower than above-ground debris. Janisch *et al.* (2005) noted that roots of *Pseudotsuga menziesii* 1–3 cm in diameter decomposed only slightly more slowly ($k = 0.014$) than logs

and stumps (k = 0.015). However, roots 3–5 cm in diameter decomposed at approximately half the rate (k = 0.008) of logs and stumps. Fahey *et al*. (1988) found that woody root decay rate of beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and red spruce (*Picea rubens* Sarg.) with diameters between 2 and 10 cm (k = 0.042 – 0.093) was much slower than decay of surface woody debris of the same species and similar (4–8 cm diameter) size classes (k = 0.131 – 0.157). They observed the same pattern with material 1–2 cm in diameter. Fahey *et al*. (1991), however, observed that roots (1–5 cm diameter) of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) decayed at about the same rate as branches of the same diameter in contact with the ground. The slower decay of below-ground roots compared to material of similar diameter above ground may in some instances be due to roots surviving after felling of the stem. The surviving roots can live for an additional 1–2 years as a result of the translocation of stored energy from root crowns to the immediate lateral roots (Yavitt & Fahey 1982). Moreover, root grafting or coppicing has been known to keep lateral roots alive for some time after felling (Will 1966; Chen *et al*. 2001; Ludovici *et al*. 2002). There appears to be no information for large-diameter material (>10 cm diameter) on comparative decay rates above and below ground.

A few studies have been undertaken on the influence of soil properties on root decay. Fahey & Arthur (1994) attempted to relate the rate of decay of coarse roots to three soils of contrasting properties (soil texture, organic matter content, and horizon development). They found no significant effect of soil on decay rate, although there was a trend towards slower decay rates in soils in cooler areas with poor drainage. Yavitt & Fahey (1982) observed slightly faster decay rates in fine textured soil than in gravelly soil. Ludovici *et al*. (2002) suggested depth may be a factor controlling decomposition of woody roots.

Decomposer fungi and invertebrate communities present in the forest can have a significant influence in determining the rate and type of wood decay. The presence of fungi can increase decay (Mattson *et al*. 1987), and the different fungal species present have been observed to be associated with specific decay patterns (Means *et al*. 1985; MacMillan 1988; Rayner & Boddy 1988; Allen *et al*. 2000; Buchanan *et al*. 2001; Chen *et al*. 2001; Hood *et al*. 2004). Chen *et al*. (2001) observed that woody roots with white rot fungi present had much higher rates of decay than those with brown rot fungi, as white rot degrades both lignin and cellulose while brown rot attacks cellulose primarily. Typically, brown rot fungi attack conifers and white rots are more frequent on angiosperms (Rayner & Boddy 1988). Invertebrate activity can also have a significant effect on the decomposition of coarse woody debris through attacking wood directly and accelerating decay by creating a suitable environment for microbes (Abbott & Crossley 1982; Hood *et al*. 2004).

RECOMMENDATIONS FOR FURTHER STUDY

Studies on the decay rates of coarse woody debris in New Zealand are limited and there are insufficient data to derive decay rates for "Kyoto Forests" at regional and national levels. Elsewhere the study focus has been on above-ground coarse woody debris and limited attention has been paid to coarse woody roots because of technical difficulties in sampling. However, it has become increasingly important to determine decay rates of all forms of coarse woody debris, particularly for New Zealand's plantation forests as such debris forms an important and dynamic carbon storage pool in these forests.

A possible approach for determining decay rates for *Pinus radiata* regionally and nationally would be to undertake time series studies, involving the change in mass of decaying samples over time, of both above- and below-ground material, on sites of varying temperature and moisture. In the time series approach sample dimension, position in relation to the soil, and, for root samples, burial depth can be controlled and included as experimental variables to determine their influence on decay rate. However, as a time series approach requires long-term studies, especially with coarse woody debris of larger diameters, only smaller pieces can practically be targeted. To obtain estimates of the decay rate of larger pieces in the shortest possible time a chronosequence approach would be required to support estimates from the time series approach at suitable study sites.

In addition, a relationship between above- and below-ground decay rate could be established for different environmental conditions, enabling root decay rate to be determined based on above-ground stem and branch decay rate which is more easily measured. Attention would need to be given to the debris diameter and position in relation to the soil surface, and the issue of root grafting enabling root masses to survive after thinning or harvesting would need to be addressed.

ACKNOWLEDGMENTS

This review was funded by the Ministry for the Environment and we appreciate the support provided.

REFERENCES

ABBOTT, D.T.; CROSSLEY, D.A. 1982: Woody litter decomposition following clear-cutting. *Ecology 63*: 35–42.

ALLEN, R.B.; BUCHANAN, P.K.; CLINTON, P.W.; CONE, A.J. 2000: Composition and diversity of fungi on decaying logs in a New Zealand temperate beech (*Nothofagus*) forest. *Canadian Journal of Forest Research 30*: 1025–1033.

ALLEN, R.B.; CLINTON, P.W.; DAVIS, M.R. 1997: Cation storage and availability along a *Nothofagus* forest development sequence in New Zealand. *Canadian Journal of Forest Research 27*: 323–330.

ARTHUR, M.A.; TRITTON, L.M.; FAHEY, T.J. 1993: Dead bole mass and nutrients remaining 23 years after clear-felling of a northern hardwood forest. *Canadian Journal of Forest Research 23*: 1298–1305.

BEETS, P.N.; ROBERTSON, K.A.; FORD-ROBERTSON, J.B.; GORDON, J.; MACLAREN, J.P. 1999: Description and validation of C_change: A model for simulating carbon content in managed *Pinus radiata* stands. *New Zealand Journal of Forestry Science 29*: 409–427.

BERG, B. 1984: Decomposition of root litter and some factors regulating the process: Long-term root litter decomposition in a Scots pine forest. *Soil Biology and Biochemistry 16*: 609–617.

BOHM, W. 1979: "Methods of Studying Root Systems". Springer-Verlag, Berlin, Germany.

BOONE, R.D.; SOLLINS, P.; CROMACK, K. 1988: Stand and soil changes along a mountain hemlock death and regrowth sequence. *Ecology 69*: 714–722.

BROWN, S.; JIANGMING, M.; McPHERSON, J.K.; BELL, D.T. 1996: Decomposition of woody debris in Western Australian forests. *Canadian Journal of Forest Research 26*: 954–966.

BUCHANAN, P.K.; CLINTON, P.W.; ALLEN, R.B. 2001: Dead wood in the forest — alive and dynamic! *New Zealand Journal of Forestry 45*: 40–42.

CAMIRE, C.; COTE, B.; BRULOTTE, S. 1991: Decomposition of roots of black alder and hybrid poplar in short-rotation plantings: Nitrogen and lignin control. *Plant and Soil 138*: 123–132.

CHEN, H.; HARMON, M.E.; GRIFFITHS, R.P. 2001: Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: a chronosequence approach. *Canadian Journal of Forest Research 31*: 246–260.

CHEN, H.; HARMON, M.E.; GRIFFITHS, R.P.; HICKS, W. 2000: Effects of temperature and moisture on carbon respired from decomposing woody roots. *Forest Ecology and Management 138*: 51–64.

ERICKSON, H.E.; EDMONDS, R.L.; PETERSON, C.E. 1985: Decomposition of logging residue in Douglas fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Canadian Journal of Forest Research 15*: 914–921.

FAHEY, T.J.; ARTHUR, M.A. 1994: Further studies of root decomposition following harvest of a northern hardwoods forest. *Forest Science 40*: 618–629.

FAHEY, T.J.; HUGHES, J.W.; PU, M.; ARTHUR, M.A. 1988: Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *Forest Science 34*: 744–768.

FAHEY, T.J.; STEVENS, P.A.; HORNUNG, M.; ROWLAND, P. 1991: Decomposition and nutrient release from logging residue following conventional harvest of Sitka spruce in north Wales. *Forestry 64*: 289–301.

GANJEGUNTE, G.K. 2001: Effects of litter and woody debris quality on decomposition and nutrient release in exotic forests in New Zealand. PhD thesis, Lincoln University, New Zealand.

GANJEGUNTE, G.K.; CONDRON, L.M.; CLINTON, P.W.; DAVIS, M.R.; MAHIEU, N. 2004: Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *Forest Ecology and Management 187*: 197–211.

GRIER, C.C. 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, M.E.; SEXTON, J. 1996: "Guidelines for Measurements of Woody Detritus in Forest Ecosystems", twentieth ed. U.S. Long-Term Ecological Research Network Office, University of Washington, Seattle, U.S.

HARMON, M.E.; KRANKINA, O.N.; SEXTON, J. 2000: Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research 30*: 76–84.

HARMON, M.E.; FRANKLIN, J.F.; SWANSON, F.J.; SOLLINS, P.; GREGORY, S.V.; LATTIN, J.D.; ANDERSON, N.H.; CLINE, S.P.; AUMEN, N.G.; SEDELL, J.R.; LIENKAEMPER, G.W.; CROMACK, K.; CUMMINS, K.W. 1986: Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research 15*: 133–302.

HODGMAN, C.D. 1948: "Handbook of Chemistry and Physics", third ed. Chemical Rubber Publishing Co., Cleveland, Ohio.

HOOD, I.A.; BEETS, P.N.; KIMBERLEY, M.O.; GARDNER, J.F.; OLIVER, G.R.; PEARCE, S. 2004: Colonisation of podocarp coarse woody debris by decomposer basidiomycete fungi in an indigenous forest in the central North Island of New Zealand. *Forest Ecology and Management 196*: 311–325.

IPCC 2003: "Intergovernmental Panel on Climate Change. Good Practice Guidance for Land Use, Land-use Change and Forestry". The Intergovernmental Panel on Climate Change (IPCC), Japan.

JANISCH, J.E.; HARMON, M.E.; CHEN, H.; FASTH, B.; SEXTON, J. 2005: Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. *Ecoscience 12*: 151–160.

KING, J.S.; ALLEN, H.L.; DOUGHERTY, P.; STRAIN, B.R. 1997: Decomposition of roots in loblolly pine: Effects of nutrient and water availability and root size class on mass loss and nutrient dynamics. *Plant and Soil 195*: 171–184.

LAMBERT, R.L.; LANG, G.E.; REINERS, W.A. 1980: Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology 61*: 1460–1473.

LUDOVICI, K.H.; ZARNOCH, S.J.; RICHTER, D.D. 2002: Modeling in-situ pine root decomposition using data from a 60-year chronosequence. *Canadian Journal of Forest Research 32*: 1675–1684.

MACKENSEN, J. BAUHUS, J. 2003: Density loss and respiration rates in coarse woody debris of *Pinus radiata*, *Eucalyptus regnans* and *Eucalyptus maculata*. *Soil Biology and Biochemistry 35*: 177–186.

MACKENSEN, J.; BAUHUS, J.; WEBBER, E. 2003: Decomposition rates of coarse woody debris — A review with particular emphasis on Australian tree species. *Australian Journal of Botany 51*: 27–37.

MacMILLAN, P.C. 1988: Decomposition of coarse woody debris in an old-growth Indiana forest. *Canadian Journal of Forest Research 18*: 1353–1362.

MATTSON, K.G.; SWANK, W.T.; WAIDE, J.B. 1987: Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. *Canadian Journal of Forest Research 17*: 712–721.

MEANS, J.E.; CROMACK, K.; MacMILLAN, P.C. 1985: Comparison of decomposition models using wood density of Douglas-fir logs. *Canadian Journal of Forest Research 15*: 1092–1098.

MINDERMAN, G. 1968: Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology 56*: 355–362.

NAESSET, E. 1999: Decomposition rate constants of *Picea abies* logs in southeastern Norway. *Canadian Journal of Forest Research 29*: 372–381.

O'LOUGHLIN, C.; WATSON, A. 1979: Root-wood strength deterioration in radiata pine after clearfelling. *New Zealand Journal of Forestry Science 9*: 284–293.

OLSON, J.S. 1963: Energy storage and the balance of producers and decomposers in ecological systems. *Ecology 44*: 322–331.

PAYTON, I.J.; NEWELL, C.L.; BEETS, P.N. 2004: "New Zealand Carbon Monitoring System: Indigenous Forest and Shrubland Data Collection Manual". New Zealand Climate Change Office, Ministry for the Environment, Wellington.

PHILLIPS, C.J.; WATSON, A.J. 1994: "Structural Tree Root Research in New Zealand: A Review". Manaaki Whenua Press, Lincoln.

RAYNER, A.D.M.; BODDY, L. 1988: "Fungal Decomposition of Wood: Its Biology and Ecology". John Wiley & Sons, Chichester, U.K.

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.

SOLLINS, P. 1982: Input and decay of coarse woody in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research 12*: 18–28.

SOLLINS, P.; CLINE, S.P.; 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.

STEWART, G.H.; BURROWS, L.E. 1994: Coarse woody debris in old-growth temperate beech (*Nothofagus*) forests of New Zealand. *Canadian Journal of Forest Research 24*: 1989–1996.

STONE, J.N.; MacKINNON, A.; PARMINTER, J.V.; LERTZMAN, K.P. 1998: Coarse woody debris decomposition documented over 65 years on southern Vancouver Island. *Canadian Journal of Forest Research 28*: 788–793.

WATSON, A.; O'LOUGHLIN, C. 1990: Structural root morphology and biomass of three age-classes of *Pinus radiata*. *New Zealand Journal of Forestry Science 20*: 97–110.

WIEDER, R.K.; LANG, G.E. 1982: A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology 63*: 1636–1642.

WILL, G.M. 1966: Root growth and dry-matter production in a high-producing stand of *Pinus radiata*. *New Zealand Forest Research Note 44*: 745–752.

YATSKOV, M.; HARMON, M.E.; KRANKINA, O.N. 2003: A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research 33*: 1211–1226.

YAVITT, J.B.; FAHEY, T.J. 1982: Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. *Canadian Journal of Forest Research 12*: 745–752.