

Nitrogen Fertilization Effects on Carbon and Nitrogen
Storage in Woody Debris in Second-growth
Douglas-fir Stands

by

Warren H. Tacey

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Approved by

Robert L. Edmonds
(Co-chairperson of Supervisory Committee)

W. H. Chappel
(Co-chairperson of Supervisory Committee)

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College of Forest Resources

Date

August 11, 1993

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University of Washington

Abstract

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by Warren Tacey

Co-chair of the Supervisory Committee: Professor Robert L. Edmonds
College of Forest Resources

Co-chair of the Supervisory Committee: Professor H. N. Chappell
College of Forest Resources

The growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is limited by N supply in much of the Pacific Northwest. Nitrogen fertilizer applications produce growth increases in about 70% of stands examined region-wide. A relationship has been demonstrated between growth response and C:N ratio in the soil and forest floor. Relationships have not been examined with coarse woody debris, which is also a major organic matter component in Pacific Northwest forests. This study examined the role of woody debris in mediating the nitrogen dynamics of unthinned second growth Douglas-fir stands which had been fertilized with urea N at 0 or 448 kg ha⁻¹.

The average biomass of fallen woody debris on 14 sites in western Washington and Oregon was 76 Mg ha⁻¹, of which 90% was greater than 76mm diameter and 79% was inferred to have been carried over from the previous stand. This was twice the quantity previously

recorded from second growth stands and represented four times the mass of C in the forest floor. The average mass of N in fallen woody debris across all sites was 205 kg ha^{-1} , about the same as the mass of N in the forest floor. The N content of wood in decay classes IV and V was significantly higher on fertilized sites than on unfertilized sites. Fallen woody debris was clearly an important storage site for N. The C:N ratios for woody debris were high, averaging from 109 to 481, suggesting that N could be retained in this wood and play an important role in forest nutrition over long cycle times.

Despite the large amount of C in fallen wood, its biomass was not a useful predictor of response to applied N. The pool of N in fallen wood increased following fertilization, and N and C contents were greater in soils on fertilized sites. These results suggest that fallen woody debris may comprise both an important short term sink for applied N as well as a long term source, and thus have an important role in the long term productivity of Douglas-fir sites.

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INTRODUCTION

The growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is limited by nitrogen (N) supply in much of the Pacific Northwest. Fertilizer applications produce positive growth responses (Gessel et al., 1969; Edmonds and Hsiang, 1987; Chappell et al., 1991; Chappell et al., 1992). The period of greatest N uptake coincides with the closure of the forest canopy and maximum growth of the forest stand in Douglas-fir and other species (Cole et al., 1990).

Extensive experimentation with N fertilization of second-growth Douglas-fir has occurred over the last 35 years throughout western Washington and Oregon (Gessel and Walker, 1956; Chappell et al., 1991; Chappell et al., 1992). The aim of that work has been to cost-effectively increase the volume of wood produced. Results from extensive trials throughout western Washington and Oregon have shown an overall increase in gross volume growth of about 20%, over four years, after a single application of either 224 or 448 kg ha⁻¹ of N, as urea (Turnbull and Peterson, 1976). Volume response was defined as the relative increase in periodic annual increment (p.a.i) of fertilized plots over unfertilized controls. These results

represented the average of 85 installations throughout western Washington and Oregon. However, about 30% of installations in the studies above showed no significant response to applied N (Gessel et al., 1990).

Operational fertilization of non-responsive sites is clearly a waste of resources. Subsequent research has therefore been directed at trying to characterize non-responsive sites (Peterson et al., 1984; Peterson and Heath, 1986). Multiple regression of 28 environmental, nutrient and growth potential variables for the 85 installations above showed that carbon to nitrogen (C:N) ratios, of either forest floor (litter plus humus) or of the top 15 cm of soil, consistently accounted for the greatest proportion of the variance in the response of unthinned, second-growth Douglas-fir throughout western Washington and Oregon, except in southwest Oregon (Edmonds and Hsiang, 1987). Response tended to decrease with increasing C:N ratio.

Even though Douglas-fir responds to applied N fertilizer, the duration of response is brief and the efficiency of use by trees is poor. Long-term correction of nitrogen deficiencies is seldom achieved with chemical fertilizers. Nitrogen added through symbiotic fixation or from applications of organic by-products like sewage sludge can provide much better long-term response (Cole et al., 1990). Sources of C in organic material already on-site, like woody debris on the forest floor, may also play a role in the long-term supply of

nutrients. Soil C has also been linked to the long-term productivity of forest stands (Edmonds, 1990).

Woody debris is a major source of C on the forest floor in the Pacific Northwest (Harmon et al., 1986). Woody debris also has the capacity to store significant quantities of N, by microbial immobilization, in the short-term and release it in the longer term in Douglas-fir forests of the Pacific Northwest (Harmon et al., 1986; Edmonds, 1987; Edmonds, 1990). Thus woody debris can be both a source and a sink for N. Decomposing woody residue, primarily as decaying logs, may be a particularly good source of N (Larsen et al., 1978; Harvey et al., 1989). The maximum quantity of woody debris accumulates in the Pacific Northwest immediately after cutting (Dell and Ward, 1971) and in the old growth stage (Spies et al., 1988). Hence the interaction of applied N and woody debris is potentially important to the nutrient dynamics of second-growth forests in the short and long term. While there has been considerable research on the quantity and role of woody debris in old-growth Douglas-fir forests (see Harmon et al., 1986 for a comprehensive review) little attention has been directed to the role of this component of the ecosystem in the nutrition of second-growth forests.

Nitrogen immobilization and release are mechanisms that mediate the availability of N to trees (Edmonds, 1979; Edmonds, 1980; Bosatta and Staaf, 1982; Edmonds, 1984; Bosatta and Agren, 1985; Edmonds, 1987). Other environmental processes, like decomposition, also

require N and thus compete for the available pool. Specifically, microbes involved in decay have been shown to immobilize N in slash and forest floor materials (Vitousek and Matson, 1984). Coarse woody debris is another substrate for microbial decay and hence N immobilization (Grier, 1978) but its role in the immobilization and release of N in fertilized Douglas-fir stands has not been examined.

My study examined the effects of N fertilization on C and N stored in soil and wood in second-growth Douglas-fir stands. I examined the potential for characterizing sites where second-growth Douglas-fir did not respond to applied N by quantifying the amount and decay class of woody debris present. I evaluated the mass and C:N ratios of all woody debris on the forest floor of a subset of the sites included in earlier studies by Edmonds and Hsiang (1987).

OBJECTIVES

Since fallen wood may be a significant reservoir for nitrogen and thus influence the response of second-growth Douglas-fir stands to applied N fertilizer, the objectives of this study were to:

1. Determine the mass of fallen wood, including both fine and large materials;
2. Determine the C and N contents of fallen wood and the soil;
3. Determine the biomass and C:N ratios in each decay class of the large fallen wood component on fertilized and unfertilized, unthinned stands;
4. Compare the C and N contents of soils in fertilized and unfertilized, unthinned stands, and
5. Determine if the biomass or C:N ratio of fallen wood related to the response of second-growth Douglas-fir to urea fertilization.

LITERATURE REVIEW

Nitrogen Availability and Uptake in Forests.

About 95% of the N in most surface soils occurs in organically combined forms. About 1-3% of this is converted annually by microorganisms to ammonium and nitrate, forms potentially available to plants, thus the availability of soil N is dependent on microbial activity (Bremner, 1965). The ammonium form is preferentially used by most conifers, including Douglas-fir (Edmonds et al., 1989).

The Nitrogen Cycle

The N cycle is described in detail in many texts; the following summary is based largely on Binkley (1986) and Edmonds et al. (1989) and illustrated in Figure 1. Microbes play a key role in N cycling and availability by decomposing organic matter to mineralize, or release, N as ammonia which, when converted to ammonium, is available for uptake by most conifers. Nitrification involves the microbial conversion of ammonium to nitrite and then nitrate under aerobic conditions. Denitrification involves microbial conversion of nitrate to nitrite and to gaseous N under anaerobic conditions.

Immobilization by microbes usually consumes most of the ammonium released in decomposition (Vitousek and Matson, 1984; Binkley, 1986). Litter with a low N concentration, and hence a high

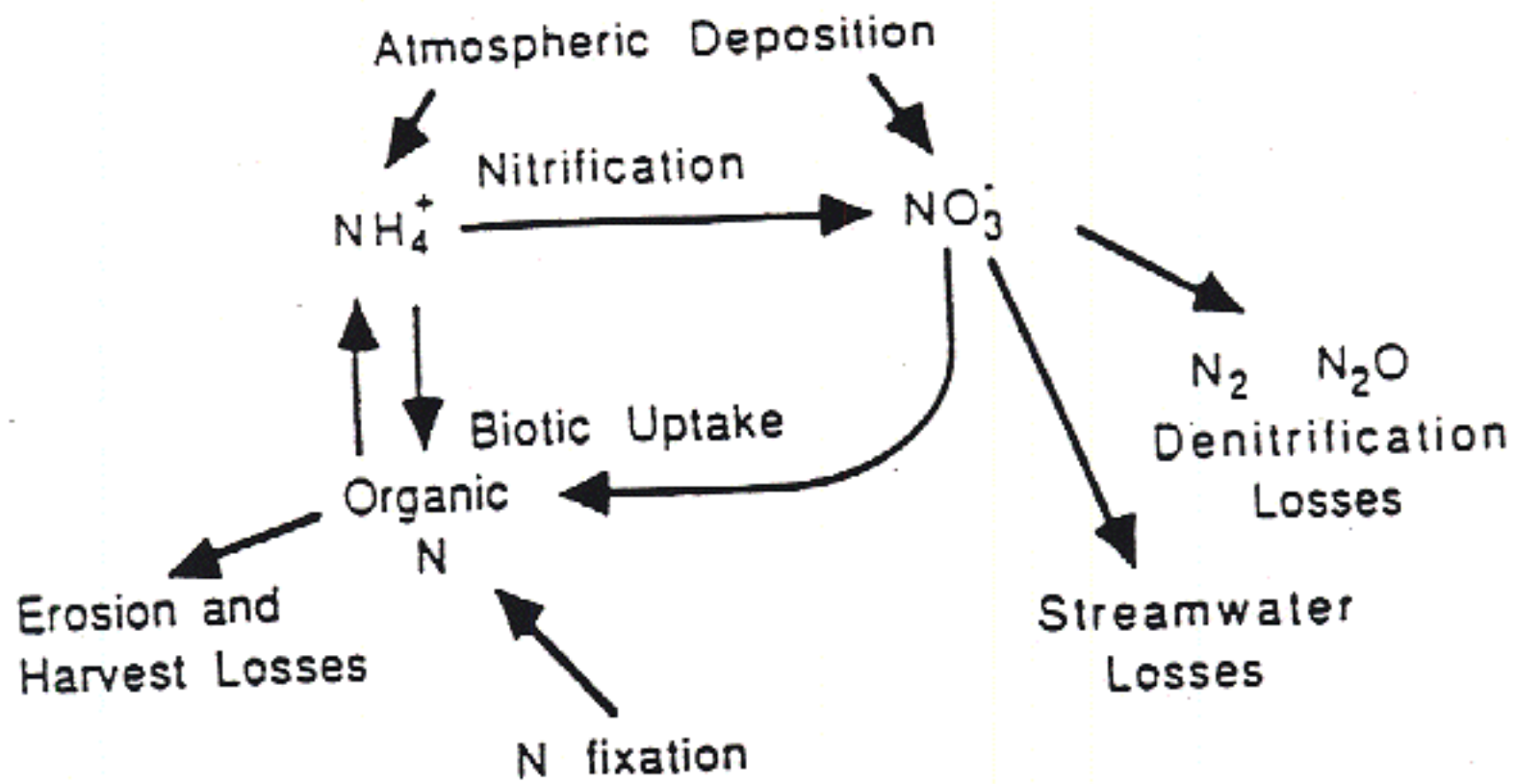


FIGURE 1: Inputs, internal transfers and outputs of nitrogen (N) in a forest ecosystem. From Edmonds et al., (1989).

C:N ratio, typically accumulates N from the soil for some years before releasing it again. The immobilization / release processes are strongly dependent on the C:N ratio of substrates. Typically, more N is available for tree growth at substrate C:N ratios below 20:1, while N is considered to be immobilized by microbes at C:N ratios above 30:1 in fine substrates (Lutz and Chandler, 1946). Release seems to depend on the nature of the substrate, as coarse woody debris appears capable of releasing N at C:N ratios above 300:1 (Edmonds, 1987).

Woody substrates such as logs, which may have C:N ratios above 300:1, could not only be an important sink for applied N in the early stages of decomposition, but also a potential source in the later stages when C:N ratios drop to 200:1 or below (Graham and Cromack, 1982). Therefore, characterization of the biomass, decay class, N content and C:N ratio of woody material on sites that have known responses to N fertilization appeared to be a potentially fruitful avenue for elucidating the relationship between Douglas-fir growth response and applied N.

The Concept of Nitrogen Availability

Nitrogen available from soil can theoretically be defined by the following formula:

$$N \text{ total} = N \text{ available} + N \text{ immobile; or, by rearranging,} \quad (1)$$

$N \text{ available} = N \text{ total} - N \text{ immobile.}$

(2)

Hence available N should be definable by the difference between total and immobile N. In many cases total N is used as a surrogate or indicator for available N (Binkley, 1986). In practice total N is not well correlated with the growth of many species and specifically not with the growth of Douglas-fir (Shumway and Atkinson, 1977). Although representative sampling can be problematic, total N is relatively simple to measure and has been used widely in both Douglas-fir fertilizer research (Peterson et al., 1984; Edmonds and Hsiang, 1987) and in studies of the nutrient dynamics of decaying wood in Northwestern forests (Grier, 1978; Graham and Cromack, 1982; Edmonds, 1987; Edmonds et al., 1989). It is useful as a common denominator for the comparison of work on tree fertilization and wood decomposition. It is, however, important to be aware of the limitations of total N measurements and of the available N concept for which total N often acts as a surrogate.

Available N can be defined as:

1. Nitrogen which the plants of interest can take up for growth; or
2. Nitrogen which can be extracted by some standard technique agreed between plant nutritionists and used as an index of 1 above.

This dichotomy is exemplified by Loneragan (1968) who wrote that "nutrient requirement has been used to mean both the concentration in the external solution, and in the plant, when these are not the same". For example, a plant with a high tissue requirement for calcium may have a low requirement for calcium concentration in a culture solution provided that it has a high rate of absorption (Loneragan, 1968; Ingestad, 1974). Nutrient requirements in the plant tissue and the external solution are also species dependent (Ingestad, 1974).

Edmonds et al. (1989) have provided a definition consistent with definition 1 above, whereby available nutrient is that which is available for uptake each year. These authors define availability more precisely as;

$$\text{Availability} = \text{nutrient capital} \times \text{turnover rate} \quad (3)$$

where capital is equivalent to the total present. They stress that nutrient availability must be related to the current requirement of trees, clearly implying that the requirement and hence the necessary availability varies with time and stage of plant development.

Even an "absolute" measure of availability may be of limited value. Plants on the most infertile sites in the field are not always most responsive to nutrient addition (Chapin et al., 1986). This is counter to the view that productivity increases with greater nutrient

abundance, based on the concept that productivity is limited simply by an inadequate store of the essential nutrient. Chapin et al. (1986) note that older individuals respond less than younger ones. This accords with Ingestad's (1981) concept that N uptake is related to relative growth rate, independent of a wide range of concentrations in the external solution. Thus, plants require most nutrient in the vigorous exponential growth phase (Ingestad, 1981; Ingestad, 1982; Axelsson, 1985; Cole et al., 1990).

Several authors circumvent the absence of an absolute measure of availability by using N availability indices (Powers, 1980; Edmonds et al., 1989). Availability indices are relationships between a parameter that is measurable and the parameter of interest, such as growth rate (Keeney and Bremner, 1966), site yield potential (Powers, 1980) or nutrient deficiency characteristics (Chapin et al., 1986). Chapin et al (1986) point out, however, that correlations between measured values and the response of natural communities to fertilization are limited and assert that this lack of success may not lie in the quality of measurements but in the nature of nutrient limitation (hence availability) in natural communities. They believe that this is at least partly due to interactions between nutrient competition and other forms of competition in mixed stands and note further that nutrient responses in controlled conditions are not the same as those in the wild.

Measurement of Available Nitrogen

"Available" N can be measured by chemical or biological means. While neither may truly represent what is taken up in the field by trees, they are the only practical methods available and hence must be used if quantitative measurements are required.

Chemical methods

There are a range of chemical methods to extract "available" N, such as;

- initial extractable inorganic N using 1 N KCl,
- extraction by boiling with water and K_2SO_4 for 1 hour and,
- autoclaving at $120^{\circ}C$.

Bremner (1965) states that "no chemical method is likely to simulate the activities of microorganisms..." and further that there had "... been little attention given to the performance of field experiments to calibrate laboratory methods." Once the available N is extracted, the quantity present can be analysed in the same way as total N.

Total N is now routinely determined using analyses based on Kjeldahl's (Kjeldahl, 1883) original procedure (Binkley, 1983). Special precautions are required to recover some forms of N such as nitrate and nitrite, which form a small part of the total, but are important biologically (Bremner, 1965).

Biological methods

In contrast to chemical methods, Bremner (1965) states that "Incubation methods provide fairly accurate indices of the availability of soil N to plants" presumably because they "...show good correlation with crop response." While this seems a practical and intuitive understanding of availability, the concept is still not explicitly defined and is difficult to apply to trees.

Biological methods include either aerobic or anaerobic incubation of soils, with distilled water, followed by chemical analysis of the leachate (Eno, 1960; Waring and Bremner, 1964; Keeney and Bremner, 1966; Powers, 1980; Westerman and Crothers, 1980; Binkley, 1983; Binkley, 1986). A drawback of these methods is that results are markedly affected by air drying and air dry storage of the samples prior to analysis whereas chemical methods are not affected by drying (Keeney and Bremner, 1966).

Incubation methods do have a place when used as originally proposed by Eno (1960). Keeney (1980) quotes the work of Shumway and Atkinson (1977, 1978), which showed high correlation of ammonium production by Waring and Bremner's (1964) anaerobic incubation method with diameter growth increment of Douglas-fir, while total soil N content was poorly correlated with growth.

An alternative biological approach involves analyzing foliar samples for nutrient content and correlating these with the results of growth

studies (Keeney and Bremner, 1966; Everard, 1973; Powers, 1980). While potentially suited to annual crop or pasture plants this method becomes confounded when working with trees since foliar levels are likely to change with season, location on the plant, age of tree, and old versus young leaves. It has however been used successfully with young Douglas-fir (Turner et al., 1988; Blake et al., 1990).

Ion exchange resins, buried in bags, combine microbiological and chemical methods to capture the products of microbial activity (Binkley, 1983). This method gave results that correlated well with six other chemical and incubation methods under controlled conditions in the glasshouse. Results were, however, more variable in the field where they were more sensitive to on-site conditions (Binkley, 1983).

Vitousek and Matson (1984) found that the activity of N fixing flora in Douglas-fir logs in Montana was related to the stage of decay and water content of the woody debris, but not to site quality. This illustrates the potential importance of environmental conditions in mediating the N status of a site.

Nitrogen Fertilization and Soil Carbon Content

Increases in soil and litter C following fertilization with N, with and without other nutrients, or, following invasion by N fixing plants, have been reported from various environments in Sweden, New Zealand, Alaska, British Columbia, Washington and Oregon (Van Cleve

and Moore, 1978; Kraemer and Hermann, 1979; Binkley, 1983; Baker et al., 1986; Nohrstedt et al., 1989). Soil C levels rose between 10% and 25% in Sweden following fertilization with 150 to 600 kg ha⁻¹ of N as ammonium nitrate and urea (Nohrstedt et al., 1989). Fertilization with 960 kg ha⁻¹ of N, plus other nutrients, increased C by 115% in the top 5 cm of sand dune soils in New Zealand (Baker et al., 1986). The increase in C, to 1 m soil depth, was 17%. The presence of N fixing red alder caused 30-100% increases in soil C in Douglas-fir stands in British Columbia and Washington (Binkley, 1983). Thus, increases in N applied as fertilizer or by biological fixation have often resulted in increased soil C levels. This has important implications for long-term site productivity (Edmonds, 1990; Jurgensen et al., 1990) and may be an important mechanism for C sequestration, with attendant benefits as a sink for excess atmospheric C (Harmon et al., 1990; Post et al., 1990).

Prediction of Tree Growth Response

Prediction of tree growth response to applied nutrients is an important component of any economic approach to improving forest tree productivity. Tree growth response has been related to many variables including a number associated with N nutrition. Soil N indices, like mineralizable N (Shumway and Atkinson, 1978; Powers, 1980; Lea and Ballard, 1982a) and foliar N (Leaf, 1973; van den Driessche, 1981; Radwan and DeBell, 1980; Lea and Ballard, 1982b) are typical examples. More often than not Douglas-fir response has been related to stand and site variables rather than soil or foliar N

indices. These stand and site variables have included site index (Radwan and DeBell, 1980), basal area (Duzan et al., 1982; Ballard and Lea, 1986), soil depth and composition (Steinbrenner, 1979) and C:N ratios in soils and forest floor material (Peterson et al., 1984; Edmonds and Hsiang, 1987). Studies relating Douglas-fir fertilization response to other environmental components, like woody debris, which may mediate N nutrition do not appear to have been undertaken.

Synthesis on Nitrogen Availability

The availability of N to plants is an intuitive and logical concept, with some evidence linking it to growth rate. The issue is more complex, however, than simply the amount of N existing in a form accessible to plants. The rate of uptake and turnover of N can profoundly affect the ability of plants to grow. These rates are in turn dependent on the species of plant involved, competition effects, site type and the physical and biological environment. These factors make the measurement of available nitrogen difficult and illustrate the importance of having a very clear definition of what is meant by the concept of available. The questions "Available to what?" and "Available for what purpose?" should be answered before the concept of "available N" is used. With this forethought the concept can be useful in a theoretical and practical sense. Given the limitations of measuring N in ways consistent with the concept of availability (i.e., measuring an index related to tree response), total N can be a useful surrogate for available N. Total N is readily measured

and allows comparison across a range of studies, provided its limitations are recognized.

Woody Debris in Forests of the Pacific Northwest

Recognition of fallen wood as a significant component of the biomass and nutrient cycles in forests of the Pacific Northwest occurred largely as a result of studies connected with the International Biological Program of the 1970's (Edmonds, 1982). Much of that work concentrated on "coarse woody debris" (CWD). Definitions of "coarse" have varied from material >1 cm diameter (Vitousek and Matson, 1984), through logs >10 cm (Dell and Ward, 1971) to only logs >15 cm in diameter (Harmon et al., 1986). This review considers all of these materials as they all contribute to the C capital of a site.

This review provides an overview of the quantities of fallen wood typically found in old-growth forests and cut-over areas, a summary of a widely used decay rating system for wood on the forest floor and an outline of efforts to age such decay classes. It also examines the density of wood in each class and concludes by examining the N and C status of decaying wood and the way it might influence forest N nutrition.

Role of Woody Debris

For many microbes, invertebrates, vertebrates and plants, woody debris represents a vital micro-environment and food source. This is

particularly true for microbes and especially fungi, including many mycorrhizal species (Frankland et al., 1982).

Woody debris provides habitat for both lower and higher plants. It is a substrate for algae, lichens, mosses and ferns as well as shrubs and trees. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings frequently establish preferentially on fallen logs (Christy and Mack, 1984; Harmon and Franklin, 1989) and red huckleberry is frequently seen on old stumps (Franklin and Dyrness, 1988). These plants trap litter and import nutrients to the logs, providing additional resources for decomposers (Harmon et al., 1986).

Woody debris also provides habitat for animals. Some salamanders are dependent on the moisture in old logs to survive the dry season (Maser and Trappe, 1984). Termites and wood-boring insects use logs as a food source and habitat (Furniss and Carolin, 1977; Edmonds and Eglitis, 1989). Woody debris also plays an important role in soil turnover and slope stability, particularly by retarding erosion and accumulating mineral and organic matter on the upslope side (Collins et al., 1983; Maser and Trappe, 1984). Logs also form pools in streams that trap sediment and provide fish habitat (Swanson et al., 1982).

The significant role of woody debris in C and N storage and cycling is intimately related to the processes above. Carbon and N dynamics in woody debris are discussed more specifically below. A key starting

point is an analysis of the quantity of woody debris present in Douglas-fir forests.

Quantity of Woody Debris in Forests

Old-growth Douglas-fir forests contain from 55 to 581 Mg ha⁻¹ of coarse (>15 cm diameter) woody debris (Grier and Logan, 1977; Harmon et al., 1986; Spies et al., 1988). Assuming 50% of the biomass is C (Harmon et al., 1990) woody debris can contain an amount of C at least comparable to and sometimes more than the amounts present in the forest floor or in soil organic matter (Table 1). The total amount of woody material, including that below 15 cm diameter and that buried below the forest floor, has not, however, been well documented.

Measurements of the amount of wood left on a site after logging, and hence at the time the second-growth stand established, have been made to assess the volume of potentially merchantable material remaining or to evaluate the fire danger (Dell and Ward, 1971; Howard, 1973; Martin and Brackebusch, 1974; Howard, 1981). It is doubtful that these have included all of the woody matter present, as neither a merchantability nor a fire risk study was likely to be concerned with highly decayed logs. These highly decayed logs may, however, have important influences on the C:N ratio of the site.

Clearcutting in western Washington resulted in an average woody residue volume of 280 m³ ha⁻¹ of sound material alone or about a

Table 1. Woody debris dry biomass and forest floor and soil C content in Douglas-fir stands (Mg ha^{-1}).

Coarse woody debris (> 15 cm)	Forest floor C	Soil organic matter C	Reference
55	43		Grier et al., 1974
0.6 - 56	15 - 39		Turner and Long, 1975
55 - 581	28 - 57	90 - 130	Grier and Logan, 1977
	2 - 20	10 - 390	Edmonds and Hsiang, 1987
20 - 66			Spies et al., 1988
4 - 96	7 - 26	56	Harmon et al., 1990
82	26	133	Jurgensen et al., 1990
89 - 140			Miller and Bigley, 1990

40% increase over the pre-harvest dead and cull materials on-site (Howard, 1981). Other studies of slash on clearcuts in the Douglas-fir region found an average of between 105 and 314 $\text{m}^3 \text{ha}^{-1}$ of residues (Howard, 1973) and an average of 520 $\text{m}^3 \text{ha}^{-1}$ (range 72 to 508 Mg ha^{-1}) of material over 10 cm diameter (Dell and Ward, 1971). Under harvesting regimes of the 1960's, 53% of logging slash was found to exceed 38.1 cm in diameter and 2.4 m in length (Howard, 1971), although changes in utilization standards have probably reduced this figure now.

An average of 140 Mg ha^{-1} was reported before burning and 89 Mg ha^{-1} after burning in the Douglas-fir region of the Cascade Range (Miller and Bigley, 1990). In eastern Washington, soil wood (i.e., woody residues incorporated in the forest floor) can comprise over 15% of the organic matter on or in the surface 30 cm of soil, equaling or surpassing the organic matter in the forest floor on highly productive sites (Jurgensen et al., 1990).

Logs may cover up to 20% and snags another 5% of the soil surface on old-growth sites (Franklin et al., unpublished, in Harmon et al., 1986). They could therefore intercept a portion of any applied fertilizer and prevent or delay its input to the soil. This point is dramatically illustrated by the amount of ash retained on logs, especially large, deeply fissured ones, around Mt. St. Helens more than 12 years after the 1980 eruption (Warren Tacey, personal observations).

It is also possible that decay fungi may import N into logs via hyphal mats that ramify through the surrounding soil (Ausmus, 1977). If hyphae can exploit the forest floor and soil one log-width either side of a log, and logs cover 20% of the ground, then N may be imported and temporarily immobilized in logs from up to 60% of the site. The rate and amount of N imported into logs would presumably depend on a range of factors including the decay status of the logs, the quantity of N present and the suitability of the substrate for fungal growth. No measurements or estimates of the quantity of N imported into logs are known from the literature.

Decay Classes of Woody Debris

Fallen logs have typically been classified by decay class (Graham and Cromack, 1982; Sollins, 1982; Maser and Trappe, 1984; Means et al., 1985; Harmon et al., 1986; Spies et al., 1988). Fallen logs in decay class I are essentially undecayed while decay class V logs are usually below the level of the forest floor and are completely soft and friable, but still identifiable (Maser and Trappe, 1984). A complete description of the characteristics of each the five decay classes recognized by Maser and Trappe (1984) is contained in Table 2.

Age of Decay Classes

The aging of decay classes, while critical to biomass and nutrient turnover rate studies, has received little attention in the literature because it is difficult and laborious to do. The only comprehensive published study in the Douglas-fir forests of the Pacific Northwest

Table 2. Decay class characteristics of fallen Douglas-fir logs. From Maser and Trappe, (1984)

Characteristics of fallen logs	Decay class				
	I	II	III	IV	V
Bark	Intact	Intact	Trace	Absent	Absent
Twigs to 3cm	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Color of wood	Original color	Original color	Original color to faded	Light brown to reddish brown	Red brown to dark brown
Portion of tree on ground	Tree elevated on support points	Elevated but sagging slightly	Tree sagging near ground	All of tree on ground	All of tree on ground
Invading roots	None	None	In sapwood	In heartwood	In heartwood

was carried out by dating scars on living trees that had been damaged by an adjacent log as it fell (Means et al., 1985). These data were supplemented by aging western hemlock trees that subsequently established on the fallen logs. The mean ages recorded for each decay class are listed in Table 3 (Means et al., 1985). The age shown is the total time, on average, that logs of that decay class have been on the forest floor. Other studies have shown that the relative fractions of organic matter in the fine forest floor material and in large woody material change with time.

The weight of forest floor material stabilizes at 30 to 40 Mg ha⁻¹ in low site-quality Douglas-fir stands between 75 and 125 years after stand establishment. The weight of large woody material on the ground continues to rise to 300 Mg ha⁻¹ about 450 years after stand establishment (Long, 1982). This suggests that the residence time of large logs may extend considerably beyond the 219 yr average inferred by Means et al (1982). At the very least the residence time could be expected to be highly variable depending on site and substrate quality, moisture status and log diameter (Erickson et al., 1985; Harmon et al., 1986; Edmonds, 1987). The presence of logs as carry-over from one rotation to the next (Spies et al., 1988) could also be expected to significantly change the balance of fine to coarse material, and hence the uptake and release of nutrients, on a site.

Forest management is believed to dramatically reduce the amount of coarse woody debris on a site. Spies et al (1988) and Harmon et al

Table 3. Mean age of decay classes of Douglas-fir logs. From Means et al., (1985).

Decay class	Mean age (yr)	Standard error of the mean	Number of samples
I	7.0	2.0	16
II	16.7	2.6	16
III	32.7	5.1	28
IV	81.6	9.3	19
V	218.7	17.9	15

(1990) suggest forest management greatly reduces the biomass of coarse woody debris to levels below the minimum found in unmanaged forests. Spies et al (1988), Edmonds (1990) and Harmon et al (1990) all report coarse woody debris levels below 30 Mg ha⁻¹ in second-growth forests. Levels were further reduced to 10 Mg ha⁻¹ in third rotation forests (Edmonds, 1990), giving rise to concern over this loss of a long-term source of organic matter, below the level contained in fine forest floor materials.

Density of Woody Debris

A range of density values exists for Douglas-fir logs, by decay class and age (Table 4). Sollins' (1982) data from the T. T. Munger Research Forest in southern Washington were most relevant to my study for several reasons; the T. T. Munger area is within the same region as the current study, Sollins took fragmentation losses into account, used a higher number of replicates than were used in other studies, took particular care to obtain representative samples and included the faster decay rate of snags in the overall values. This last point is particularly relevant because up to 33% of the gross standing volume in old-growth Douglas-fir stands can be cull material, including snags, when those stands are logged (Martin and Brackebusch, 1974). All stands sampled in my study were logged 50 to 70 years ago when old-growth was still common in the Pacific Northwest, so it may be reasonable to assume that the range of woody debris quantities left on the sites I sampled was in the same range Sollins (1982) measured for logged old growth stands. Sollins'

Table 4. Measured densities (g cm^{-3}) of fallen Douglas-fir logs by decay class.

Decay class					Reference
I	II	III	IV	V	
0.4	0.4	0.4	0.3	0.3	Brown, 1974
0.35	0.28	0.28	0.21	0.14	Sollins, 1982
0.42	0.32	0.27	0.22	0.08	Means et al., 1985
0.34-0.52					Erickson et al., 1985
0.20				0.16	Harmon et al., 1986
0.39	0.37	0.22	0.17	0.13	Spies et al., 1988
0.31	0.34	0.29	0.23	0.16	Average

density figures are generally lower than those of other workers in decay classes I, II and III and slightly higher in classes IV and V.

Nitrogen and Carbon in Woody Debris

The N content of fallen logs (expressed as mass of N ha⁻¹ in wood of each decay class) rises for some time as they decay and then drops again. Harmon et al (1986) reported that the N content rose as logs progressed to decay class IV, then declined again in class V (Figure 2). This pattern could imply that N is initially immobilized in logs and then released again. Grier (1978) found that the N content of western hemlock logs rose for 25 years after they fell to the forest floor, and inferred that net N immobilization occurred within the logs. Vitousek and Matson (1984) have shown, however, that woody debris (stems >1cm diameter) were a sink for only 5% of applied N¹⁵ and that the litter on the forest floor took up the greatest fraction (26%) of applied N.

Increasing N content through decay class IV was also reported by Graham and Cromack (1982) for Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock from the Hoh rainforest of western Washington. Spruce logs 68 years old and western hemlock logs 33 years old were both in decay class IV, hence N contents continued to rise for at least that long in each case. Graham and Cromack (1982) interpreted this to mean that net mineralization had not occurred even though both species had sustained a weight loss of over 45%.

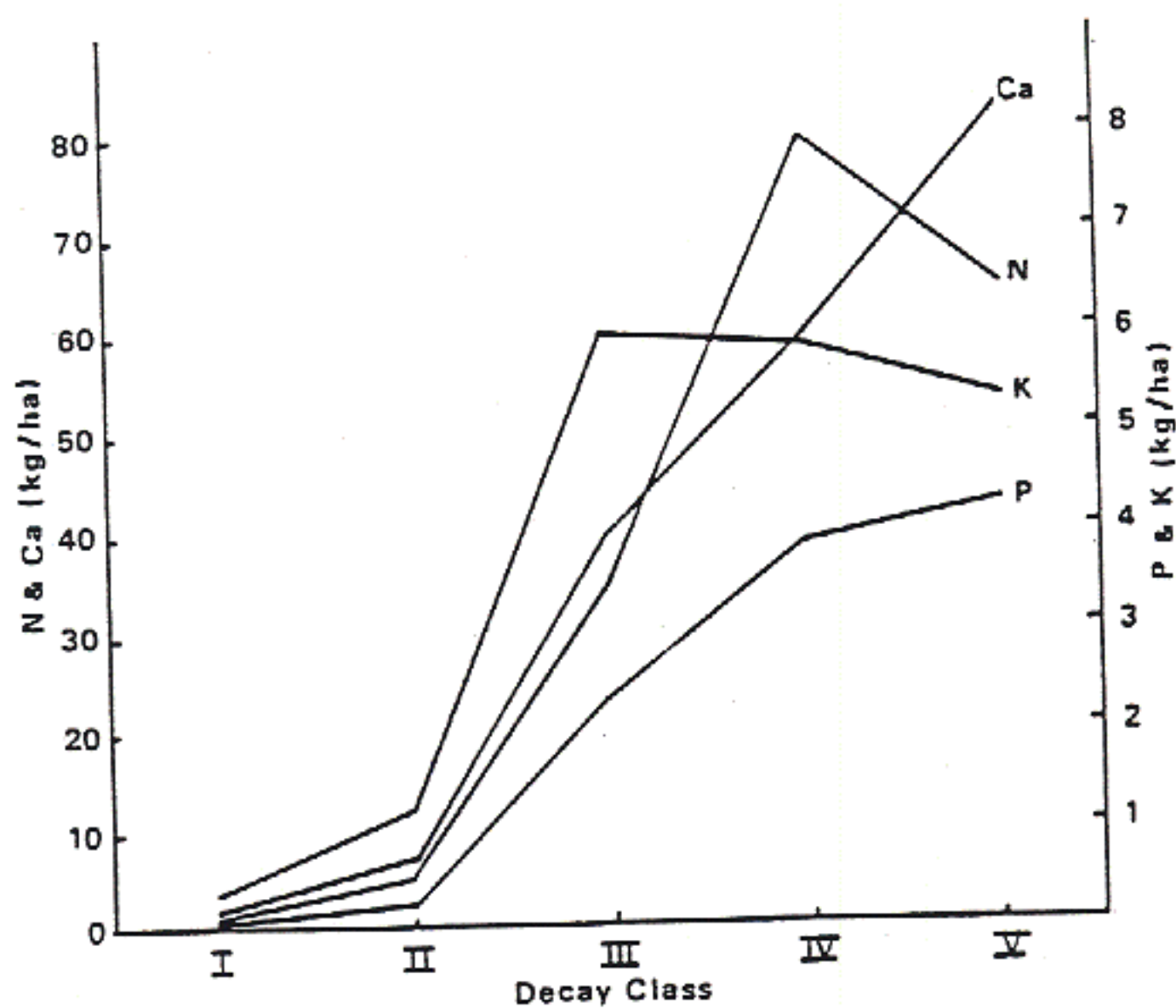


FIGURE 2: Distribution of N, P, K and Ca over decay classes in seven *Pseudotsuga menziesii*-dominated stands from the Cascade Range of Oregon and Washington. From Harmon et al., (1986).

Logs are also an important site for microbial fixation of N (Larsen et al., 1978) and thus aid in the net addition of N to the ecosystem.

Immobilization of N in coniferous litter is usually associated with C:N ratios greater than about 30:1 with mobilization occurring at ratios of 20:1 or less in needles and other fine materials (Edmonds, 1990). Carbon to N ratios of between 998 and 1488:1 have been found in Douglas-fir logs (Edmonds and Eglitis, 1989), although net N release was believed by these authors to occur after 10 years, when the ratios were still well in excess of between 100 and 300:1.

Synthesis on Woody Debris

Fallen wood has the potential to intercept, possibly import, and probably immobilize significant quantities of N when it is fresh and release N in the later stages of decay. The nutrient immobilization capacity of a site mediates the amount of applied N that becomes available to trees following fertilization. Long term response to fertilization only occurs when the immobilization capacity is overcome (Prescott et al., 1992).

Whether to retain or get rid of wood on the forest floor has attracted considerable debate. The following two quotations characterize the debate: "Soil organic matter is an important factor for the continued productivity of Inland Northwest forests" (Jurgensen et al., 1990) versus "decline in growth of conifer plantations is caused by progressive N immobilization in the forest floor during stand

development" (Miller, 1979). In either case, the role of fallen woody material is of considerable interest to forest managers with regard to its role in forest nutrition. Fallen wood has the potential to play an important role in the N dynamics of a forested site and may have significant consequences for cost-effective fertilization of second-growth Douglas-fir stands.

METHODS

This study builds on work on Douglas-fir nutrition carried out since 1969 as part of the Regional Forest Nutrition Research Project (RFNRP; now the nutrition project of the Stand Management Cooperative - SMC). A full description of the design and methods used then have been published previously (Hazard and Peterson, 1984). A brief description of the elements relevant to this study follows.

Study Sites

Fourteen unthinned (Phase I) installations established as RFNRP fertilizer response experiments in 1969 and 1970 were used for this study. This allowed the existing, extensive RFNRP-SMC database on fertilizer response and site conditions to be used.

The fourteen installations sampled were located within the three RFNRP geographic provinces covering western Washington and the northwest corner of Oregon (Figure 3). Province 1 loosely coincides with the Puget Sound lowlands, generally comprising gravelly soils formed following deposition of material by the retreat of the continental Vashon glaciation about 10,000 years ago (Franklin and Dyrness, 1988). Province 1 extends roughly from sea-level to 460 m elevation. Province 2 encompasses the western foothills and slopes of the Cascade Range from 460 m to the Cascade crest.

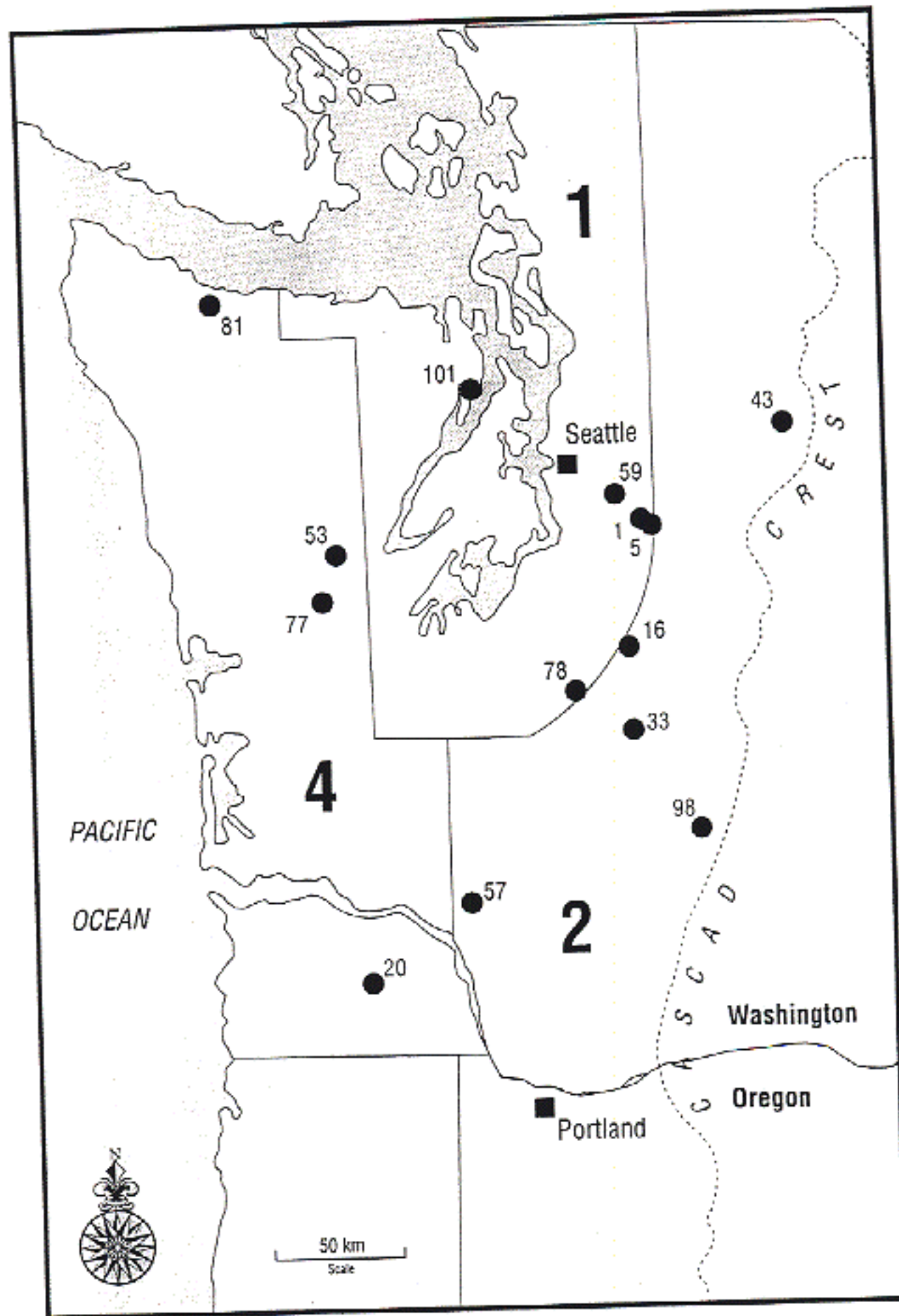


FIGURE 3: Location of RFNRP provinces 1, 2 and 4 (large numerals), showing the 14 experimental installations sampled (small numerals).

In practice, sample sites are confined below the upper limit of the vegetation zone dominated by Douglas-fir. Podzolized residual soils predominate on these sites (Franklin and Dyrness, 1988). Province 4 occupies the coastal zone of Washington and northwest Oregon, the southern half of which was not glaciated but much of which is characterized by high rainfall and gravelly to sandy, glacial outwash soils (Franklin and Dyrness, 1988). Elevations range from sea-level to 430 m.

The design of my study recognized that there were likely to be wide variations in environmental conditions and hence in the results obtained across the region. This variation might have been limited by sampling in one province only. For the results to have practical application in the future, however, sampling across a range of site conditions was required. At the same time, the need for meaningful stratification still needed to be taken into account. To extend the range of data collected as widely as possible with the available resources, sites were chosen to represent the widest possible range of growth responses based on existing RFNRP data.

All sites comprised unthinned Douglas-fir stands only, selected to avoid the confounding effect of thinning on growth response. Selected stands ranged in breast height age from 22 to 50 years at the time of fertilization in either 1969 or 1970. All stands were at or approaching the stem exclusion stage (Oliver and Larson, 1990) at the time of the present study. Because many installations had been

logged since establishment, insufficient candidates were available across the range of responses to stratify by site index class (King, 1966). Consequently, installations ranged from site index class I (index height >41 m at age 50 yr) to class IV (index height 23 to 29 m at age 50 yr). A description of the installations sampled appears in Table 5. Each RFNRP installation consisted of six square 0.04 ha plots measuring 20 m by 20 m plus a treated buffer. Initial values of stand variables are listed in Table 6.

At the time of establishment in 1969 or 1970, urea fertilizer was applied to two plots at 224 kg N ha^{-1} , to two plots at 448 kg N ha^{-1} and two further plots served as unfertilized controls. Using the procedure of Stegemoeller and Chappell (1990), growth response was calculated as the relative difference in net total volume periodic annual increment between the two 448 kg N ha^{-1} plots and the two controls for the 4 yr period after fertilization. For the purposes of my study, three relative growth response classes were arbitrarily defined as follows: low 0-20 %, medium 20-40 % and high 40+ %. For my study, one plot fertilized at 448 kg N ha^{-1} and one unfertilized control plot were randomly selected for assessment at each sampling installation. All measurements and samples for this study were collected in June and July of 1992.

Table 5. Description of installations sampled.

Prov	Instn No.	Installation Name	Plot No.	Treatmt N ha ⁻¹	Site Index m @	Age * mm	Rain fall mm	Parent material/Soil order	Elevation m	Volume Response % #	Response Class *
1	1	Cedar Falls	4	0	36.0	43	2032	Glacial Till	344	58	High
			2	448	33.2			inceptisol			
5		Power Line	25	0	32.3	38	1778	Glacial Till	274	59	High
			29	448	30.2			inceptisol			
59		Tiger Mtn	354	0	29.6	42	1905	Sandstone	387	21	Medium
			351	448	28.6						
78		Eatonville Triangle	468	0	31.7	50	1194	Glacial Till	250	0.4	Low
			463	448	36.6			inceptisol			
101		Thorndyke Homestead	602	0	37.8	31	889	Glacial Till	140	34	Medium
			601	448	36.0						
2	16	South Fork Ohop Crk	91	0	25.6	42	1651	Glacial Till	610	6	Low
			92	448	27.7						
33		Mineral Creek	193	0	34.1	26	2286	Igneous inceptisol	511	35	Medium
			195	448	38.1						
43		Skykomish	253	0	25.9	45	2667	Granite spodosol	457	66	High
			256	448	30.2						
57		Headquarters Camp	342	0	37.8	35	1651	Igneous ultisol	536	8	Low
			338	448	43.0						
98		Tongue Mountain	584	0	37.2	45	2159	Pyroclastic	488	22	Medium
			583	448	40.2						

Table 5. continued.

Prov	Instn	Installation	Name	Plot	Treatmt	Site	Age	Rain	Parent	Elevation	Volume	Response
No.				No.	kg N ha ⁻¹	Index	*	mm	material/Soil	m	% #	Class *
4	20	Deep Creek		118	0	44.8	32	1778	Sediments	373	43	High
				117	448	42.1			inceptisol			
53		Camp Grisdale		317	0	36.3	28	2921	Glacial Till	421	8	Low
				315	448	39.0			inceptisol			
77		Mid Fork Satsop River		462	0	41.5	22	2286	Glacial Till	162	6	Low
				461	448	32.0			spodosol			
81		North Point Lookout		485	0	31.4	39	2540	Basalt	390	38	Medium
				484	448	33.8						

@ King, 1966.

* Breast height age at fertilization.

Relative pa difference at 8 yr in volume between plots fertilized with 448 kg N ha⁻¹ and control plots.

< 0-20% Low; 21-40% Medium; >40% High.

Table 6. Stand variables assessed during RFNRP studies.

Variable	Measurement	Procedure
Site index	Meters at 50 yr	King, 1966
Age	Stand age, yr	Breast height core at initial treatment
Rainfall	Millimeters yr ⁻¹	Nearest weather station
Soil type	Parent material and soil order	Soil pit in unfertilized area between plots
Soil nutrients	0 - 15 cm soil	Hazard and Peterson, 1983
Elevation	Meters	Topographic map or altimeter
Volume response	Net volume increment, %	Difference between fertilized and control plot

Fallen Woody Debris

Biomass

The biomass of wood on the forest floor was measured using a modified form of the planar intersect method (Brown, 1974), a variant of the line intersect method. These methods have been developed to obtain estimates of woody fuels in forests (Warren and Olsen, 1964; van Wagner, 1968; Brown, 1971; Brown, 1974) and are suited for rapid estimation of wood fuel loads over large areas.

The usual planar intersect procedure involves using two to four transects, each 60 m long, over a 20 ha area to obtain an estimate within 10 to 20% of the true load. The true load is assessed by measuring the dimensions of each piece of woody debris over 76 mm diameter and by weighing finer material in a sub-sample area (Brown, 1974). Transects are laid out on a randomly chosen radial from a random starting point. Radial sampling is recommended to avoid bias due to the non-random orientation of fallen logs after harvesting operations, especially if cable logging is used (Warren and Olsen, 1964; van Wagner, 1968; Brown, 1971).

The biomass of all woody material was measured on the RFNRP fertilizer response plots by setting out 10 transects, 2 m apart, across the full 20 m width of the previously established plots (Figure 4). On steep slopes transects were usually laid across the slope for ease of access. While this approach did not result in sampling on random radii, the closeness of the transects ensured sampling was

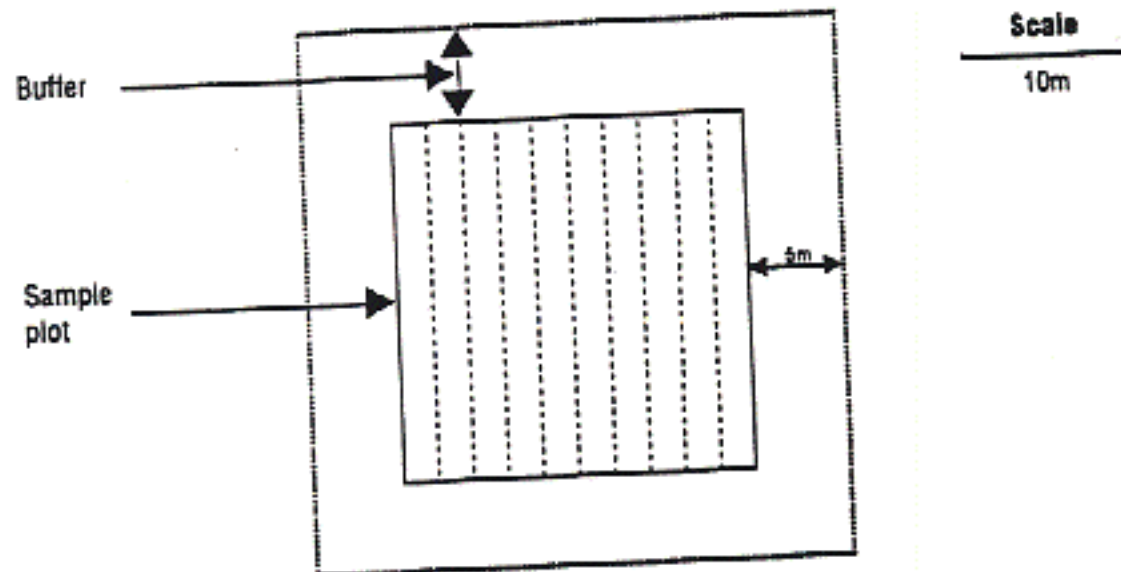


Figure 4a. Layout of sample plots.

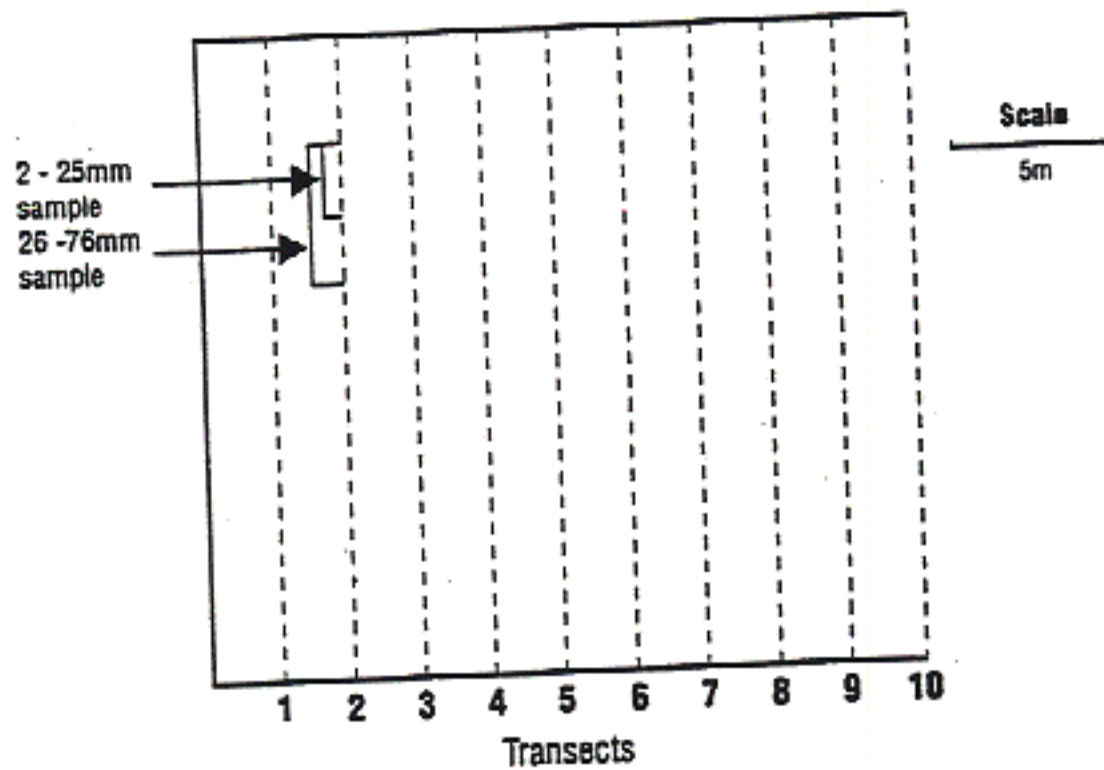


Figure 4b. Layout of transects in 20m x 20m sample plot.

comprehensive without the risk of infrequent sample lines falling between concentrations of wood.

The diameter of every log (> 76 mm) that intersected the transect was measured, to the nearest centimetre, perpendicular to the centre line of the log. This material was referred to as "large wood." The same log was often measured more than once due to the closeness of the transects. This would not be expected to lead to over-estimation of the volume of wood because the planar intersect method works by integrating the area of "slices" through logs to obtain volumes (van Wagner, 1968). Division of the sum of these areas by the number of slices measured provides the integration necessary to obtain volume.

The more times a log is measured, the more accurate the calculated volume since integration assumes addition of an infinite number of slices, each with no thickness. No patterns of log orientation due to harvest method were obvious, although logs did tend to lie across the slope on the steepest sites. Stumps were omitted as they are not accurately estimated by the planar intersect method (Brown, 1974).

All fine woody material was also assessed using the planar intersect method and combined into a single total from measurements of two sub-classes. The number of pieces in the 2 to 25 mm diameter range was counted over a randomly selected 1.8 m segment of each transect. The same random origin was used to count the number of pieces in the 26 to 76 mm diameter range over a 3.7 m segment of

each transect (Brown, 1974). The combined amount of all wood 2-76 mm in diameter was referred to as "fine wood." The terms "large wood" and "fine wood" were chosen to avoid confusion with the somewhat loosely defined term "coarse woody debris."

The width of stumps was recorded along their line of intersection with the transect but these data were not included in the analyses because Brown (1974) specifically recommends that they be excluded. This is because the butt-swell can give a grossly exaggerated value to the diameter figure, which is squared in the calculation step and thus vastly over-estimates the volume of these items. There were never more than two stumps intersected on any plot, so this step was regarded as introducing only a small underestimate into the total wood load present. Some account has been taken of butt-swell in calculations of stump volumes in the past (Grier and Logan, 1977) but that method was not used here because the line intersect procedure did not record stump diameter at "standard" breast height. It would be possible in future to record stump diameters and calculate volumes separately.

The total biomass of fallen wood was also estimated visually by comparing the amount of wood visible with a standard series of photographs developed for estimating the mass of logging slash in Douglas-fir - western hemlock forests (Ottmar et al., 1990). The intent was to see if this very rapid estimation method yielded results

that correlated satisfactorily with results from the planar intersect method.

Decay Class

Decay class was assessed visually according to the scheme of Maser and Trappe (1984) each time a piece of wood was encountered along the transects (Table 2). This approach gave a realistic assessment of the quantity of each decay class present, without the usual problems of having to assign a log to a single class when the extent of decay varied along its length (Graham and Cromack, 1982).

In addition to assessing the usual characteristics like the presence or absence of bark or branches, the degree of sagging and the color and texture of the wood (Maser and Trappe, 1984), probing with a 25 cm steel spike (Lang and Forman, 1978; Lambert et al., 1980) assisted in the determination of the extent of decay, especially where logs were covered by moss or buried in the soil. Decay class I logs were sound, with bark and fine branches intact. They could not be penetrated with the spike. Large decay class II logs had bark and larger branches present and the sapwood was only partially softened by decay. If the log was large and intact, but the bark was missing entirely and the spike only penetrated a short way, then the sapwood was judged to be decayed and the log assigned to decay class III. If the log was large, essentially intact and the spike penetrated to the heart of the log or the full length of the spike it was classified as decay class IV. Decay class V logs were soft

throughout and offered little resistance to penetration by the spike. Decay class IV and V logs were also typified by the characteristic red-brown color of the decayed wood.

Small logs, especially when saturated, were often soft enough for the spike to penetrate even though bark was present and the wood was still pale yellow in color. These logs were assigned to decay class III. If small logs could be penetrated a short distance, only the sapwood was judged to be rotted and they were classified as decay class II. The spike would not penetrate even small decay class I logs.

Soil and Wood Sampling for Nutrient Analysis

Soil Sampling

Samples of the top 15 cm of mineral soil were collected using a 25 mm diameter Oakfield sampler (Oakfield Apparatus Co., Oakfield, WI). Twenty samples were collected from each plot, 10 at equal intervals across each diagonal. These samples were thoroughly mixed and returned to the laboratory in sealed 500 ml plastic bags. Soil samples were air-dried, sieved through a 2 mm mesh and the fine fraction retained for analyses.

Wood Sampling

A sample of wood from a representative log larger than 76 mm in diameter from each decay class was collected from both the fertilized and control plots at eight of the installations. Wood samples were

collected using a hatchet to cut a wedge from each log, since fire restrictions prohibited the use of a chain saw as recommended by Sollins (1982). Care was taken to collect a sample yielding representative proportions of bark (where present), sapwood and heartwood, within the limitations of the technique used. These samples were not collected volumetrically. Samples were returned to the laboratory in new kraft paper bags and oven-dried at 70° C. Largely intact wood in decay classes I, II and III was ground using a heavy-duty Wiley mill, while material from decay classes IV and V was ground using a mortar and pestle. All wood samples were ground to pass a 2 mm mesh.

Samples were collected to represent the full range of provinces and response levels for this study (Table II, Appendix). Due to cost constraints, analyses were not done for all plots and no analyses were done on the fine wood fraction less than 76 mm diameter. N and C contents for this material exist in the literature (Edmonds, 1987).

Site Description

At each sampling location aspect, slope, understory vegetation cover, litter depth and depth of the O1 horizon were recorded. Slope was measured to the nearest percentage point with a hand-held clinometer and aspect was recorded to the nearest degree using a hand-held compass. Vegetation was characterized by a visual

estimate of the percentage cover of the predominant species. The depths of litter and O1 horizon on the forest floor were recorded to the nearest 5 mm at 10 locations across one diagonal of each plot. General descriptions of the stand structure, composition, soil type and evidence of burning were also recorded.

Laboratory Analyses and Calculations

Nutrient Analyses

Total N as ammonia was determined on wood and soil samples using a micro-Kjeldahl method following lithium sulfate digestion (Bremner and Mulvaney, 1982) using a Technicon AutoAnalyzer II (Technicon Instruments Corp., Tarrytown NJ). Carbon was determined by weight loss following combustion (Nelson and Sommers, 1982) using a LECO WR-12 analyzer (LECO Corp., St Joseph, MI).

Calculations of Wood Mass and Constituents

The mass of fallen wood in each decay class on each site was calculated using the following formulas (Brown, 1974);

$$\text{2-76 mm material:} \quad \text{mass} = (26.07 \cdot n \cdot d^2 \cdot s \cdot a \cdot c) / Nl \quad (4)$$

$$\text{76+ mm material:} \quad \text{mass} = (26.07 \cdot \Sigma d^2 \cdot s \cdot a \cdot c) / Nl \quad (5)$$

where; n = total number of intersections for the size class
 d^2 = diameter² tables (Brown, 1974) of 2-76mm wood
 Σd^2 = sum of squares of measured log diameters >76mm
 s = density
 a = non-horizontal angle correction (Brown, 1974)
 c = slope correction factor (Brown, 1974)
 Nl = total length of sampling line for each size class
 26.07 = a constant to convert to $Mg\ ha^{-1}$.

The density values used were from Brown (1974) for 2-76 mm material and Sollins (1982) for larger material. Since Sollins' density figures are generally lower than those developed by others (Table 4) in decay classes I, II and III and slightly higher in the top two classes, the mass of fallen wood calculated as present on the sites studied here could be regarded as a low end estimate in the lower classes and a little higher in classes IV and V.

The mass of N and C present in wood on-site was calculated by taking the percentage of each element in the samples from each decay class and multiplying by the mass of wood greater than 76 mm diameter in each class. Carbon to nitrogen ratios for each decay class were expressed as the ratio of percentage weights of each element from laboratory analyses of each wood sample. Total C:N ratios for all wood greater than 76 mm diameter on a site were calculated by summing the total mass of C across all decay classes on a site and dividing by the total mass of N.

Retrospectivity of Wood Measurements

Clearly the wood present at the time of this study and its decay status had changed compared to when the plots were established 23 years ago. Published data for the average age of each decay class (Table 3) were used to help account for these changes (Means et al., 1985). Since the mean residence time on the forest floor of logs in decay classes I and II was 7 and 17 years respectively, all wood in these classes at the time of this study was discounted from linear regressions of tree growth response versus fallen wood volume because growth response was measured over the four years following plot establishment, when the current decay class I and II wood was not on the ground.

Some of the wood now in decay class III may not have been present at the time of establishment either. However, those logs from the new stand would all have been of small diameter and a small component of the total compared to the volume in the large logs carried over from the previous stand. Decay class III wood was not discounted, because many of the larger logs could be more than 23 yr old. This may have slightly over-estimated the amount of wood in decay class III at the time of plot establishment. Wood that was in decay classes IV through V at the time of the present study was judged present at the time of establishment. A few, small diameter pieces from the stand may have reached these decay classes since establishment but the volume would have been very small compared to the totals.

Some of the wood measured during this study would have changed decay class since plot establishment and some would have moved out of decay class V to become soil organic matter. Since there was no accurate way to know how much was in each class at the beginning, no useful estimate of these changes could be made. Loss from decay class V would lead to a slight underestimate of the wood present at establishment.

Density of wood decreases with time as it decays (Table 4), so measurements today would tend to underestimate the biomass present earlier. Mass of N per hectare present in each decay class tends to stabilize as the wood decays beyond decay class III (Harmon et al., 1986) so time elapsed since establishment was not expected to unduly influence the amount of N present in wood at the time of this study compared to the amount present soon after fertilization. Carbon to N ratios may have fallen slightly if N remained while C was consumed by decomposer organisms.

Calculations of Soil Constituents

Total mass of N and C in the top 15 cm of mineral soil was calculated by multiplying the percentage values from the laboratory analyses by the depth sampled, bulk density and the fine fraction of soil passing a 2 mm sieve. Fine fraction was calculated as the difference between total soil and the percentage gravel recorded for each installation in the RFNRP-SMC database. Bulk density for each installation was also obtained from the RFNRP-SMC database.

Statistical Analyses

Means and standard errors were calculated for the depth of the litter and O1 layers and for the C and N contents in each decay class, using the statistical package in Microsoft® Excel version 3.0a (Microsoft Inc., Redmond, WA). A linear regression was fitted to a plot of estimated versus measured biomass of woody debris for all installations, using the facilities of Cricket Graph® version 1.3.2 (Cricket Software, Malvern, PA).

Data on biomass, mass of carbon, mass of nitrogen and the C:N ratio of woody debris by decay class on fertilized and control plots was tabulated and means and standard variations calculated using the Systat® version 5.2.1 statistical package (Systat Inc, Evanston, IL). Systat was also used to carry out analyses of variance on these data, using independent t tests with equal sample sizes and, where significant differences in means existed between decay classes, Tukey tests were used to make multiple comparisons between the decay class means.

RESULTS AND DISCUSSION

Biomass of Woody Debris

Amount of Wood

Biomass of wood beneath unthinned second growth Douglas-fir stands averaged 73.5 Mg ha⁻¹ on unfertilized sites and 79.2 Mg ha⁻¹ on fertilized sites (Table 7). Total biomass on individual plots ranged from 9.8 to 234.2 Mg ha⁻¹ (Table I, Appendix). The differences in biomass of "large" fallen wood in each decay class and in the total across both "large" and "fine" sizes, and all decay classes, were not significant between fertilized and control plots (Table 7). The standard deviation within all groups was, however, of the same order as the mean in each case, indicating the wide variation in the amount of fallen wood across these sites. There was more wood in the older decay classes III through V. These differences were significant on control plots but not on fertilized plots. The larger amount of wood in decay classes III through V was most likely carried over from the previous stand. The relatively lower mass of decay class V wood recorded may at least partly reflect a failure to detect all of this material below the forest floor. The smaller amount of decay class I and II wood probably reflected the early developmental stage of the new stands. The trend to higher biomass of new decay class I wood on fertilized plots, while not significant, is indicative of their greater productivity after fertilization (Stegemoller and Chappell, 1990).

Table 7. Dry mass of wood components by decay class (Mg ha^{-1}) - means with $n=14$, standard deviations in parentheses. Means within columns are not significantly different ($p > 0.05$). Decay class means within same row with different letters are significantly different ($p < 0.05$).

Treatment	2-76mm	Decay class				Total	
		I	II	III	IV		V
Control	7.01 (4.44)	1.56 a (2.02)	4.02 ab (3.66)	23.65 c (30.46)	22.30 bc (23.13)	14.92 ac (14.74)	73.46 (48.10)
Fertilized	7.94 (4.58)	6.16 a (9.71)	6.04 a (5.45)	24.35 a (27.73)	21.85 a (38.68)	12.79 a (15.17)	79.15 (68.12)
Average	7.48	3.86	5.03	24.00	22.08	13.86	76.31

An average of 7.5 Mg ha^{-1} of fine wood was present on these second growth plots. There was no difference in this component between control and fertilized plots. Fine wood made up from 2% to 65% of the total wood biomass on a per plot basis. The amount of fine wood present is noteworthy as this component may have been overlooked in past studies where only coarse woody debris ($>15\text{cm}$) and forest floor material have been considered. While the finest part of this component may have been considered as part of the forest floor in the past, the part nearer 76 mm may not have fallen into either the coarse woody debris or the forest floor category and may not have been recorded (Grier and McColl, 1971).

Litter

The depths of litter and the O1 soil layer were not significantly different between fertilized and control treatments, with wider variation in organic layer depth than in the thickness of litter (Figure 5). Hence fertilization did not result in a significant difference in the net quantity of forest floor material or of fine or large wood on the ground.

Synthesis on Woody Biomass

The range and average values for fallen woody biomass recorded in this study fall within the range of values previously recorded for second growth Douglas-fir forests in the Pacific Northwest (Cole et al., 1968; Grier and Logan, 1977; Harmon et al., 1990). The overall average of 76 Mg ha^{-1} is more than double the value of 30 Mg ha^{-1}

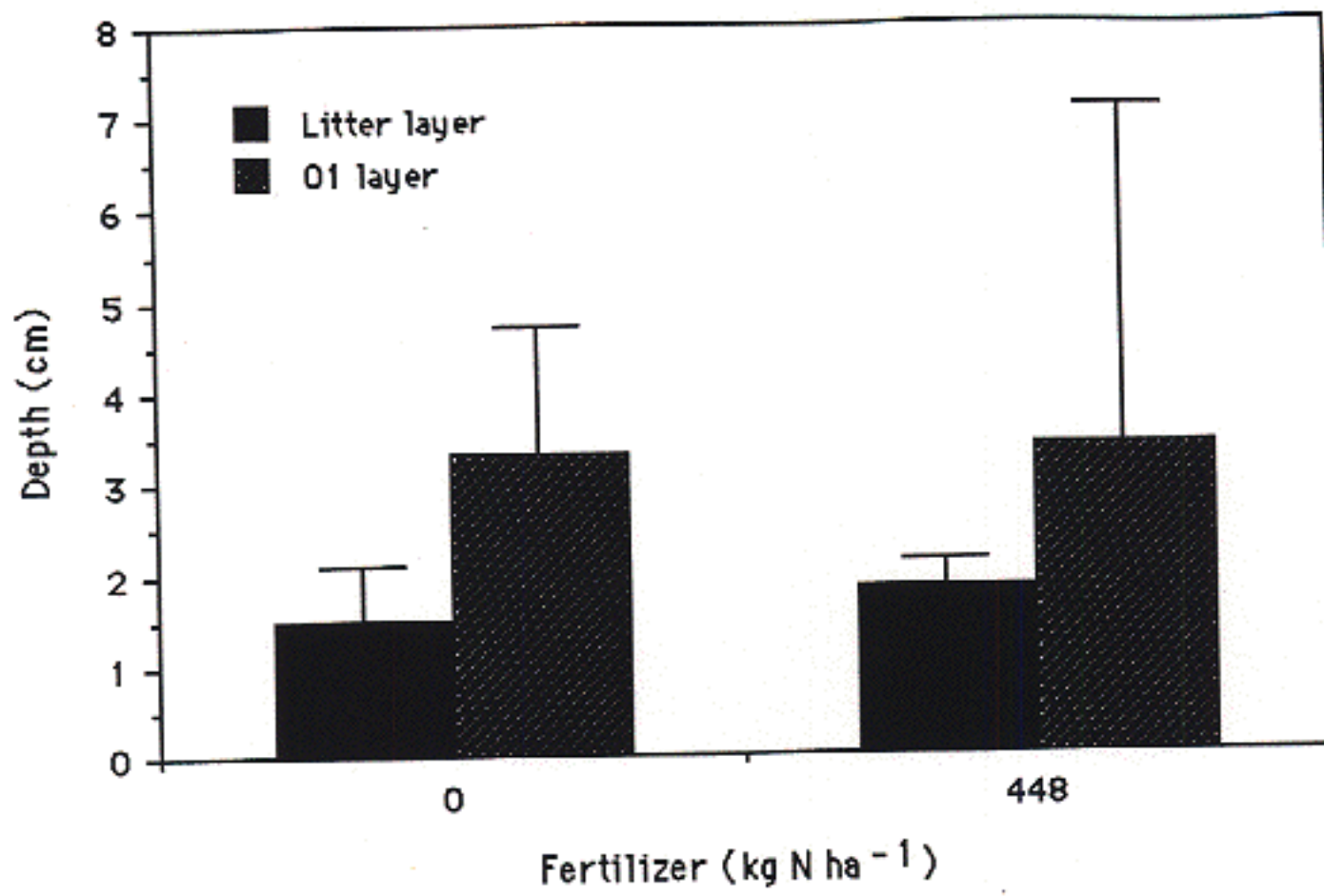


FIGURE 5: Depths of litter and O1 organic layers on plots fertilized with 0 or 448 kg N ha⁻¹ up to 22 yr earlier. Bars show standard error of the mean (n=14).

commonly accepted as typical on second-growth sites (Spies et al., 1988; Edmonds, 1990) and values varied widely across the study area. This suggests that the contribution of fallen wood to the nutrient dynamics of second-growth sites may be more significant than previously supposed.

The wide range of values recorded doubtless reflects variation in operational practices, as noted by Howard (1973), who found that the quantity of slash remaining after harvest averaged three times more on public than private land due to different utilization standards. The range of biomass values in this study overlaps the lower half of the range reported by Dell and Ward (1971) for material over 10 cm diameter on freshly logged sites. The average of 76 Mg ha⁻¹ is somewhat lower than the average of 89 Mg ha⁻¹ reported immediately after burning logged sites (Miller and Bigley, 1990). Charcoal was noted on almost all sites in this study. It is reasonable that the biomass of fallen wood should decline in the 45-90 yr since cutting and burning. If wood biomass levels do indeed drop to a minimum 60-80 yr after stand re-establishment (Spies et al., 1988) then the levels measured here represent that age range and may be up to twice as great as previously thought. The 7.5 Mg ha⁻¹ of fine wood measured here was about half of the 14.2 Mg ha⁻¹ for fine woody debris and forest floor in a 60 yr old stand of Douglas-fir measured by Grier and McColl (1971), whose samples comprised all organic material, including mosses and litter but excluded "larger pieces of rotting wood." Hence the fine wood recorded here could be

regarded as additional to the forest floor and having about the same biomass.

The importance of woody debris carryover from previous Douglas-fir stands has been noted by Spies et al (1988). They estimated that approximately 76% of the coarse woody debris beneath naturally regenerated stands 60-80 yr old in the Cascade Range originated in the previous stand and speculated that sites with high woody debris accumulations may consequently be more productive, in part due to the suitability of logs as sites for mycorrhizal activity in dry periods.

The average wood biomass of 76 Mg ha^{-1} recorded here was very similar to values of 81 Mg ha^{-1} (Sollins, 1982) and 82 Mg ha^{-1} (Franklin et al., unpublished, in Harmon et al., 1986) recorded for all fallen logs $>15\text{cm}$ diameter in old-growth Douglas-fir stands 450yr old. This indicates that the carryover from the previous stand is indeed an important contribution to the wood load on the forest floor of second-growth stands, even after slash burning.

Carbon and Nitrogen in Wood

Carbon

The C concentration of large fallen wood ranged from 46.6% to 54.7%, with significant differences ($p<0.05$) between decay classes within treatments (Table II, Appendix). Values were 2 to 8% greater in decay classes IV and V than in classes I through III (Figure 6). There

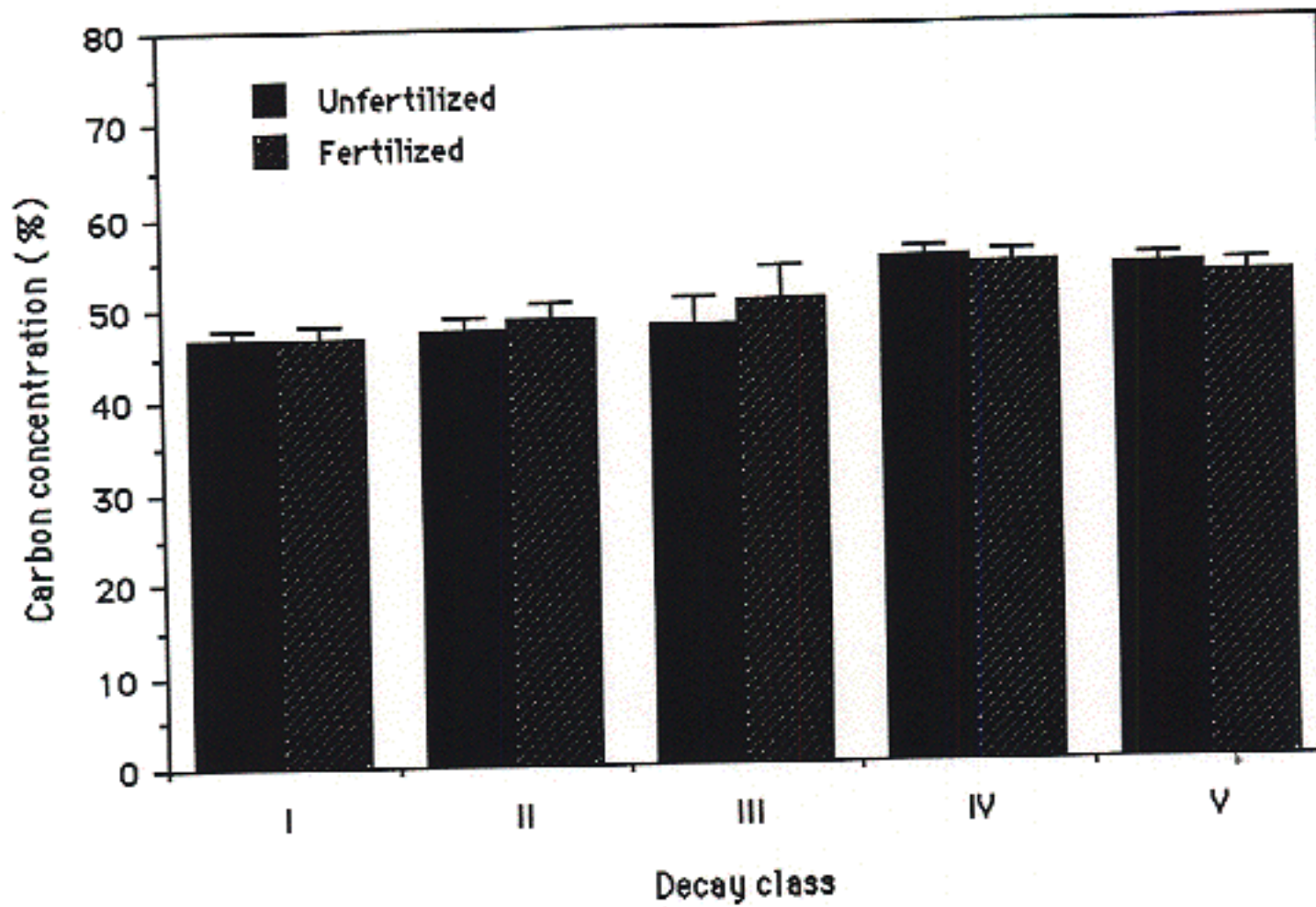


FIGURE 6: Carbon concentration (Weight %) in woody debris by decay class on Douglas-fir plots fertilized with 0 (Unfertilized) and 448 (Fertilized) kg N ha^{-1} up to 22 years earlier. Bars show standard error of the mean ($n=14$).

were no significant differences in C concentrations of wood between fertilized and control treatments within the same decay class. Consequently, average C concentration for each decay class within each fertilizer level was used to calculate the mass of C on each plot.

Total mass of C in all fallen wood averaged 32.5 Mg ha^{-1} and did not differ between control and fertilized plots (Table 8). Mass of C contained in wood of decay classes III, IV and V was up to an order of magnitude greater than the amount in wood of classes I and II, largely due to the greater biomass in decay classes III through V, although the standard deviations were in the same range as the means. There were consequently no significant differences in mass of C, within decay classes, between fertilized and control plots.

Nitrogen

Nitrogen concentration of large fallen wood ranged from 0.109 to 0.559% and generally increased as the decay class rose (Table III, Appendix; Figure 7). There were significant differences between decay classes within fertilization levels. Average N concentrations of fallen wood on fertilized plots were consistently greater than the averages for control plots, although these differences were only significant in decay classes IV and V ($p < 0.05$). Average N concentration for each decay class within each fertilizer level was thus used to calculate the mass of N on each site. The calculated total mass of N in large wood averaged 176.6 kg ha^{-1} on unfertilized sites and 233.9 kg ha^{-1} on fertilized sites, although

Table 8. Mass of carbon by decay class of woody debris (Mg ha^{-1}) - means with $n=14$, standard deviations in parentheses. Means within columns are not significantly different ($p > 0.05$). Means within rows with different letters are significantly different ($p < 0.05$). Forest floor data from Edmonds and Hsiang, (1987).

Component	Treatment	Decay class					Total
		I	II	III	IV	V	
Wood	Control	0.73 a (0.94)	1.90 ab (1.73)	11.33 b (14.59)	12.20 b (12.66)	8.03 b (7.93)	34.20 (25.14)
	Fertilized	2.88 a (4.53)	2.86 a (2.58)	11.67 a (13.28)	11.96 a (21.17)	6.88 a (8.16)	36.25 (34.96)
Soil 0-15 cm	Control						45.58 (22.60)
	Fertilized						62.02 (30.79)
Forest floor							8.18 (3.00)

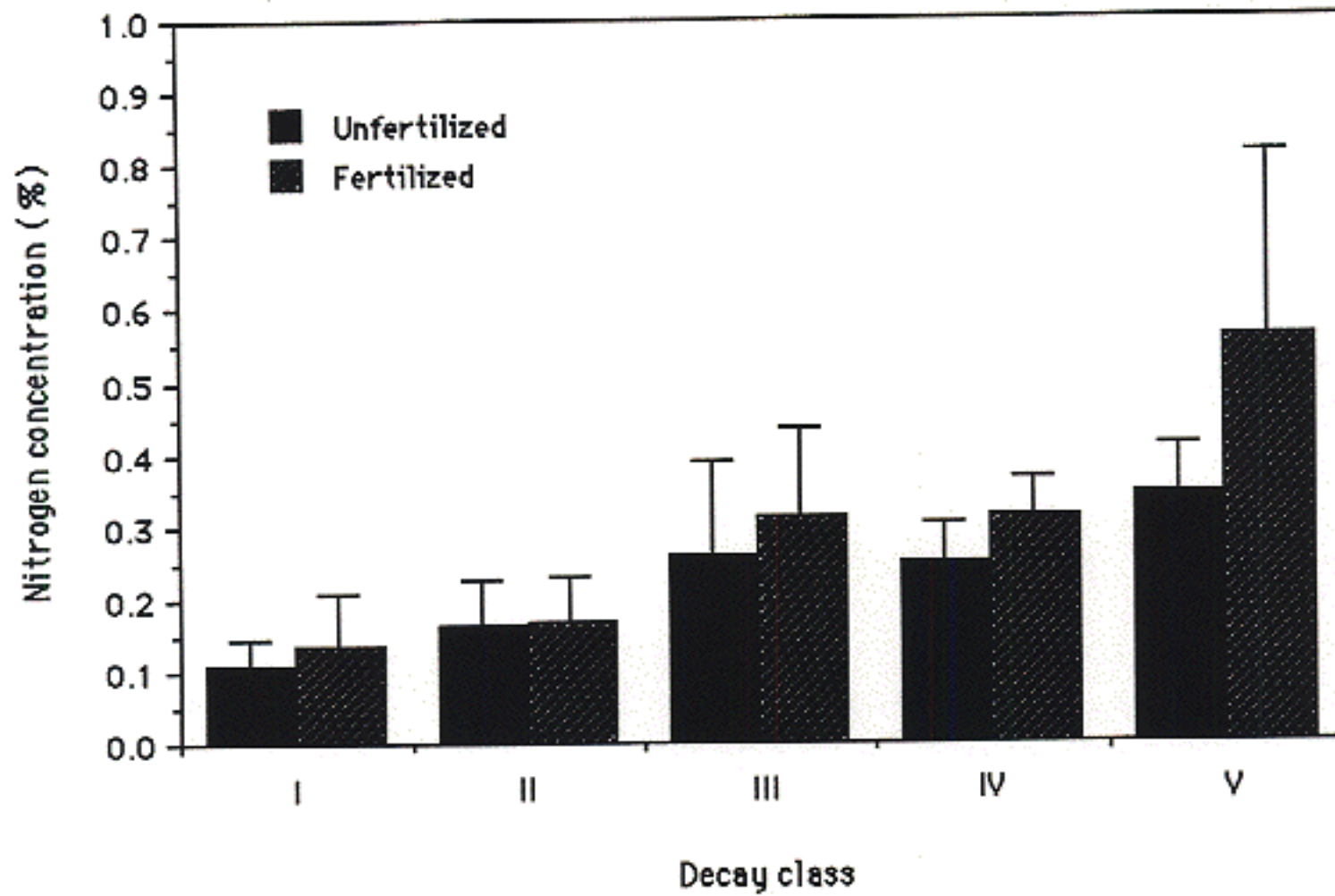


FIGURE 7: Nitrogen concentration (Weight %) in woody debris by decay class on Douglas-fir plots fertilized with 0 (Unfertilized) or 448 (Fertilized) kg N ha⁻¹ up to 22 years earlier. Bars show standard error of the mean (n=14).

these differences were not statistically significant due to the large variations in biomass. The N mass in decay classes III, IV and V was consistently an order of magnitude higher than in classes I and II (Table 9, Figure 8), although the standard deviations were of the same range as the means. There was a consistent trend towards more N in wood on the fertilized sites but the wide variation in levels within a decay class meant that these differences were not significant.

Carbon to Nitrogen Ratio

Carbon to N ratios generally dropped, from a high of 481 to a low of 109, with increasing decay class (Table 10). A statistically significant difference between higher and lower ratios appeared at class II on the unfertilized treatment and at class III on the fertilized treatment. Average C:N on fertilized plots tended to be lower than the averages for control plots in decay classes III to IV, but these differences were not statistically significant. Mean C:N across all fertilized plots was lower (245) than for control plots (284) but the difference was not significant.

Synthesis on Wood Carbon and Nitrogen Content

Fallen wood contains a significant proportion of the C on the ground surface and in the soil beneath second growth Douglas-fir stands (Table 11), making up 38.9% of the total and exceeding the fraction in the forest floor more than four-fold. Carbon in large wood

Table 9. Mass of nitrogen by woody debris decay class (kg ha^{-1}) - means with $n=14$, standard deviations in brackets. Means within columns are not significantly different ($p > 0.05$). Means within decay classes in rows with different letters are significantly different ($p < 0.05$). Forest floor data from Edmonds and Hsiang, (1987).

Component	Treatment	Decay class					Total
		I	II	III	IV	V	
Wood	Control	1.70 a (2.21)	6.63 a (6.04)	61.25 b (78.90)	55.97 ab (58.05)	51.04 ab (50.40)	176.59 (131.69)
	Fertilized	8.32 a (13.10)	10.21 a (9.20)	75.74 a (86.23)	68.19 a (120.68)	71.49 a (84.78)	233.95 (235.23)
Soil 0-15 cm	Control						2164 (1312)
	Fertilized						2703 (1436)
Forest floor							205 (73)

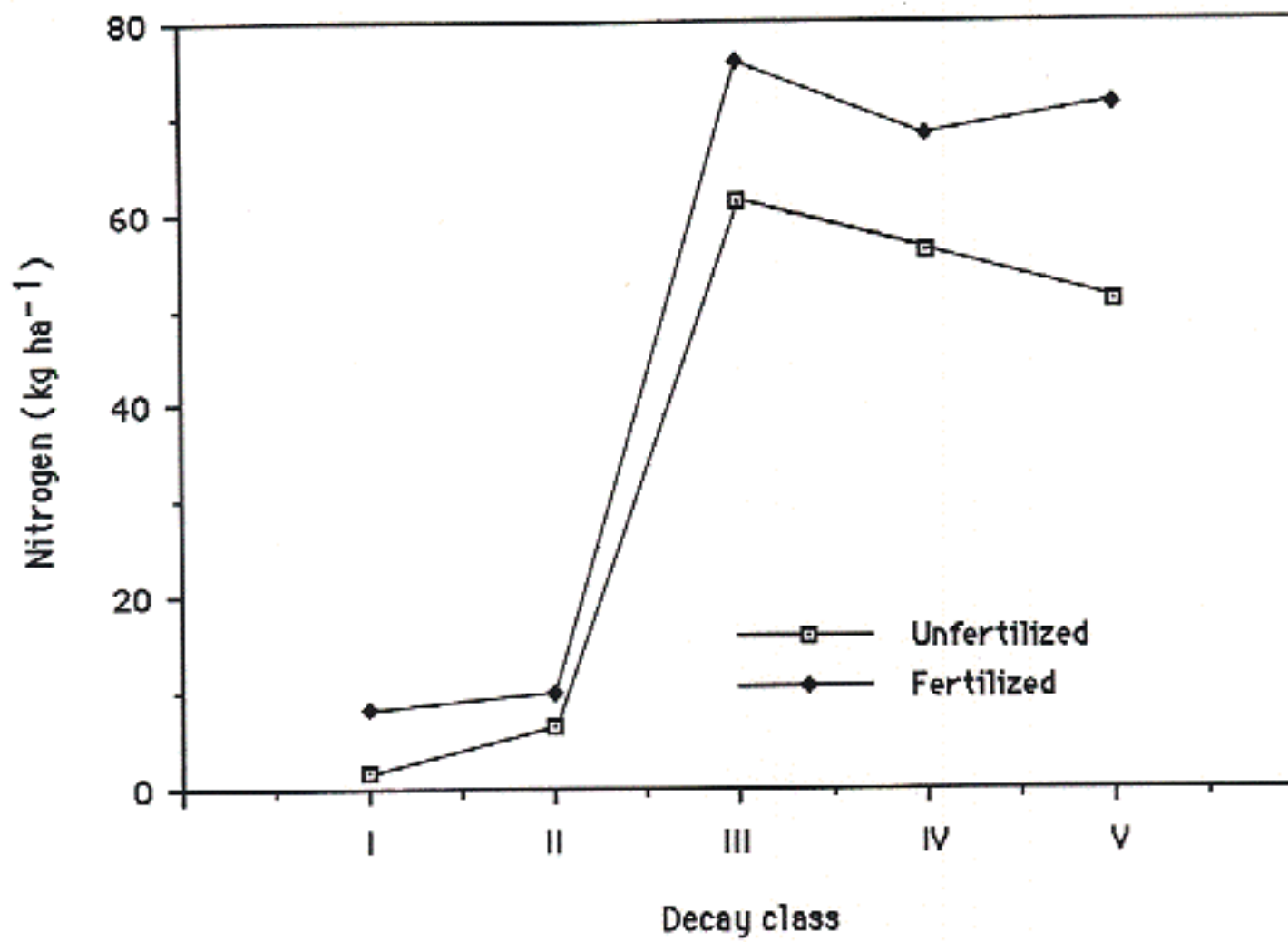


FIGURE 8: Mass of nitrogen (kg ha⁻¹) in woody debris by decay class on Douglas-fir plots fertilized with 0 (Unfertilized) and 448 (Fertilized) kg N ha⁻¹ up to 22 years earlier. (n=14).

Table 10. C:N ratio by decay class of woody debris - means with $n=8$, standard deviations in parentheses. Means within columns are not significantly different ($p > 0.05$). Means in decay classes within rows with different letters are significantly different ($p < 0.05$). Forest floor data from Edmonds and Hsiang, (1987).

Component	Treatment	Decay class					Average
		I	II	III	IV	V	
Wood	Control	481 a (184)	327 ab (132)	224 b (103)	227 b (52)	164 b (35)	284 (157)
	Fertilized	433 a (219)	325 b (121)	182 c (66)	178 c (37)	109 c (40)	245 (163)
Soil 0-15 cm.	Control						24 (8)
	Fertilized						24 (6)
Forest floor							41 (6)

Table 11. Mass of carbon and nitrogen in wood, soil and forest floor beneath second growth Douglas-fir stands. Differences between treatments within parameters are not significant ($p > 0.05$). Forest floor data from Edmonds and Hsiang, (1987).

Parameter									
Treatment (kg ha ⁻¹ N)	Carbon (Mg ha ⁻¹)			Nitrogen (kg ha ⁻¹)			C:N		
	0	448	% change	0	448	% change	0	448	% change
Component									
Wood	34.2	36.2	6	177	234	32	203	178	12
Soil	45.6	62.0	36	2164	2703	25	24	24	0
Forest floor	8.2	-	-	205	-	-	41	-	-
Total	88.0			2546					

was almost double ($34.2 - 36.2 \text{ Mg ha}^{-1}$) the $3.8 - 19 \text{ Mg ha}^{-1}$ range from a previous report (Cole et al., 1968).

The mass of N in fallen wood forms about the same proportion of the total as that in the forest floor (Table 11), but the dynamics and timing of its availability to the crop trees are likely to be very different because the C:N ratio is so much higher (Table 11). Although the 57 kg ha^{-1} (177 to 234 kg ha^{-1} or 32%) increase in combined N content of all wood following fertilization was not significant (Table 11), this increase indicates an overall trend towards continuing N immobilization in the decaying wood. The dynamics of this may be such that N is being both taken up and released from older wood where the C:N ratio is between 100 and 300 (Edmonds et al., 1989). Nitrogen mass appeared to peak in decay class III wood and decline slightly from there (Figure 8). The data for control plots in this study were very similar to values published previously by Harmon et al., 1986.

The increased, but variable, mass of N in large wood on fertilized sites was consistent with the finding by Heilman (1961) regarding the fate of N applied at $560\text{-}672 \text{ kg ha}^{-1}$ to Douglas-fir stands in western Washington. Nitrogen held in wood is likely to form an important reservoir in the longer term. The increase of 57 kg ha^{-1} of N in wood on fertilized sites represents 13% of the 448 kg ha^{-1} applied to the RFNRP plots. This compares with -6% to 8% of applied N reported by Heilman (1961) as being taken up by "old stumps,

debris etc." Heilman's debris component did not include buried (class V) logs, which contained 30% of the N in wood on my sites, making the two sets of results quite similar.

Woody biomass on and in the forest floor is thus likely to have an important influence on long-term site productivity for two reasons. First, it comprises a greater carryover of biomass and N from the previous stand than was previously appreciated for second-growth sites. Second, its long residence time on the forest floor, coupled with the retention of a significant mass of N right into decay class V, implies that it could provide N to the ecosystem for over a century into the future, with attendant benefits for long-term site productivity.

Carbon and Nitrogen in Soil

Carbon

Soil C concentrations ranged from 2.03% to 8.96% (Table IV, Appendix). There was a trend towards a higher average level of C on fertilized sites but the differences were not statistically significant. Average mass of C was 62.0 Mg ha^{-1} in fertilized soil and 45.6 Mg ha^{-1} in unfertilized soil, although this difference was not significant (Table 8). Average mass of C for the total soil depth (range 4 to 184 cm, average 116 cm) over 120 control plots sampled at the time of plot establishment 22-23 yr ago was 143.5 Mg ha^{-1} (Edmonds and Hsiang, 1987).

Increases in N applied as fertilizer or by biological fixation have often led to increased soil C levels (Kraemer and Hermann, 1979; Binkley, 1983; Baker et al., 1986; Nohrstedt et al., 1989) and this was also demonstrated in this study. This has positive implications for long-term site productivity (Edmonds, 1990; Jurgensen et al., 1990) and may be an important mechanism for C sequestration, with attendant benefits as a sink for excess atmospheric C (Harmon et al., 1990; Post et al., 1990).

Nitrogen

Soil N content was generally higher on fertilized sites, but the differences were not statistically significant. (Table IV, Appendix). Calculated average mass of N in fertilized soil was 2703 kg ha⁻¹, compared to 2164 kg ha⁻¹ for untreated soil but this difference was not significant (Table 9). These values are reasonable compared to the average N mass of 7106 kg ha⁻¹ (range 245 to 21,432 kg ha⁻¹) for the total soil depth reported by Edmonds and Hsiang (1987) from 120 RFNRP control plots sampled at the time of establishment.

Carbon to Nitrogen Ratio

There were no consistent trends in C:N ratios in soils (Table IV, Appendix). The average value was 24 for both fertilized and unfertilized soils (Table 10), which is similar to the value of 27 reported by Edmonds and Hsiang (1987) for samples from all control plots at 120 RFNRP installations at establishment.

Synthesis on Site Carbon and Nitrogen Content

There was a significant increase in the N concentration of wood in decay classes IV and V (Table III, Appendix) and an accompanying trend (although statistically insignificant due to the high variability in wood biomass) to increased mass of N per hectare in decay classes III through V following fertilization (Table 9). There was also a trend for increased mass of C (Table 8) and N (Table 9) in the soil 23 years after fertilization, although the variance once again rendered this statistically insignificant. There were, however, no significant relationships between mass of N in the soil or wood and tree volume response. This means that 23 years after fertilization of a site there was increased storage of N in soil or wood or both even though there had been no response to the fertilizer at the time of application. Thus, even though a response to applied N did not occur in the present crop, due to factors other than N limiting tree growth, at least some of the N remains in the ecosystem and has been accompanied by an increase in soil C.

A possible explanation for increased soil C mass without a corresponding increase in above-ground production to provide increased litterfall has been offered by Nohrstedt et al (1989). They felt that the increase in soil C could be due to reduced microbial activity per unit of C (ie., decomposition).

Woody Debris and Growth Response

Relative net periodic annual increment responses for stands sampled in my study ranged from 0 to 66% (Table 12). Linear regression of the relative volume growth response of trees against wood biomass did not show any significant relationships with either the total biomass of wood in decay classes III through V or with the biomass in each of these decay classes alone (Figure 9). There was a non-significant upward trend in each decay class whereby response was greater when more fallen wood was present. This trend was clearest with decay class V wood, but still not statistically significant. This was consistent with the expectation that sites with a higher load of wood would have a higher N demand leading to higher response from the trees when this demand was satisfied by fertilization. Only analyses involving wood in decay classes equal to or above III were considered valid since all fine wood and large wood in decay classes I and II was likely to have fallen to the ground since the response experiments were conducted (Means et al., 1985).

Linear regression of relative volume growth response against wood C:N ratio did not show any significant relationships with either the overall C:N ratio for all wood in decay classes III through V or with the C:N ratio in each of these decay classes alone (Figure 10). There was a non-significant upward trend in each class implying more response to applied N with higher C:N ratio. Linear regression did not show any significant relationship between percentage growth

Table 12. Relative net volume periodic annual increment response after 8 yr for second-growth Douglas-fir stands fertilized with 448 kg N ha⁻¹ as urea. Data from RFNRP - SMC database.

Province	Installation	Response (%)
1	1	58
	5	59
	59	21
	78	0.4
	101	34
2	16	6
	33	35
	43	66
	57	8
	98	22
4	20	43
	53	8
	77	6
	81	38

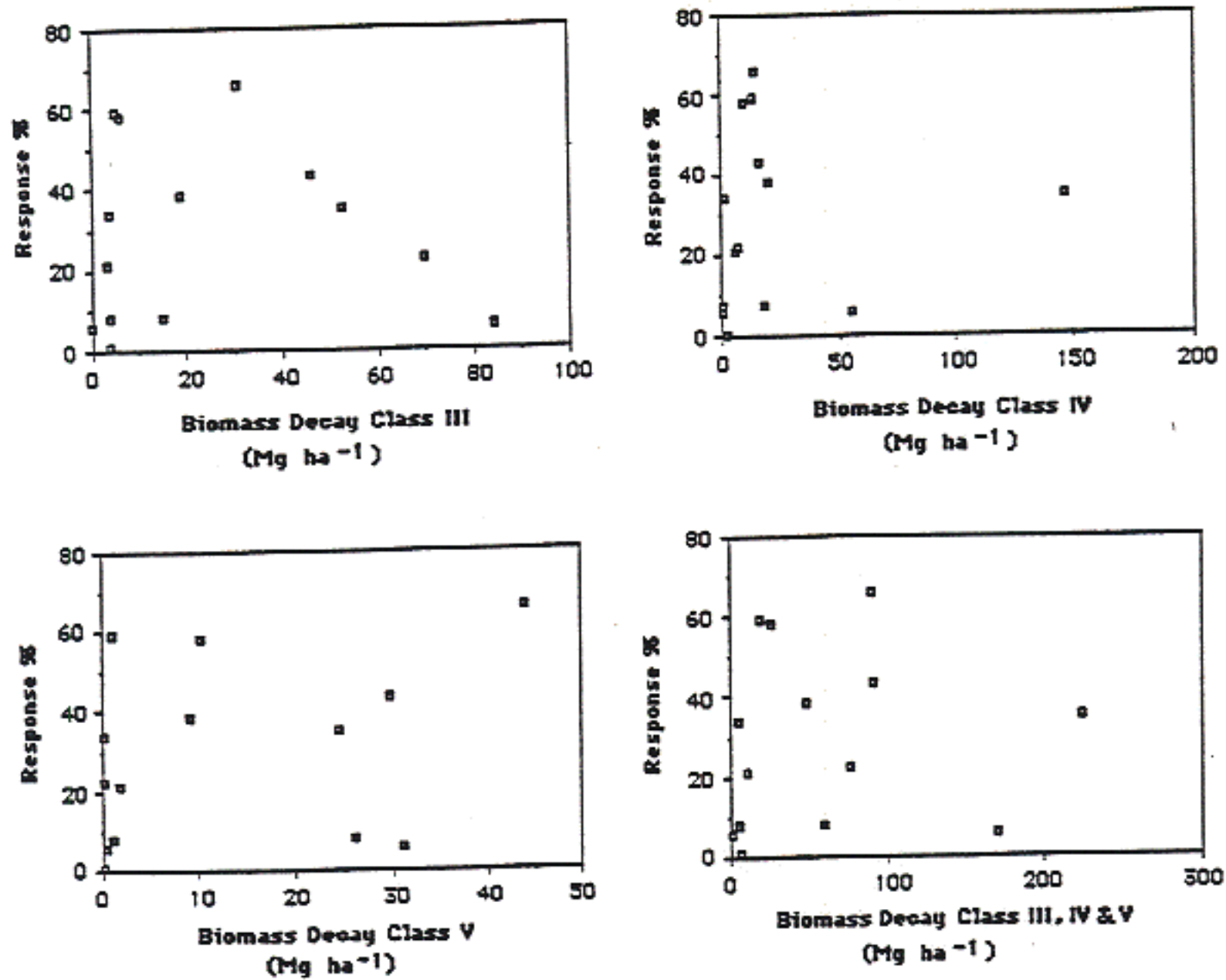


FIGURE 9: Relative net volume periodic annual increment response of second-growth Douglas-fir at 8 yr, plotted against woody debris biomass on sites fertilized with 448 kg N ha^{-1} . ($n=14$).

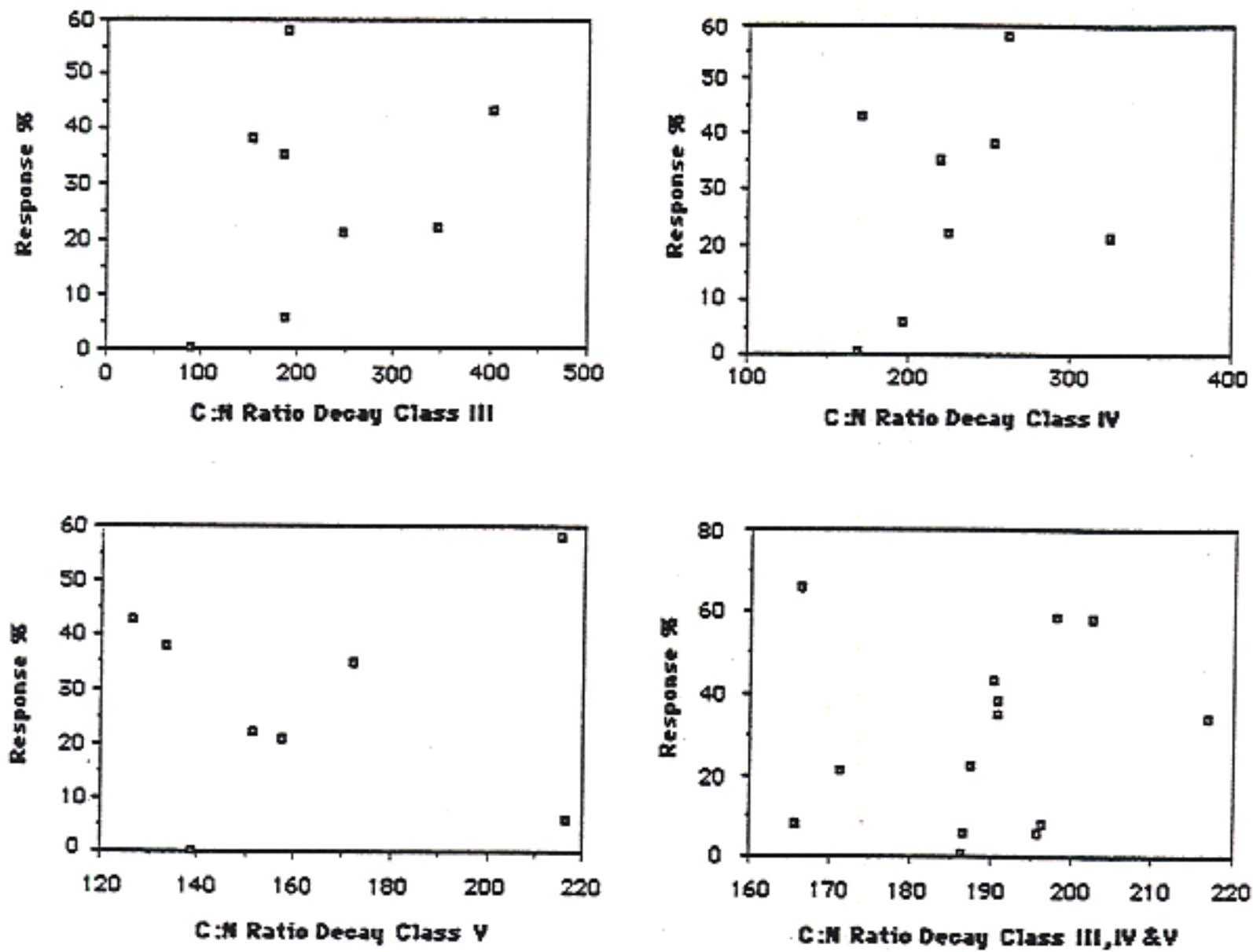


FIGURE 10: Relative net volume periodic annual increment response of second-growth Douglas-fir at 8 yr, plotted against woody debris C:N ratio on sites fertilized with 448 kg N ha⁻¹. (n=14).

response of trees and soil C:N ratio, although the trend was slightly upwards implying more response to applied N at higher C:N ratios. Since fertilization did not significantly change the mass of N in the wood component and this change was only 11% of the change in the mass of N in the soil component, the change in the wood N could not be expected to be a useful predictor of tree growth.

Thus it was not surprising that there was no significant relationship between the biomass or N content of the fallen wood and crop tree response. This suggests that the large pool of C in the logs, with a high C:N ratio, was not sufficient to have a negative affect on tree response to applied N fertilizer. Thus the positive benefits of fallen wood (Edmonds, 1990; Franklin, 1992) could be realized without interfering with the response of the crop trees to the applied fertilizer, at least in young, unthinned stands.

It was quite possible that the amount of N taken up by the fallen wood was not significant in terms of the total applied and the amount that was utilized by the living trees. The average growth response of unthinned Douglas-fir to 448 kg N ha^{-1} was only marginally greater than the response to 224 kg N ha^{-1} after four years ($4.14 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ compared to $3.65 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$; Peterson and Heath, 1986; Stegemoeller and Chappell, 1990). Hence the 448 kg N ha^{-1} applied to unthinned stands may have been more than the trees could utilize effectively. Consequently, the 57 kg N ha^{-1} taken up by fallen wood may have simply been part of what was in excess

to the requirements of the trees. This would then account for the lack of a relationship between the quantity or nutrient content of fallen wood and tree growth. A logical extension of this work would be to examine the relationship between wood parameters and tree growth response on sites fertilized at the application rate of 224 kg N ha^{-1} normally used in commercial operations. The other extension would be to examine the same relationship on thinned stands where up to 60% of growth response was predicted by the C:N ratio of the forest floor when 448 kg ha^{-1} of N was applied (Edmonds and Hsiang, 1987). The role of fallen wood in site nutrient dynamics may be quite critical on these sites where either the amount of applied N is lower, or the trees remaining after thinning are more able to respond.

The overall C:N ratio of all wood and C:N ratios of wood in each decay class were also unsuccessful predictors of tree response to applied N. The change in C:N ratio following fertilizer application was only 12% and this was not significant (Table 11) hence this ratio could not be expected to be a useful predictor. Unless the C:N ratios of decaying wood are normally close to the level at which N immobilization switches to N release, then the ratio is unlikely to predict response to applied N. This may explain why the C:N ratio of the forest floor before fertilization was a useful predictor (Edmonds and Hsiang, 1987) while the same ratio for soil was not. The forest floor is normally at a C:N ratio of about 40, which is closer to the level where a switch from immobilization to release occurs so that it offers better

predictive value because sites with a starting ratio below about 30 respond markedly less than those above 40 (Edmonds and Hsiang, 1987). The forest floor C:N may thus be more sensitive to the available N status as it affects tree response.

Measurement of the C:N ratio of the forest floor on the fertilized RFNRP sites may cast useful light on why forest floor C:N ratio does have predictive value. It is also possible that the necessity in this study to sample sites from a range of site index classes may have confounded any potential relationship between wood C:N ratio and tree response. Edmonds and Hsiang (1987) found that response was best predicted by the composite soil C:N ratio while forest floor C:N ratio was a better predictor on site classes 1 and 2 than on site classes 3, 4 and 5. Unfortunately my sample size was too small to stratify the data by site index, but this may be a useful avenue for future research.

The greater surface area of forest floor material is also more likely to be intimately in contact with the ground than logs of an equivalent mass. Therefore changes in the C:N status of the forest floor are more likely to reflect the true N availability of the substrate in contact with the tree roots. Similarly, if the logs are not evenly spread over the surface, as the forest floor material is, then their "zone of influence" may include few tree roots and have little impact on tree nutrient uptake. A useful extension of these preliminary studies might be to conduct a manipulative experiment to compare the

effects between sites with a quantity of wood concentrated into a few large logs, sites with an equal amount evenly dispersed as a uniform layer and sites from which the large wood had been removed.

Planar Intercept versus Visual Estimation of Biomass

There was a significant relationship between the biomass calculated from the planar intercept measurements and the visual estimates of biomass based on the stereo photo series (Figure 11). The planar intercept method is the means used to obtain the actual values ascribed to the photo series (Ottmar et al., 1990) so this result is not unexpected. Since this result occurred even though I had no previous experience with this visual estimation method, it may be a useful tool if estimates of fallen wood biomass are required from many plots in the future. Improvements in reliability with increasing user experience are apparently the norm with this methodology (Maxwell and Ward, 1976).

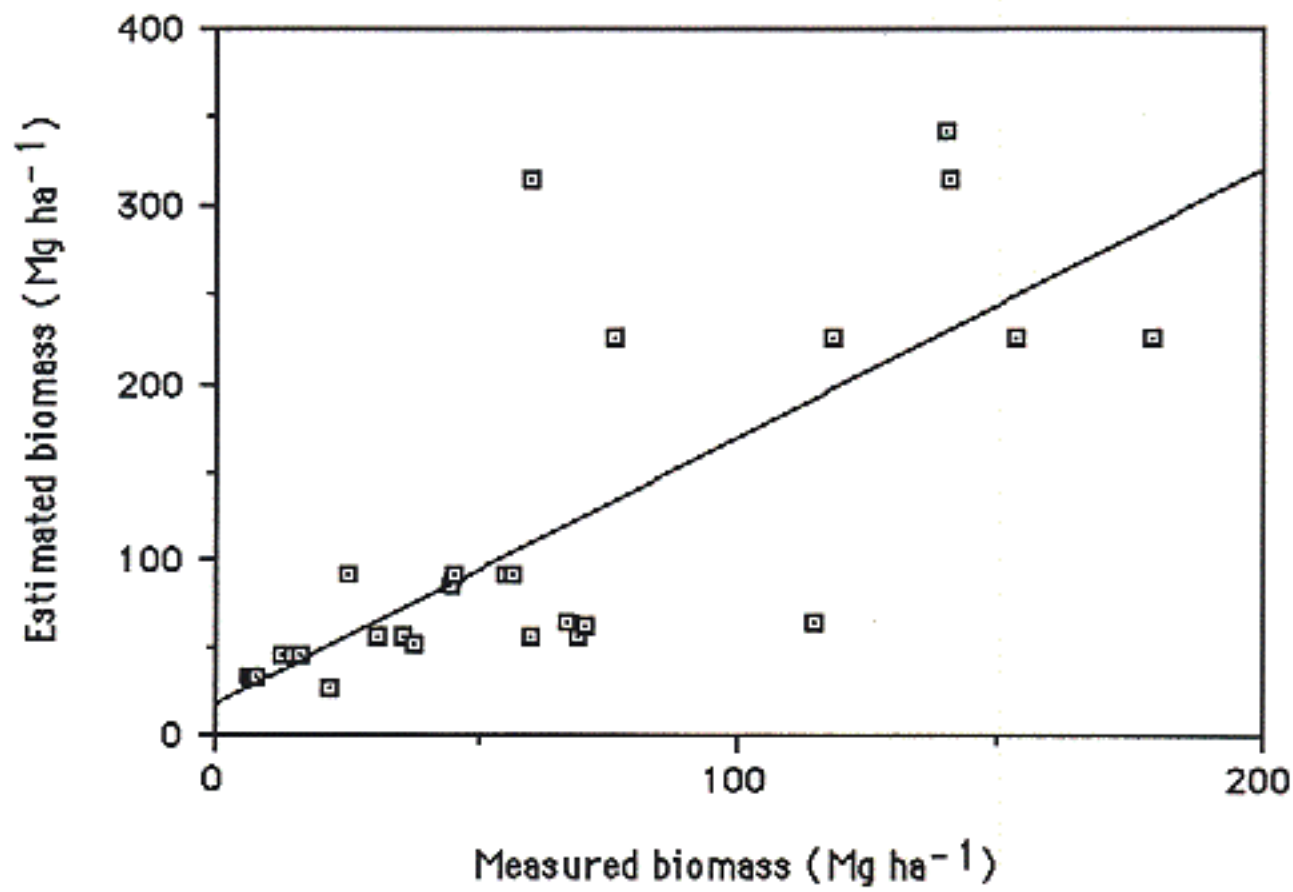


FIGURE 11: Linear regression of estimated against measured biomass of all woody debris in second-growth Douglas-fir stands. (n=28; $y=18.603 + 1.517x$; $r=0.729$; $p<0.001$).

CONCLUSIONS

1. The biomass of wood beneath second-growth Douglas-fir stands averaged 76.3 Mg ha^{-1} (range 9.8 to 234.2 Mg ha^{-1}) and did not differ significantly between unfertilized plots and plots fertilized with 448 kg N ha^{-1} . Fine wood $<76\text{mm}$ diameter made up 10% of this biomass and 79% was wood in decay classes III to V, which had largely been carried over from the previous stand.
2. The total biomass of wood was about twice as much as previous reports have indicated for second rotation forests. The importance attributed in the literature to carryover from the previous stand was confirmed. There was no evidence for increased productivity on sites with higher accumulations of wood on the ground.
3. The mass of C in wood averaged 32.5 Mg ha^{-1} and did not differ between fertilizer treatments. This mass represented 32% of the combined amount of C on the ground and in the top 15 cm of soil and exceeded the amount in the forest floor material by four times.
4. The N concentration in wood on fertilized sites consistently exceeded the concentration on control sites. These differences were significant in decay classes IV and V. The N concentration in older decay classes was significantly higher than in younger classes within treatments.

5. The mass of N in large (>76 mm diameter) wood averaged 176.6 kg ha⁻¹ on unfertilized sites and 233.9 kg ha⁻¹ on fertilized sites 23 years after application. Although these differences were not significant due to the wide variations in wood biomass, woody biomass was clearly a significant storage site for N following fertilization. The mass of N in wood was about the same as that in the forest floor, with each of these comprising about 9% of the total laying on and in the top 15 cm of soil.

6. Average C:N ratio of wood dropped from a high of 481 in decay class I on the unfertilized sites to 109 in decay class V on the fertilized sites. There was a significant change in the C:N ratio around decay classes II and III. The C:N ratio of the wood was much higher than the values of 24 for the soil and 41 for the forest floor on these same sites, suggesting that the store of N in the wood will be retained for a longer period and play a role over longer cycle times.

7. Woody debris is likely to have an important role in retaining applied fertilizer N on-site in second-growth Douglas-fir forests. Coupled with the contribution to the organic C store, this suggests that wood carried over from the previous stand may be important to the long term productivity of these sites.

8. There was a trend to higher N and C levels in soils that had been fertilized. This suggests that fertilization with N could contribute to the fixation of C in forest soils as well as improving the productivity of trees. This may have important implications for offsetting increases in global atmospheric C levels.

9. Biomass of fallen wood beneath second-growth Douglas-fir was not a predictor of response to applied N. This wood, however, contained a significant pool of N, which increased by 57 kg ha^{-1} (32%) after N fertilizer was applied to the site, without interfering with the volume response of the crop trees.

BIBLIOGRAPHY

- Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. *Ecol. Bull.*, 25, 180-192.
- Axelsson, B. 1985. Increasing forest productivity and value by manipulating nutrient availability. In Ballard, R., Farnum, P., Ritchie, G. A. and Winjum J. K. (Eds). *Forest potentials - productivity and value* (pp. 5-38). Tacoma, Washington: Weyerhaeuser Corp., Centralia, Washington.
- Baker, T. G., Oliver, G. R. and Hodgkiss, P. D. 1986. Distribution and cycling of nutrients in *Pinus radiata* as affected by past lupin growth and fertiliser. *For. Ecol. Manage.*, 17, 169-187.
- Ballard, R. and Lea, R. 1986. Foliar analysis for predicting quantitative fertilizer response. The importance of site and stand variables to the interpretation. In Gessel, S. P. (Ed). *Forest Site and Productivity*. Boston, Massachusetts: Martin Nijhoff.
- Binkley, D. 1983. Ecosystem production in Douglas-fir plantations: Interactions of red alder and site fertility. *For. Ecol. Manage.*, 5, 215-227.
- Binkley, D. 1986. *Forest Nutrition Management*. New York: John Wiley.
- Blake, J. I., Chappell, H. N., Bennett, W. S., Webster, S. R. and Gessel, S. P. 1990. Douglas-fir growth and foliar nutrient responses to nitrogen and sulfur fertilization. *Soil Sci. Soc. Am. J.*, 54, 257-262.
- Bosatta, E. and Agren, G. I. 1985. Theoretical analysis of decomposition of heterogeneous substrates. *Soil Biol. Biochem.*, 17, 601-610.
- Bosatta, E. and Staaf, H. 1982. The control of nitrogen turnover in forest litter. *Oikos*, 39, 143-151.

- Bremner, J. M. 1965. Total nitrogen. *In* Black, C. A. (Ed). Methods of Soil Analysis. Madison, Wisconsin: American Society of Agronomists.
- Bremner, J. M. and Mulvaney, C. S. 1982. Total nitrogen. *In* Page, A. L., Miller, R. H. and Keeney, D. R. (Eds). Methods of Soil Analysis. Part 2 (pp. 595-624). Madison, Wisconsin: American Society of Agronomy.
- Brown, J. K. 1971. A planar intersect method for sampling fuel volume and surface area. *For. Sci.*, 17, 96-102.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. Gen. Tech. Rep. No. INT-16. USDA For. Serv. Intermountain Forest and Range Res. Exp. Stn. Ogden, Utah.
- Chapin, F. S., Vitousek, P. M. and Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. *Am. Nat.*, 127, 48-58.
- Chappell, H. N., Cole, D. W., Gessel, S. P. and Walker, R. B. 1991. Forest fertilization research and practice in the Pacific Northwest. *Fert. Res.*, 27, 129-140.
- Chappell, H. N., Omule, S. A. Y. and Gessel, S. P. 1992. Fertilization in Coastal Northwest forests: Using response information in developing stand-level tactics. *In* Chappell, H. N., Weetman, G. F. and Miller, R. E. (Eds). Forest fertilization: Sustaining and improving nutrition and growth of western forests. Institute of Forest Resources Contrib. No. 73. College of Forest Resources, University of Washington, Seattle.
- Christy, E. J. and Mack, R. N. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *J. Ecol.*, 72, 75-91.
- Cole, D. W., Ford, E. D. and Turner, J. 1990. Nutrients, moisture and productivity of established forests. *Forest Ecol. Manage.*, 30, 283-299.

- Cole, D. W., Gessel, S. P. and Dice, S. F. 1968. In Young, H. E. (Ed). 13th Annual Meeting of the American Association for the Advancement of Science (pp. 197-233). University of Maine Press.
- Collins, B. D., Dunne, T. and Lehre, A. K. 1983. Erosion of tephra-covered hillslopes north of Mt. St. Helens. *Z. Geomorphol.*, 46, 103-121.
- Dell, J. D. and Ward, F. R. 1971. Logging residues on Douglas-fir region clearcuts - weights and volumes. Res. Pap. No. PNW-115. USDA For. Serv. Forest and Range Res. Stn. Portland, Oregon.
- Duzan, H. W., Allen, H. L. and Ballard, R. 1982. Predicting fertilizer response in established loblolly pine plantations with basal area and site index. *South. J. App. For.*, 6, 15-19.
- Edmonds, R. L. (Ed). 1982. Analysis of Coniferous Forest Ecosystems in the Western United States. US/IBP Synthesis Series, Vol 14. Stroudsburg, Pennsylvania: Hutchinson Ross Publishing.
- Edmonds, R. L. 1979. Litter decomposition and nutrient release in Douglas-fir needle litter in relation to stand development. *Can. J. For. Res.*, 9, 132-140.
- Edmonds, R. L. 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. *Can. J. For. Res.*, 10, 327-337.
- Edmonds, R. L. 1984. Long-term decomposition of and nutrient dynamics in Pacific silver fir needles in western Washington. *Can. J. For. Res.*, 14, 395-400.
- Edmonds, R. L. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest eco-systems in Washington, U.S.A. *Can. J. For. Res.*, 17, 499-509.

- Edmonds, R. L. 1990. Organic matter decomposition in western United States forests. *In* Proc. Symposium on Management and Productivity of Western Montane Forest Soils (pp. 118-128). Boise, Idaho: Intermountain Research Station, U. S. Forest Service, Ogden, Utah.
- Edmonds, R. L., Binkley, D., Feller, M. C., Sollins, P., Abee, A. and Myrold, D. 1989. Nutrient cycling: Effects on productivity of Northwest forests. *In* Perry, D. A., Meurisse, R., Thomas, B., Miller, R., Boyle, J., Means, J., Perry, C. R. and Powers, R. F. (Eds). *Maintaining the Long-term Productivity of Pacific Northwest Forest Ecosystems* (pp. 17-35). Portland, Oregon: Timber Press.
- Edmonds, R. L. and Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. *Can. J. For. Res.*, 19, 853-859.
- Edmonds, R. L. and Hsiang, T. 1987. Forest floor and soil influence on response of Douglas-fir to urea. *Soil Sci. Soc. of Am. J.*, 51, 1332-1337.
- Eno, C. F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Sci. Soc. Am. Proc.*, 24, 277-279.
- Erickson, H. E., Edmonds, R. L. and Peterson, C. E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Can. J. For. Res.*, 15, 914-921.
- Everard, J. 1973. Foliar analysis sampling methods: Interpretation and application of results. *Quart. J. For.*, 67, 51-66.
- Frankland, J. C., Hedger, J. N. and Swift, M. J. (Eds) 1982. *Decomposer Basidiomycetes: Their Biology and Ecology*. London: Cambridge University. Press.
- Franklin, J. F. 1992. Scientific basis for new perspectives in forests and streams. *In* Naiman, R. J. (Ed). *Watershed Management: Balancing Sustainability and Environmental Change*. Springer Verlag, New York.

- Franklin, J. F. and Dyrness, C. T. 1988. Natural Vegetation of Oregon and Washington. Corvallis, Oregon: Oregon State University Press.
- Furniss, R. L. and Carolin, V. M. 1977. Western forest insects. Misc. Publ. No. 1339. USDA For. Serv. Washington, D. C.
- Gessel, S. P., Miller, R. E. and Cole, D. W. 1990. Relative importance of water and nutrients on the growth of coast Douglas-fir in the Pacific Northwest. *Forest Ecol. and Manage.*, 30, 327-340.
- Gessel, S. P., Stoate, T. N. and Turnbull, K. J. 1969. The growth behavior of Douglas-fir with nitrogenous fertilizer in western Washington. Institute of Forest Products Contribution No. 7. College of Forest Resources, University of Washington, Seattle, Washington.
- Gessel, S. P. and Walker, R. B. 1956. Height growth response of Douglas-fir to nitrogen fertilization. *Soil Sci. Soc. Am. Proc.*, 20, 97-100.
- Graham, R. L. and Cromack Jr, K. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.*, 12, 511-521.
- Grier, C. C. 1978. A *Tsuga heterophylla*-*Picea sitchensis* ecosystem of coastal Oregon: Decomposition and nutrient balances of fallen logs. *Can. J. For. Res.*, 8, 198-206.
- Grier, C. C., Cole, D. W., Dyrness, C. T. and Fredriksen, R. L. 1974. Nutrient cycling in 37- and 450-year-old Douglas-fir ecosystems. In Waring, R. H. and Edmonds, R. L. (Eds). Integrated research in the coniferous forest biome. *Coniferous Forest Biome Bull.* No. 5, pp 21-34. University of Washington, Seattle.
- Grier, C. C. and Logan, R. S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. *Ecol. Monogr.*, 47, 373-400.

- Grier, C. C. and McColl, J. G. 1971. Forest floor characteristics within a small plot in Douglas-fir in western Washington. *Soil Sci. Soc. Am. Proc.*, 35, 988-991.
- Harmon, M. E., Ferrell, W. K. and Franklin, J. F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science*, 247, 699-702.
- 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 Jr, K. and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15, 133-302.
- Harmon, M. J. and Franklin, J. F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology*, 70, 48-59.
- Harvey, A. E., Meurisse, R. T., Geist, J. M., Jurgensen, M. F., McDonald, G. I., Graham, R. T. and Stark, N. 1989. Managing productivity processes in the Inland Northwest - Mixed conifers and pines. *In* Perry, D. A., Meurisse, R., Thomas, B., Miller, R., Boyle, J., Means, J., Perry, C. R. and Powers, R. F. (Eds). *Maintaining the Long-term Productivity of Pacific Northwest Forest Ecosystems* (pp. 164-184). Portland, Oregon: Timber Press.
- Hazard, J. W. and Peterson, C. E. 1984. Objectives and analytical methods of the Regional Forest Nutrition Project. Contribution No.53. Inst. of Forest Resources, University of Washington, Seattle.
- Heilman, P. E. 1961 Effects of Nitrogen Fertilization on the Growth and Nitrogen Nutrition of Low-site Douglas-fir stands. PhD, University of Washington, Seattle, Washington.
- Howard, J. O. 1971. Forest products residues - their volume, use and value. 1. Volume of residues from logging. *For. Ind.*, 98, 22-23.

- Howard, J. O. 1973. Logging residue in Washington, Oregon and California - volume and characteristics. Res. Bull. No. PNW-44. USDA For. Serv. Forest and Range Experiment Station, Portland, Oregon.
- Howard, J. O. 1981. Ratios for estimating logging residue in the Pacific Northwest. Res. Pap. No. PNW-288. USDA For. Serv. Forest and Range Experiment Station, Portland, Oregon.
- Ingestad, T. 1974. Towards optimum nutrition. *Ambio*, 3, 49-54.
- Ingestad, T. 1981. Nutrition and growth of birch and grey alder seedlings in low conductivity solutions and at varied rate of nutrient addition. *Physiol. Plant.*, 52, 454-466.
- Ingestad, T. 1982. Addition rate and concentration. Relative addition rate and external concentration; driving variables used in plant nutrition research. *Plant Cell and Environ.*, 5, 443-453.
- Jurgensen, M. F., Harvey, A. E., Graham, R. T., Larsen, M. J., Tonn, J. R. and Page-Dumroese, S. 1990. Soil organic matter, timber harvesting and forest productivity in the Inland Northwest. In Lacate, D. S., Gessel, S. P., Weetman, G. F. and Powers, R. F. (Eds). *Sustained Productivity of Forest Soils. Proc. 7th Nth Am. Forest Soils Conf.* (pp. 392-415). Vancouver, Canada: University of British Columbia.
- Keeney, D. R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. *Forest Sci.*, 26, 159-171.
- Keeney, D. R. and Bremner, J. M. 1966. Comparison and evaluation of laboratory methods of obtaining an index of soil nitrogen availability. *Agron. J.*, 58, 498-503.
- King, J. E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser For. Pap. No. 8. Weyerhaeuser Forestry Research Centre, Centralia, Washington.

- Kjeldahl, J. 1883. Neue methode zur bestimmung des stickstoffs in organischen korpen. *Z. Anal. Chem.*, 22, 366-382.
- Kraemer, J. F. and Hermann, R. K. 1979. Broadcast burning: 25-year effects on forest soils in the western flanks of the Cascade Mountains. *For. Sci.*, 25, 427-439.
- Lambert, R. C., Lang, G. E. and Reiners, W. A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology*, 61, 1460-1473.
- Lang, G. E. and Forman, R. T. T. 1978. Detritus dynamics in a mature oak forest: Hutchenson Memorial Forest, New Jersey. *Ecol.*, 61, 1460-1473.
- Larsen, M. J., Jurgensen, M. F. and Harvey, A. E. 1978. Nitrogen fixation associated with wood decayed by some common fungi in western Montana. *Can. J. For. Res.*, 8, 341-345.
- Lea, R. and Ballard, R. 1982a. Predicting loblolly pine response from N fertilizer using soil-N availability indices. *Soil Sci. Soc. Am. J.*, 46, 1096-1099.
- Lea, R. and Ballard, R. 1982b. Relative effectiveness of nutrient concentrations in living foliage and needle fall at predicting response of loblolly pine to N and P fertilization. *Can. J. For. Res.*, 12, 713-717.
- Leaf, A. L. 1973. Plant analysis as an aid in fertilizing forests. In Walsh, L. and Beaton, J. (Eds). *Soil Testing and Plant Analysis* (pp. 427-457). Madison, Wisconsin: Soil Science Society of America.
- Loneragan, J. F. 1968. Nutrient requirements of plants. *Nature*, 220, 366-382.

- Long, J. N. 1982. Productivity of western coniferous forests. In Edmonds, R. L. (Ed). Analysis of Coniferous Forest Ecosystems in the Western United States. US/IBP Synthesis Series. Vol. 14 (pp. 419). Stroudsburg, Pennsylvania: Hutchinson Ross Publishing.
- Lutz, H. J. and Chandler, R. F. 1946. Forest Soils. New York: John Wiley and Sons.
- Martin, R. E. and Brackebusch, A. P. 1974. Fire hazard and conflagration prevention. In Cramer, O. P. (Ed). Environmental Effects of Forest Residues Management in the Pacific Northwest (pp. G1-G27). Portland, Oregon: USDA For. Serv. Gen. Tech. Rep. PNW-24.
- Maser, C. and Trappe, J. M. 1984. The Seen and Unseen World of the Fallen Tree. Gen. Tech. Rep. No. PNW-164. USDA For. Serv. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Maxwell, W. G. and Ward, F. R. 1976. Photo series for quantifying forest residues in the coastal Douglas-fir-hemlock type, coastal Douglas-fir-hardwood type. Gen. Tech. Rep. No. PNW-51. USDA For. Serv. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Means, J. E., Cromack Jr., K. and MacMillan, P. C. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. Can. J. For. Res., 15, 1092-1098.
- Miller, H. G. 1979. The nutrient budgets of even-aged forests. In Malcolm, D. C., Atterson, J. and Ford, E. D. (Eds). The Ecology of Even-aged Forest Plantations (pp. 221-256). Cambridge: Institute of Terrestrial Ecology.
- Miller, R. E. and Bigley, R. E. 1990. Effects of Douglas-fir logging slash on stand development and site productivity. In Gessel, S. P., Lacate, D. S., Weetman, G. F. and Powers, R. F. (Eds). Sustained Productivity of Forest Soils, (pp. 362-376). Vancouver, Canada: University of British Columbia.

- Nelson, D. W. and Sommers, L. E. 1982. Total carbon, organic carbon and organic matter. In Page, A. L., Miller, R. H. and Keeney, D. R. (Eds). *Methods of Soil Analysis. Part 2* (pp. 539-579). Madison, Wisconsin: American Society of Agronomy.
- Nohrstedt, H., Arnebrant, K., Baath, E. and Soderstrom, B. 1989. Changes in carbon content, respiration rate, ATP content and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. *Can. J. For. Res.*, 19, 323-328.
- Oliver, C. D. and Larson, B. C. 1990. *Forest Stand Dynamics*. New York: McGraw Hill.
- Ottmar, R. D., Hardy, C. C. and Vihnanek, R. E. 1990. Stereo photo series for quantifying forest residues in the Douglas-fir-hemlock type of the Willamette National Forest Gen. Tech. Rep. No. PNW-GTR-258. USDA For. Serv. Pacific Northwest Res. Stn. Portland, Oregon.
- Peterson, C. E. and Heath, L. S. 1986. Volume growth and volume growth response after fertilization of unthinned Douglas-fir stands. Regional Forest Nutrition Research Project Report No. 6. College of Forest Resources, University of Washington, Seattle, Washington.
- Peterson, C. E., Ryan, P. J. and Gessel, S. P. 1984. Response of northwest Douglas-fir stands to urea: Correlations with forest soil properties. *Soil Sci. Soc. of Am. J.*, 48, 162-169.
- Post, W. M., Peng, T.-H., Emmanuel, W. R., King, A. W., Dale, V. H. and DeAngelis, D. L. 1990. The global carbon cycle. *American Scientist*, 78, 310-326.
- Powers, R. F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. *Soil Sci. Soc. Am. J.*, 44, 1314-1320.
- Prescott, C. E., Corbin, J. P. and Parkinson, D. 1992. Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. *Plant and Soil*, 143, 1-10.

- Radwan, M. A. and DeBell, D. S. 1980. Site index, growth, and foliar chemical composition relationships in western hemlock. *Forest Science*, 26, 283-290.
- Shumway, J. S. and Atkinson, W. A. 1977. Measuring and predicting growth response in unthinned stands of Douglas-fir by paired tree analysis and soil testing. DNR Note No. 15. Wash. State Dept. Natural Resources, Olympia, Washington.
- Shumway, J. S. and Atkinson, W. A. 1978. Predicting nitrogen fertilizer response in unthinned stands of Douglas-fir. *Commun. Soil Sci. Plant Anal.*, 9, 529-539.
- Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.*, 12, 18-28.
- Spies, T. A., Franklin, J. F. and Thomas, T. B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology*, 69, 1689-1702.
- Stegemoeller, K. A. and Chappell, H. N. 1990. Growth and response of unthinned Douglas-fir stands to single and multiple applications of nitrogen. *Can. J. For. Res.*, 20, 343-349.
- Steinbrenner, E. C. 1979. Forest soil productivity relationships. In Heilman, P. E., Anderson, H. W. and Baumgartner, D. M. (Eds). *Forest Soils of the Douglas-fir Region* (pp. 199-230). Pullman, Washington: Washington State University.
- Swanson, F. J., Gregory, S. V., Sedell, J. R. and Campbell, A. G. 1982. Land-water interactions: The riparian zone. In Edmonds, R. L. (Ed). *Analysis of Coniferous Forested Ecosystems in the Western United States* (pp. 267-291). Stroudsburg, Pennsylvania: Hutchinson Ross.

- Turnbull, K. J. and Peterson, C. E. 1976. Analysis of Douglas-fir growth response to nitrogenous fertilizer (Part I: Regional Trends). Contribution No. 13. Institute of Forest Products, College of Forest Resources, University of Washington, Seattle, Washington.
- Turner, J. and Long, J. N. 1975. Accumulation of organic matter in a series of Douglas-fir stands. *Can J. For. Res.*, 5, 681-690.
- Turner, J., Lambert, M. J. and Gessel, S. P. 1988. Nitrogen requirements in young Douglas-fir of the Pacific Northwest. *Fert. Res.*, 15, 173-179.
- Van Cleve, K. and Moore, T. A. 1978. Cumulative effects of nitrogen, phosphorus, and potassium fertilizer additions on soil respiration, pH and organic content. *Soil Sci. Soc. Am. J.*, 42, 121-124.
- van den Driessche, D. 1981. Estimating potential response to fertilizer based on tree tissue and litter analysis. In Gessel, S. P., Kenady, R.M. and Atkinson, W. A. (Eds). *Proc. Forest Fertilization Conf.* (pp. 214-220). Union, Washington: Contrib. 40. Inst. For. Res., Coll. For. Res., University of Washington, Seattle, Washington.
- van Wagner, C. E. 1968. The line intersect method for forest fuel sampling. *For. Sci.*, 14, 20-26.
- Vitousek, P. M. and Matson, P. A. 1984. Mechanisms of nitrogen retention in forest ecosystems. A field experiment. *Science*, 225, 51-52.
- Waring, S. A. and Bremner, J. M. 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. *Nature*, 201, 951-952.
- Warren, W. G. and Olsen, P. F. 1964. A line intersect method for assessing logging waste. *For. Sci.*, 10, 267-276.
- Westerman, D. T. and Crothers, S. E. 1980. Measuring soil nitrogen under field conditions. *Agron. J.*, 72, 1009-1012.

APPENDIX: DATA TABLES

Table I. Wood biomass data (Mg ha⁻¹) for all plots.

Province	Installation	Plot	Fertilizer kg N ha ⁻¹	Coarse Wood					Fine Wood 2 -76 mm	Total
				Decay Class I	Decay Class II	Decay Class III	Decay Class IV	Decay Class V		
1	1	4	0	0.00	6.35	6.55	19.44	3.00	2.11	37.45
		2	448	0.00	4.89	6.03	9.13	10.40	1.93	32.38
	5	25	0	0.00	0.92	60.36	72.54	11.86	1.97	147.65
		29	448	0.00	3.09	5.27	12.96	1.08	1.88	24.28
	59	354	0	0.13	0.31	0.11	7.11	17.87	6.17	31.70
		352	448	2.44	3.14	3.05	5.83	1.64	11.05	27.15
	78	468	0	2.11	11.84	4.39	7.76	6.12	7.40	39.62
		463	448	22.96	23.14	3.95	1.79	0.00	15.18	87.02
	101	602	0	3.72	4.01	0.00	1.32	0.00	16.53	25.58
		601	448	7.33	6.17	3.65	0.38	0.00	14.17	31.70
2	16	91	0	6.08	8.09	9.62	42.56	16.68	15.49	98.54
		92	448	1.95	7.87	83.75	55.14	31.37	14.06	194.14
	33	193	0	0.54	0.61	55.83	69.35	34.55	7.02	167.90
		195	448	3.32	0.11	52.60	147.05	24.40	6.75	234.23
	43	253	0	0.00	2.74	1.52	11.59	50.97	10.61	77.43
		256	448	0.63	6.01	30.92	14.04	44.06	12.22	107.88
	57	342	0	4.93	2.04	1.70	6.12	31.01	4.80	50.60
		338	448	8.57	7.98	14.75	17.53	26.08	5.90	80.81
	98	584	0	0.87	4.57	82.92	11.50	3.23	4.93	108.02
		583	448	32.47	7.92	69.51	6.30	0.00	4.57	120.77
4	20	118	0	0.00	5.79	16.05	20.18	10.49	2.87	55.38
		117	448	0.00	4.84	45.32	16.37	29.71	7.51	103.75
	53	317	0	0.00	0.61	0.38	3.88	1.52	6.70	13.09
		315	448	0.00	1.95	3.54	0.13	0.81	3.36	9.79
	77	462	0	2.35	0.00	74.47	24.84	16.08	5.11	122.85
		461	448	1.75	3.50	0.09	0.07	0.34	6.39	12.14
	81	485	0	1.12	8.39	17.18	13.95	5.94	6.39	52.97
		484	448	4.89	3.99	18.52	19.24	9.17	6.19	62.00
		Grand Mean	Avg - 0 SEM - 0	1.56 2.02	4.02 3.66	23.65 30.46	22.30 23.13	14.92 14.74	7.01 4.44	73.46 48.10
			Avg - 448 SEM - 448	6.16 9.71	6.04 5.45	24.35 27.73	21.85 38.68	12.79 15.17	7.94 4.58	79.15 68.12

Table II. Carbon in wood (Wt %) by decay class for all samples analysed.

Province	Installation	Plot	Fertilizer kg N ha ⁻¹	Carbon Wt %				
				Decay Class I	Decay Class II	Decay Class III	Decay Class IV	Decay Class V
1	1	4	0	48.8	46.3	48.6	56.0	54.1
		2	448	46.8	45.6	46.1	51.8	53.6
	59	354	0	45.8	46.8	48.1	56.0	53.4
		352	448	49.3	47.9	52.3	52.2	51.6
2	78	465	0	46.2	50.6	48.3	54.1	54.1
		463	448	46.2	51.1	55.9	53.9	50.3
	16	91	0	45.1	46.6	44.4	53.9	52.9
		92	448	45.3	47.0	50.0	54.6	52.6
	33	193	0	48.4	47.7	51.1	53.7	53.4
		195	448	47.0	48.3	54.4	54.9	51.1
	98	584	0	46.9	47.5	51.0	52.7	52.8
		583	448	44.8	51.2	46.0	55.8	53.2
4	20	118	0	45.3	47.0	48.0	55.2	54.0
		117	448	44.9	48.8	48.6	54.7	53.8
	81	485	0	46.6	46.7	43.7	56.2	55.8
		484	448	48.5	49.0	49.5	54.0	54.6
Grand Mean				46.6	47.4	47.9	54.7	53.8
SEM - 0				1.4	1.4	2.7	1.3	1.0
Avg - 448				46.6	48.6	50.4	54.0	52.6
SEM -448				1.7	1.9	3.6	1.4	1.5

Table III. Nitrogen in wood (Wt %) by decay class for all samples analysed.

Province	Installation	Plot	Fertilizer kg N ha ⁻¹	Nitrogen Wt %				
				Decay Class I	Decay Class II	Decay Class III	Decay Class IV	Decay Class V
1	1	4	0	0.120	0.091	0.259	0.215	0.252
		2	448	0.101	0.245	0.286	0.351	0.451
	59	354	0	0.055	0.179	0.195	0.172	0.341
		351	448	0.098	0.12	0.172	0.275	0.59
	78	465	0	0.075	0.227	0.539	0.32	0.388
		463	448	0.191	0.106	0.291	0.327	1.1
	16	91	0	0.151	0.146	0.238	0.275	0.245
		92	448	0.144	0.256	0.366	0.349	0.416
	33	193	0	0.138	0.264	0.28	0.244	0.311
		195	448	0.277	0.204	0.256	0.225	0.73
	98	584	0	0.092	0.087	0.148	0.234	0.35
		583	448	0.137	0.107	0.319	0.252	0.501
4	20	118	0	0.154	0.184	0.12	0.325	0.428
		117	448	0.076	0.167	0.221	0.376	0.352
	81	485	0	0.087	0.145	0.289	0.223	0.42
		484	448	0.057	0.143	0.58	0.343	0.334
Grand Mean				0.109	0.165	0.259	0.251	0.342
SEM - 0				0.037	0.062	0.129	0.053	0.070
Avg - 448				0.135	0.169	0.311	0.312	0.559
SEM -448				0.071	0.060	0.124	0.054	0.254

Table IV. Soil element parameters and physical properties for all plots. Bulk density and gravel data for top 0-15 cm of soil, from between plots at time of treatment.

Province	Installation	Plot	Fertilizer kg N ha ⁻¹	Soil N Wt %	Soil C Wt %	Soil C:N Ratio	Bulk Density	Gravel Wt %
1	1	4	0	0.285	7.240	25	1.000	50
		2	448	0.334	6.470	19		
	5	25	0	0.151	4.300	28	1.105	25
		29	448	0.266	8.740	33		
	59	354	0	0.130	4.430	34	0.875	35
		352	448	0.205	5.610	27		
	78	468	0	0.104	2.260	22	1.321	57
		463	448	0.143	2.800	20		
	101	602	0	0.117	2.030	17	1.113	10
		601	448	0.158	3.400	22		
2	16	91	0	0.279	4.490	16	1.142	20
		92	448	0.345	5.990	17		
	33	193	0	0.122	2.740	22	0.983	18
		195	448	0.184	6.970	38		
	43	253	0	0.071	2.310	33	0.728	0
		256	448	0.073	2.090	29		
	57	342	0	0.171	3.190	19	0.838	35
		338	448	0.226	5.890	26		
	98	584	0	0.053	2.200	42	0.553	0
		583	448	0.100	2.640	26		
4	20	118	0	0.207	3.230	16	0.815	0
		117	448	0.247	4.310	17		
	53	317	0	0.306	6.080	20	0.962	3
		315	448	0.313	5.460	17		
	77	462	0	0.386	7.790	20	1.200	45
		461	448	0.345	8.100	23		
	81	485	0	0.298	5.750	19	1.188	25
		484	448	0.408	8.960	22		