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THE ADDITION, DECOMPOSITION AND ACCUMULATION  
OF ORGANIC MATTER IN SOME NATIVE  
*NOTHOFAGUS* spp. FORESTS AND *PINUS RADIATA*  
PLANTATIONS IN THE SOUTH ISLAND  
OF NEW ZEALAND

A thesis  
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of the requirements for the Degree  
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by  
Sammy Heng

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The addition, decomposition and accumulation of organic matter in beech (*Nothofagus* spp.) forests and radiata pine (*Pinus radiata*) plantations were compared in a study conducted over a two-year period from November 1976 to December 1978. A pair of adjacent beech and radiata pine stand was selected in each forest at Granville, Hanmer and Golden Downs (Nelson), located in the South Island of New Zealand. In Golden Downs, a regenerated radiata pine stand was also used.

A quantification of the organic matter content of the forest floor and top-soil (0-20cm) was undertaken in six pairs of adjacent native forest and radiata pine stands, including those at the three forests mentioned above. In Granville forest, carbon dioxide evolution rates from forest

floor and mineral N levels in humus and top-soil (0-20cm) were measured directly in the field over two years in both the beech and radiata pine stands used.

Litter-fall data obtained included biomass of litter-fall, three-monthly and annual litter-fall budgets of nutrients (N, P, K, Mg, Ca), carbon, water-soluble components (simple carbohydrates, polyphenols and total water-soluble materials), and annual litter-fall budgets of the organic constituents (ether-extractable components, aqueous ethanol-extractable components, holocellulose and residual lignin).

These data showed that in the forests at Granville, Hanmer and Nelson, total annual litter-fall was between 3915 to 7471 kg/ha in beech stands and between 1445 to 5522 kg/ha in radiata pine stands. In all these stands, peak litter-fall occurred in spring (October - November). Beech stand was returning larger amounts of these macro-nutrient elements, and water-soluble and organic constituents than the adjacent radiata pine stand in all forests studied. Annual total macro-nutrient (N + P + K + Mg + Ca) budgets in radiata pine stand accounted between 35 and 65 percent of those in adjacent beech stand.

In the forests at Granville, Hanmer and Nelson, decomposition of the litter in each of the stands used was measured using litter-bag technique from October 1976 to December 1978. Beech (leaf + twig) litter and radiata pine (needle) litter were used in the respective stands. Weights of litter remaining in litter-bags at the end of the 26-month period were between 46 and 54 percent of initial litter



weight used for beech, and between 37 and 54 percent for radiata pine. Average first-year weight loss rates (k values) obtained for beech litter ranged from 0.40 to 0.47 and for radiata pine litter from 0.33 to 0.48.

Macro-nutrient concentrations and distribution of the water-soluble and organic constituents in leaf, twig and needle litter determined at various stages of litter decomposition showed that concentrations generally declined with time except those of N and residual lignin. First-year weight loss rates for the macro-nutrient elements and other constituents in all forest stands ranged from low values for residual lignin (0.05 to 0.17) and N (0.10 to 0.27) to high values for water-soluble polyphenols (0.91 to 1.55) and K (0.43 to 1.47). Loss rates of P, K, ether-extractable components and holocellulose for radiata pine litter were greater than those for beech litter, although the reverse order was found for Mg, carbon and residual lignin.

In the quantification of organic matter accumulation in forest stands, the forest floor depths and top mineral soil (0-20cm) in six pairs of adjacent native forest and radiata pine stands at Granville, Hanmer (2 pairs), Nelson, Hochstetter and Peel forest were sampled. Average weight of the forest floor in native forest stands ranged from 25 to 464 tonnes/ha and those in radiata stands ranged from 9 to 79 tonnes/ha. Native forest stands accumulated apparently larger amounts of nutrients in forest floor than their adjacent radiata pine stands. These differences were smaller in the top-soil and in some cases radiata pine stands apparently accumulated larger amounts of top-soil nutrients. In

addition, higher levels of exchangeable cations and available phosphorus (Bray-P) were also evident in the top-soil of radiata pine stands, compared to those of beech.

The carbon mineralization field data obtained at Granville forest showed a close relationship existed between  $\text{CO}_2$  evolution rates and air temperatures ( $r = 0.846^{***}$  for beech and  $r = 0.897^{***}$  for radiata pine). However, no significant relationship was found between  $\text{CO}_2$  evolution rates and soil and/or humus moisture contents. Total  $\text{CO}_2$  evolution was about three times greater than expected from the amount of carbon released from annual litter-fall, and this was attributed to contributions from root respiration. Both clearcutting a forest stand and burning of the forest floor were found to result in apparent increases in  $\text{CO}_2$  evolution rates.

Mineralization of N in the humus and top-soil (0-20cm) layers in both the beech and radiata pine stands at Granville was found to result mainly in the form of ammonium. Nitrate was frequently not detected ( $< 0.1 \mu\text{g/g}$ ) or was present in negligibly low concentrations. In the beech stand, ammonium-N levels ranged from 11.0 to 63.1  $\mu\text{g/g}$  for the humus layer and 1.5 to 13.3  $\mu\text{g/g}$  for the top-soil in the period between March 1977 to December 1978. Corresponding values for the radiata pine stand were 22.6 to 85.4  $\mu\text{g/g}$  for the humus layer and 1.4 to 12.2  $\mu\text{g/g}$  for the top-soil. No significant correlations were found between ammonium-N levels and either temperatures, moisture contents or total-N contents for both humus and top-soil samples.

A laboratory incubation experiment was undertaken to evaluate the effects on soil CO<sub>2</sub> evolution and N mineralization due to water extracts of beech and radiata pine litter, particularly those of carbohydrates and polyphenols. It was found that carbohydrates stimulated CO<sub>2</sub> production but had no apparent effect on mineral N levels. Polyphenolic compounds in water extracts of litter and also catechin solution depressed the rate of CO<sub>2</sub> evolution and N mineralization.

A method for the extraction of lipid components of plant materials, suitable for a large number of samples was developed. This method produced consistent results (C.V. ranged from 1 to 7 percent). In the method, plant materials were initially extracted with petroleum ether at 49°C and then followed by 75%-aqueous ethanol at 62°C. The duration was 22 hours for both extractions.

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## CHAPTER 1

### INTRODUCTION

The study of the forest ecosystem or any ecosystem is essentially the elucidation of complex and sometimes perplexing processes, their interactions, and how they act, individually or in concert, to change or maintain stability within a unit of vegetation. Inevitably, some of this complexity is reflected in the course of this kind of study.

One of the characteristic features of a mature forest ecosystem is undoubtedly the accumulation of organic matter largely on the mineral soil surface. This does not generally occur in the agricultural counterpart. The rate at which forest floor develops depends primarily on the amount of litter produced and its subsequent rate of decomposition, which varies according to forest species and climatic conditions (Bray and Gorham, 1964; Singh and Gupta, 1977). These two processes also constitute the major pathways governing the recycling of nutrients. In addition, the litter constitutes a substantial fraction of energy and carbon fixed in forests, and is therefore regarded as an index of ecosystem productivity.

In recent years, numerous studies of litter production, litter decomposition and chemical composition

of litter have been reported (e.g. Phillipson et al., 1975; Ewel, 1976; Rogers and Westman, 1977; Reiners and Reiners, 1970; Likens et al., 1979). However, few of these studies examined the changes in the litter organic constituents such as fats, waxes, carbohydrates and lignin. Decomposer organisms, important and active in the role of nutrient mineralization, rely mainly on some of these constituents as sources of energy for their growth. Consequently, chemical composition changes in forest litter exert a strong influence on biological activity. This amply demonstrates the need to integrate this aspect of research into the framework of ecosystem study. Such information, together with that on the intimate relationships between litterfall, litter decomposition, litter accumulation, microbial activity, mineralization and abiotic environmental factors, provide a better understanding of the dynamic nature and the functioning of the forest ecosystem and may lead to more effective measures aimed at maintaining and increasing the productivity of forests to the best advantage possible.

Apparently, few studies of this nature and broadness in scope have been reported in the South Island of New Zealand. This could represent a serious disadvantage in the understanding of organic matter turnover in forest stands and especially in areas associated with extensive or proposed programmes of forest conversion. The need for such investigations is made more critical since many regions of the South Island constitute major established areas of reafforestation, such as Golden Downs and Hanmer. However, on the west coast of the South Island, conversion



of indigenous forest to *Pinus radiata* is still only in the infant stage. Consequently, it was proposed to initiate a study aimed at the characterization of soil organic matter and measuring organic matter turnover of existing stands of indigenous forest and radiata plantation. This characterization programme was extended to a number of regions in the South Island in an effort to make the results more applicable to a wider range of soils and climatic conditions. However, the main emphasis was placed in the West Coast region where supplementary carbon and nitrogen mineralization studies were also conducted.

Precisely, the four major objectives of the present study were:

- (1) to quantify the organic matter accumulated in the forest floor and in the top-soil of adjacent stands of indigenous forest and radiata plantation in the major forest areas, including the West Coast, Hanmer, Golden Downs (Nelson), so as to provide some information on the general changes due to forest conversion,

- (2) to estimate the annual total biomass and different litter constituents returned to the forest floor by way of litter-fall. These constituents include the macro-nutrients (N, P, K, Mg, Ca), carbon, water-soluble litter constituents (simple carbohydrates, polyphenols) and organic constituents (ether-extractable materials, holocellulose and residual lignin),

- (3) to estimate the rate of litter decomposition and the rate of loss of the different constituents of

litter, and

(4) to determine the carbon and nitrogen mineralization rates occurring in beech and radiata pine stands on the west coast (Granville forest), and to relate these processes to prevailing biotic and abiotic factors.

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## CHAPTER 2

### REVIEW OF LITERATURE

#### 2.1 LITTER PRODUCTION

##### 2.1.1 Introduction

In the forest ecosystem, the organic matter is an important source of nutrients for micro-organisms and plants. The major supply of organic matter is the litter. In this way, litter production continuously replenishes the nutrient status of the forest floor. In addition, nutrients are also derived from rainfall which includes leaching of nutrients from tree canopy; the atmosphere, either in gaseous form or in particulate matter; animal deposits, mainly as faeces; and, soil weathering. According to Foster and Morrison (1976), between 71 and 89 percent of the elements taken up annually by trees are returned by way of litterfall and throughfall. Other nutrients may also be made available through biological fixation.

Although litterfall remains the main source of nutrient return to the forest floor, no single input process could be regarded as sufficient to provide all the nett nutrient demands of any forest ecosystem (Westman, 1978). However, the relative importance of the other sources depend upon the element in question. For example, Henderson

et al. (1977) measured nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg) and calcium (Ca) in the throughfall of four forest types and concluded that the importance of throughfall in comparison to litter-fall as a nutrient return mechanism decreases in the order  $K > Ca = Mg > P = N$ .

### 2.1.2 Litter-fall Components

Leaf litter comprises the largest proportion of litter-fall, and can constitute between 60 to 76 percent of the total (Bray and Gorham, 1964). Other major components include branches and stems (12 - 15%), fruit (1 - 17%), and the miscellaneous fractions (1 - 16%). Bark litter can become predominant in some forests, particularly where *Eucalyptus* has been planted. For example, data of Rogers and Westman (1977) indicated that in a mature *Eucalyptus* forest in Australia, bark component constituted 22.8 percent of the total litter-fall. These minor components are therefore of sufficient quantity in biomass, and contain enough nutrients not to be neglected in any litter study.

Under closed canopy, leaf litter is relatively uniformly distributed over the forest floor. Greater variation is more commonly observed in branch litter-fall primarily because branch-fall is often very erratic and thus difficult to estimate. The relative contribution from each litter component to the total litter-fall varies during different seasons of the year, and is influenced by meteorological events such as storms and droughts.

### 2.1.3 Factors Affecting Litter Production

Several factors can influence litter production and these have been reviewed comprehensively by Bray and Gorham (1964). The present review only discusses the more essential features of the major factors involved.

#### 2.1.3.1 Climate

The relationship between climate and litter production is best illustrated by the data of annual litter production in various climatic regions of the world (Bray and Gorham, 1964). In equatorial forests, the annual total litter production averages 10.9 tonnes/ha while in warm temperate forests the mean is 5.5 tonnes/ha. Corresponding values for forests in the cool temperate and arctic-alpine regions are 3.5 and 1.0 tonnes/ha respectively. These data suggest that there is an inverse and linear relationship between annual total litter production and latitude.

The range of mean annual temperature and the length of growing season have been attributed to account for the variation in the mean annual litter production in the various regions. In equatorial regions, higher temperature is often experienced all the year round. Estimates by Bray and Gorham (1964) using Black's (1956) data suggest that the total amount of solar radiation received in the arctic-alpine, cool temperate and equatorial regions is approximately in the ratio 1:3:5 respectively.

Litter production is also affected by seasonal variations. There is a relatively continuous fall of litter throughout the year in equatorial regions, except for



periods of dry and wet spells. For example, in the equatorial forests of Congo, maximum litter-fall was observed to occur in the dry seasons, and minimum in the wet seasons (Laudelot and Meyer, 1954). However, in New Zealand, maximum litter-falls for *Pinus nigra* and *Pinus radiata* occurred in the autumn months of March, April and May (Will, 1959). For *Nothofagus truncata*, maximum leaf-fall was found in the spring months of October and November, and this was attributed to the development of new leaves (Miller and Hurst, 1957; Levett, 1978).

#### 2.1.3.2 Site Properties

Major site properties which have been shown to affect litter production include soil fertility, and site altitude and aspect.

Forests sited on more fertile soils have been reported to produce a greater amount of litter than those on less fertile soils (Bonnievie-svendson and Gjems, 1957).

Effects of altitude and aspect of forest site in mountainous regions are demonstrated by the data of Ebermayer (1876) as quoted by Bray and Gorham (1964). The results showed that a lower litter production was obtained in the westerly than in the easterly quadrants in Germany. High litter production occurred at the intermediate elevations (450 - 850m), where rainfall and temperature were suspected to be optimum for plant growth.

In addition, results obtained by a number of workers (Bormann et al., 1970; Siccama et al., 1970) showed that a lower rate of nett primary productivity is correlated with higher elevations. Some measurements such

as basal area per hectare, basal area per tree, deciduousness and canopy height decreased with increasing elevation (from 546m to 791m), whereas density, evergreenness and species diversity increased. Increase in elevation also promoted increased diversity and productivity of the under-storey, which was coincident with a decrease in the productivity of the over-storey. These effects are likely to influence litter production.

Topographical features appear not to have any dramatic effect on litter production. For example, litter-fall in four contrasting situations, a ridge, a broad ridge, a steep slope and in a valley were found not to differ significantly (Edwards, 1977).

#### 2.1.3.3 Forest Type and Age

The change in litter production with forest succession is not well documented. Hurd (1971) studied the annual tree litter production by successional forest stands and concluded that no significant difference was apparent between the stands. Ohmasa and Mori (1937) observed no significant difference in the mean litter-fall in both plantations and natural forests of *Pinus densiflora* and *Chamaecyparis obtusa*.

In forests where under-storey vegetation is widespread, contribution to the total litter-fall from this sector can be significant. Such contributions range from 3 to 28 percent of the total litter-fall (Bray and Gorham, 1964). In this connection Tappeiner and Alm (1975) found that higher nutrient concentration of the under-storey vegetation increased the total nutrients in the litter-fall.

The distribution of under-storey vegetation litter is closely related to the density of the forest and light penetration through the canopy to the forest floor.

Except for the very early stages of stand development, litter production generally does not show an inherent trend to change with age once canopy closure is reached (Bray and Gorham, 1964). In the older stands, under-storey contribution may increase as the crowns become more open thereby allowing light penetration, thus promoting the growth of under-storey vegetation.

In the lowlands of eastern Guatemala, however, litter-fall was found to increase with increasing age of vegetation, up to an age of 14 years (Ewel, 1976). The maximum annual litter-fall of 10 tonnes/ha produced by the 14-year-old stand did not differ significantly from that produced by a mature forest. Zavitkovski and Newton (1971) also found that in stands of red alder in western Oregon, annual litter production increased with stand age up to an age of 10 years.

Another effect of age of forest on litter production could be due to wood litter-fall. This has been observed to increase especially in the older stands (Gessel and Turner, 1976).

#### 2.1.3.4 Treatment

In a closed canopy forest, there appears to be no significant correlation between tree density and litter production (Sviridova, 1960). However, changes in density brought about by thinning of a forest stand with full canopy caused a decrease in litter production (Dimock, 1958;

Wright, 1957; Reukema, 1964). For example, data of Wright (1957) showed that stands of *Picea abies*, thinned to 460, 237 and 52 trees/ha, produced annual litter-fall of 5.7, 4.3 and 3.7 tonnes/ha respectively. In later years subsequent to thinning, it is likely that litter-fall increases in association with increase in leaf production (Sviridova, 1960; Levett, 1978).

Removal of forest litter may reduce forest litter production in later years, since this results in the loss of nutrients from the site (Mayer-Krapoll, 1956). In this respect, timber harvesting may have a similar effect.

## 2.2 CHEMICAL COMPOSITION OF PLANT MATERIALS

### 2.2.1 Introduction

Except for a small proportion of mineral constituents, plant tissue is largely composed of complex organic compounds. These include fats, oils, waxes and resins (0.5 - 5%), water-soluble carbohydrates (5 - 20%), cellulose (15 - 60%), hemicelluloses (10 - 30%), crude protein (5 - 15%) and lignin (5 - 30%). The mineral constituents normally comprise between 1 to 8% of the dry weight (Alexander, 1977; Allen, 1974). Another important group of organic compounds present in plant material is that of the phenolic compounds (see also Section 2.4.3).

The proportion of each different organic constituent varies according to the plant species and tissues (Waksman and Tenney, 1928; Nykvist, 1961; Daubenmire and Prusso,

1963; Kononova, 1966; Anderson, 1973b; present study).

This also applies to the constituents present in the different groups of organic compounds. For example, Nykvist (1961) showed that the proportion of each of the different sugars in the water extracts of leaf litter of 7 forest species were dissimilar. Glucose and fructose (Figure 2.2.1.1) were found in all species while sucrose was found only in two species.

### 2.2.2 Chemical Properties of Some Plant Organic Constituents

In the present section, only a few of the organic compounds mentioned in Section 2.2.1 are reviewed in detail. A comprehensive review of most of the important aspects of phytochemistry is given in a treatise edited by Miller (1973).

The ether-extractable organic compounds, which include fats, waxes and terpenes (frequently referred to as lipids), is one broad group of organic compounds commonly fractionated in organic matter studies (Stevenson, 1965). These organic compounds form a convenient analytical group rather than a structural group. Due to their hydrophobic properties, these compounds generally function as plant structural materials and energy resources.

Some of the more common plant lipids include cutin, which covers the epidermis of leaves, stems and fruits and, terpenes, such as menthols, camphor and pinene (Figure 2.2.2.1) which are responsible for the fragrance of mint, of eucalyptus leaves and of pine needles. Other plant lipids include fats (Figure 2.2.2.2) and the straight long-

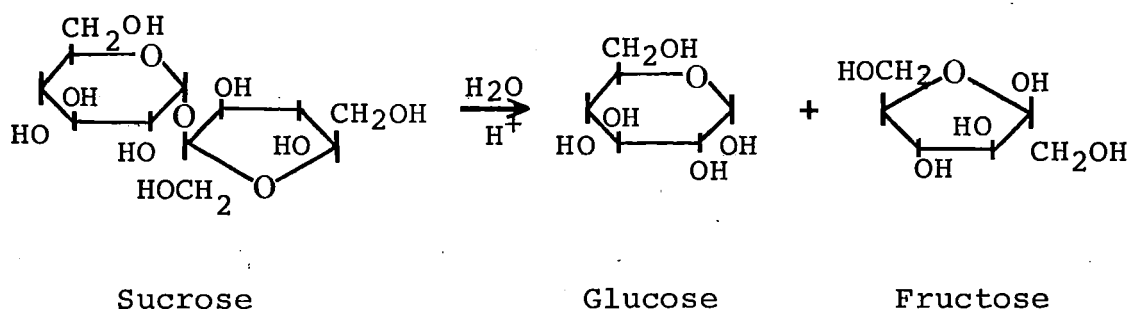
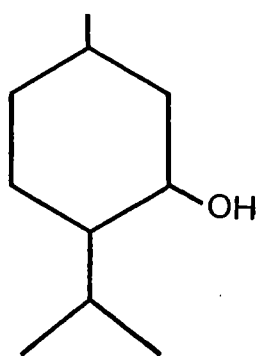
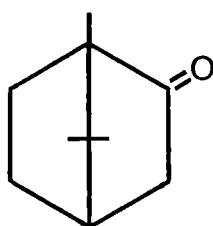


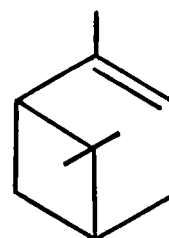
FIGURE 2.2.1.1 Acid hydrolysis of sucrose



Menthol



Camphor



$\alpha$ -pinene

FIGURE 2.2.2.1 Some common plant terpenes

TABLE 2.2.2.1 Some common plant fatty acids

Saturated	
Lauric acid	$\text{CH}_3(\text{CH}_2)_{10}\text{COOH}$
Palmitic acid	$\text{CH}_3(\text{CH}_2)_{14}\text{COOH}$
Stearic acid	$\text{CH}_3(\text{CH}_2)_{16}\text{COOH}$
Unsaturated	
Oleic acid	$\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CH}(\text{CH}_2)_7\text{COOH}$
Linoleic acid	$\text{CH}_3(\text{CH}_2)_3(\text{CH}_2\text{CH}=\text{CH})_2(\text{CH}_2)_7\text{COOH}$

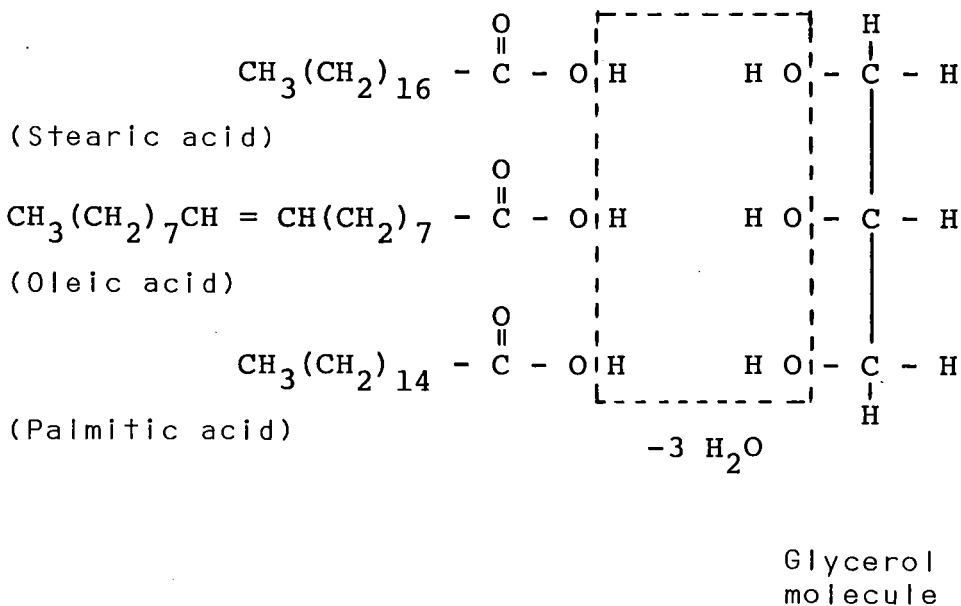


FIGURE 2.2.2.2 Formation of a molecule of fat from three fatty acids and a glycerol molecule

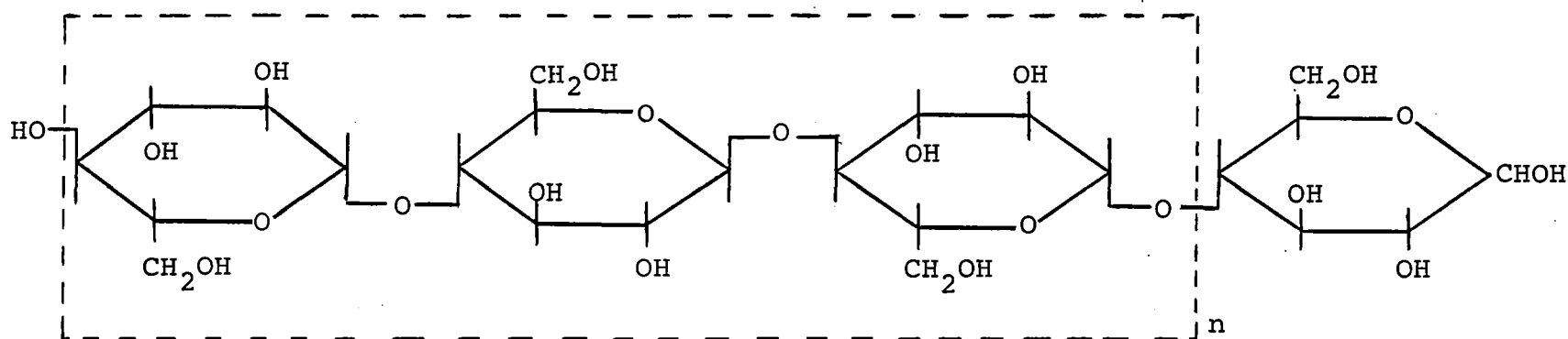
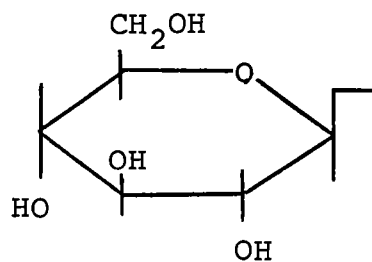


FIGURE 2.2.2.3 The Structure of cellulose



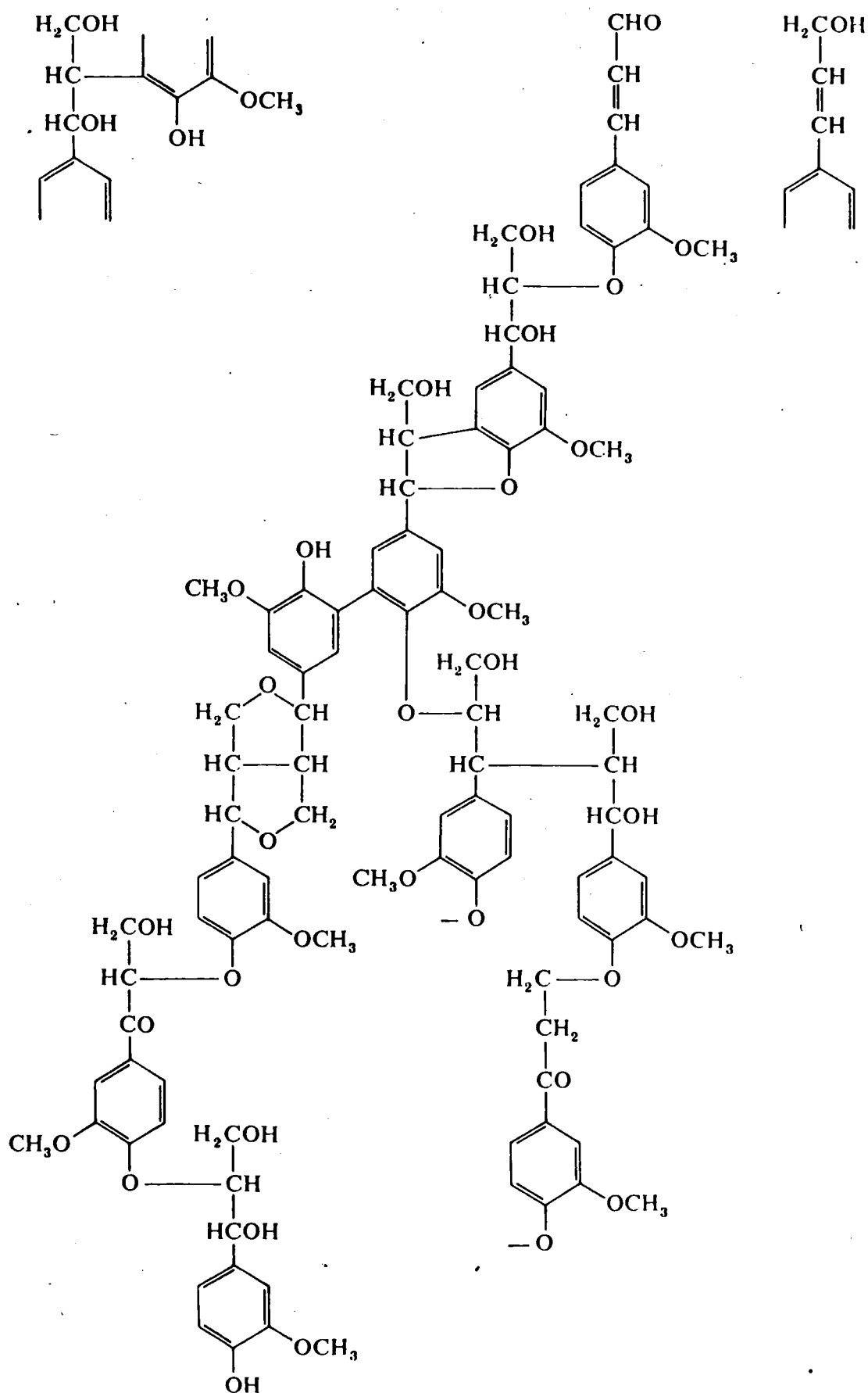


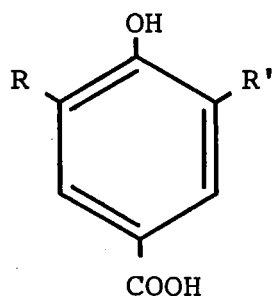
FIGURE 2.2.2.4 The structure of lignin (according to Brauns).

chain saturated and unsaturated fatty acids; examples of some of the more common ones are given in Table 2.2.2.1 .

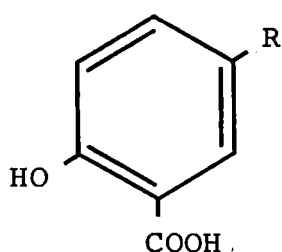
The structures of some of the other plant organic constituents such as cellulose (Figure 2.2.2.3) and hemicelluloses are also complex. Both are found as constituents of plant cell walls. Cellulose occurs in almost pure form in cotton and certain other plant fibres (e.g. flax). Cellulose is a condensation polymer of glucose and complete hydrolysis gives a nearly quantitative yield of this sugar (Geissman, 1968), while hemicelluloses yield hexoses (six-carbon sugars), pentoses (five-carbon sugars), and frequently uronic acids. Collectively, cellulose and hemicelluloses are often referred to as holocellulose.

The structure of lignin is exceedingly complex (Figure 2.2.2.4). In association with cellulose and hemicellulose, lignin constitutes the structural material of woody plants. Such intimate interlinkage makes the chemical isolation of cellulose, hemicellulose and lignin difficult. In addition, because of the resistant nature of lignin, it is often difficult to be sure that lignin fraction obtained by the different techniques represent anything like native lignin.

Phenolic compounds are perhaps one of the more reactive chemical substances found in plant materials (see Section 2.3.4.1.2), derived from lignin or formed by microbial synthesis. These compounds include phenolic acids (Figure 2.2.2.5) and the flavonoid compounds (Figure 2.2.2.6). Of these acids, p-hydroxybenzoic, vanillic and syringic acids occur in considerable amounts as combined

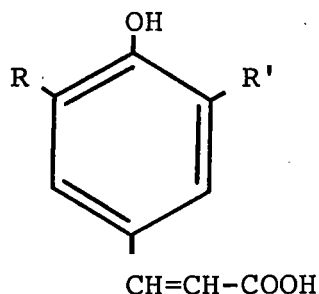


$R = R' = H$     p-hydroxybenzoic acid  
 $R = OH; R' = H$     protocatechuic acid  
 $R = OMe; R' = H$     vanillic acid  
 $R = R' = OMe$     syringic acid



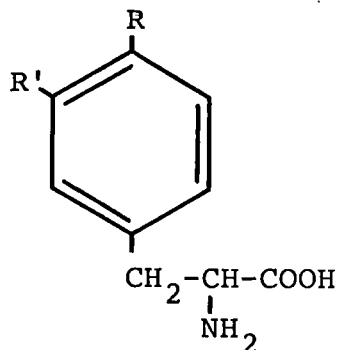
$R = H$     salicylic acid  
 $R = OH$     gentisic acid

#### A. SUBSTITUTED BENZOIC ACIDS



$R = R' = H$     p-coumaric acid  
 $R = OH; R' = H$     caffeic acid  
 $R = OMe; R' = H$     ferulic acid  
 $R = R' = OMe$     sinapic acid

#### B. SUBSTITUTED CINNAMIC ACIDS



$R = R' = H$     phenylalanine acid  
 $R = OH; R' = H$     tyrosine acid  
 $R = R' = OH$     dihydroxyphenylalanine acid

#### C. SUBSTITUTED PHENOLIC AMINO ACIDS

FIGURE 2.2.2.5    Some plant phenolic acids

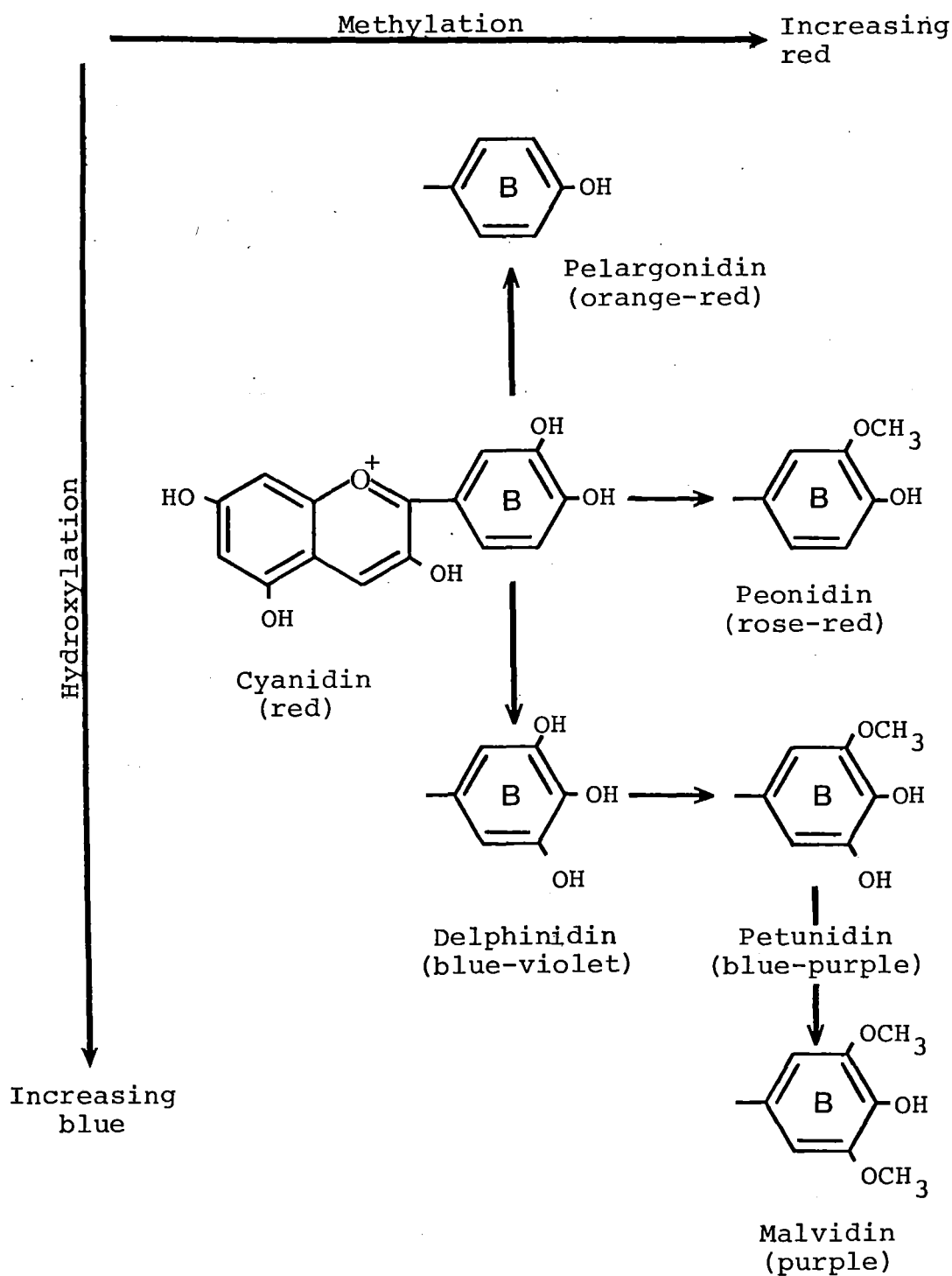


FIGURE 2.2.2.6 Relationship of anthocyanidin colour to the substitution pattern of the B-ring (after Walker, 1977)

forms in lignin. Consequently, these three acids are commonly associated with the degradation products of lignin (Kononova, 1966; Flaig et al., 1975). The flavonoid compounds (which are soluble in water) include the anthocyanidins and are widely distributed in leaves, flowers and fruits of higher plants. Anthocyanidins are responsible for most of the red, violet and blue colours of fruits and flowers (Figure 2.2.2.6). Tannins, which are high molecular weight polyphenolic compounds, and lignin, constitute the most abundant and widely distributed phenolic polymers of higher plants (Swain, 1965; White, 1957).

### 2.2.3 Isolation of Plant Chemical Constituents

A wide range of methods has been employed in the analysis of plant chemical constituents. This topic has been reviewed extensively (Black, 1965; Allen, 1974; A.O.A.C.). Although the methodology of plant analysis is beyond the scope of this study, chemical analytical methods nevertheless form an integral part of the present study. A detailed outline of some of the chemical procedures used, including those employed in the present study, is shown in Figure 2.2.3.1. Detailed aspects of the methods used are described in later chapters.

### 2.2.4 Factors Affecting Chemical Composition Of Litter

In general, the relative proportions of organic and inorganic constituents in litter are affected by several factors such as plant species, kind and age of plant tissue,

ELEMENTAL ANALYSIS

PROXIMATE ANALYSIS

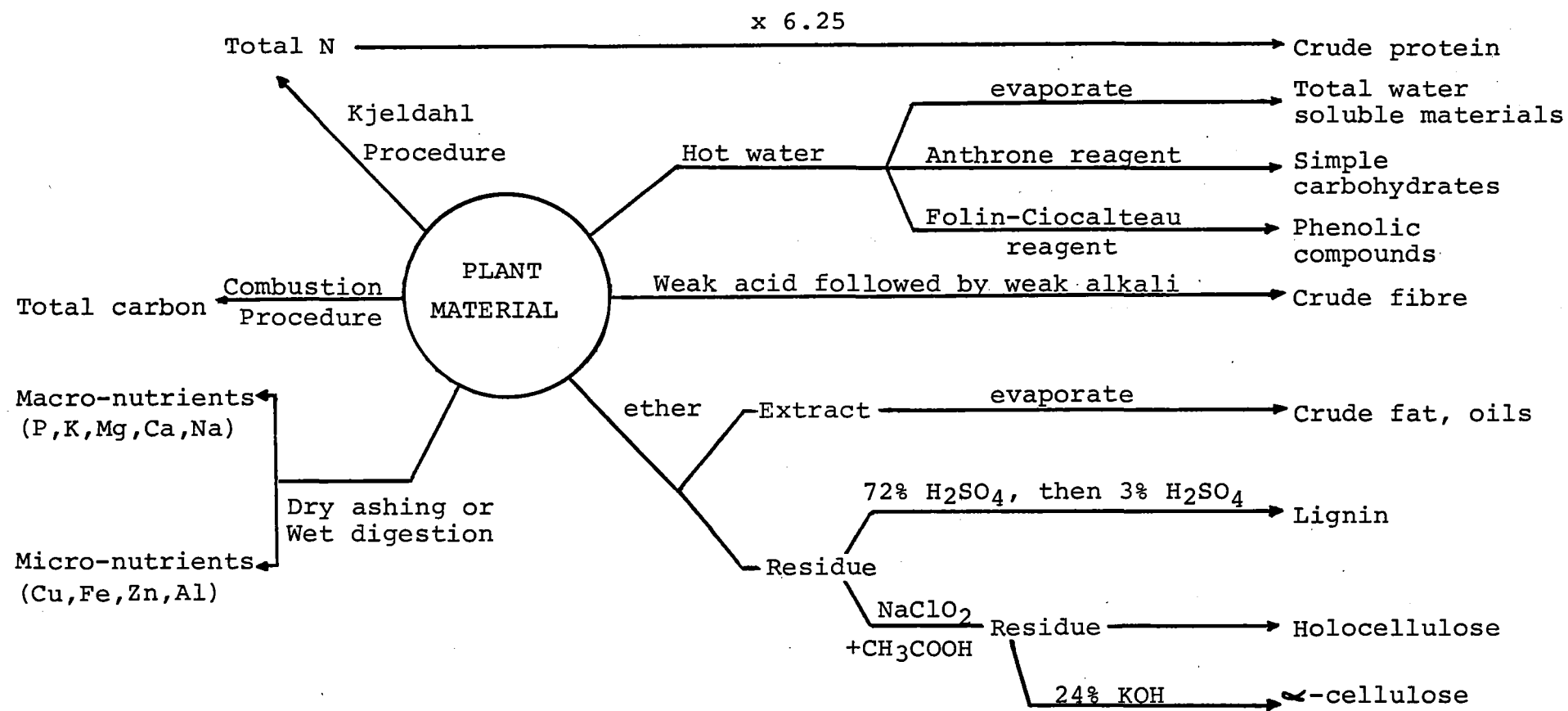


FIGURE 2.2.3.1 DIAGRAMMATIC OUTLINE SHOWING CHEMICAL PROCEDURES USED IN THE ANALYSIS OF PLANT MATERIALS

soil status on which the vegetation is growing and the time of litterfall. In this present review, all these factors mentioned above are considered under the general headings of Internal and External Factors.

#### 2.2.4.1 Internal Factors

Generally speaking, the chemical composition of the plant tissues while still green on the plant is substantially different from that when the tissue falls to the forest floor as litter. Normally the period where most dramatic changes occur appear to be from the time of onset of senescence in green plant tissues to the time of abscission. For example, Mälkönen (1974) followed the changes in the amounts of nutrients in Scots pine needles of increasing ages and found considerable decrease in the amounts of N, P, K in the transition from the fourth year stage to the yellowing stage. Calcium, on the other hand, showed an increase. This effect has been related to the translocation of the mobile elements into the more permanent parts of the plant prior to litter-fall. Calcium, being immobile, is not involved in the translocation. Translocation was also attributed to account for substantially reduced N, P, K levels in the litter compared to freshly cut leaves of *Eucalyptus* (Rogers and Westman, 1977).

Cromack (1973) found that cellulose and lignin content of senescent leaves were generally higher than those in the corresponding green leaves of several forest tree species. Changes in lignin content appeared to be relatively greater than those shown by cellulose content. However,

senescent leaves had lower N concentrations than green leaves.

Concentration of some leaf lipids have also been reported to be significantly higher in green than yellow leaves of a number of plants (Hawke, 1973). However, there are indications that this effect may have been influenced by the varying light intensities (insolation) incident on the leaves.

There is extensive literature to indicate that chemical composition of litter varies according to species and components of litter (e.g. Lutz and Chandler, 1946; Waksman and Tenney, 1928; Whittaker et al., 1979; Woodwell et al., 1975; Gosz et al., 1972). For example, Heine (1973) reported differences in the K, Mg and Ca content of freshly fallen leaves of red, silver and mountain beech. According to Lutz and Chandler (1946), except for N, major nutrient content of hardwoods is generally greater than that of conifers. Most perennial tissues, such as branches and stems, have lower contents of nutrients when compared with those in leaf tissue, especially in N, P and K (Woodwell et al., 1975).

However, it is also not uncommon to find that similar plant tissues within a stand or from the same tree can vary considerably in their chemical composition. A spatial variation in the chemical content of leaves within a tree has also been observed (Will, 1957).

#### 2.2.4.2 External Factors

Seasonal variations have been reported to affect the chemical composition of litter. For example, Spain (1973) found peak levels of N, P and ash in spring and early summer



litter-fall of some Australian pines. Mean nutrient concentrations in whole leaves reported by Whittaker et al. (1979) indicated that levels of N, P, K, Ca and Mg were higher in summer than autumn leaves. Mead (1971) found a decline in total P and N content of young slash pine needles as the growing season progressed.

The chemical composition of litter is also affected by storm events. The ratio of mobile to immobile elements is higher in plant tissues brought down prematurely by storms. This could be due to incomplete translocation of elements within the plant. Immobile elements have been observed to accumulate in tissues which are becoming senescent up to the time of abscission (Mälkönen, 1974).

Water-soluble substances are one of the constituents most susceptible to changes in total amount and composition due to leaching effect. Compounds such as simple sugars are easily leached out of plant tissues or readily utilized by the microbial population even before litter-fall, or immediately after the litter reaches the forest floor. From a study of water-soluble organic compounds in various species of tree litter, Nykvist (1963) showed that amino acids (e.g. glutamic acid) and sugars (e.g. glucose and fructose) were leached out more easily from leaf than needle litter.

Nutrient concentrations of plant tissue have been found to relate to the soil fertility status of the stand (Chekalova, 1967). The relatively low nutrient concentrations of the Hubbard Brook trees as compared with those in other broad-leaf forests of the world have been attributed

by Whittaker et al. (1979) to the acid and infertile soil at Hubbard Brook. The effect of soil fertility on nutrient concentrations can be best illustrated by the increase in nutrient concentrations of the intact foliage and litter after fertilization (Miller et al., 1976; Paavilainen, 1977). In addition, mineral deficiencies of N and P in soil may lead to an increase in polyphenol concentrations of litter (Davies et al., 1964b).

## 2.3 LITTER DECOMPOSITION

### 2.3.1 Introduction

The litter decomposition process represents an important link in the nutrient cycle of forest ecosystems. It constitutes a process by which nutrients immobilized in the structure of plant tissues are released for re-use by plants through their root systems. The process of decomposition is complex and is facilitated by the activities of a wide range of micro- and macro-organisms. These activities are influenced by numerous factors such as plant species, chemical composition and physical structure of litter, and environmental conditions such as temperature, moisture and aeration.

Litter decomposition is primarily due to the action of micro-organisms which may account for as much as 90 per cent of the total organic litter degradation (Macfadyen, 1963; Odum, 1971). Most of the litter decomposition occurs on the forest floor, although substantial microbial

colonization and decomposition may have already begun prior to litter-fall. Plant exudates promote such colonization, and this may explain the rapid immobilization of nutrients observed in litter systems (Patten and Witkamp, 1967; Witkamp, 1971).

### 2.3.2 Rates of Leaf Litter Decomposition

Decomposition rates vary according to the plant material, the surrounding environment and the methods of measurement used. The latter topic is discussed in Section 2.3.5 on a wider aspect of litter decomposition measurements.

Anderson (1973a) found a lower rate of decomposition for beech than chestnut leaf litter placed in bags in the chestnut site, with weight losses of 45.4 and 70.5 percent recorded, respectively, in a period of 31 months. In a corresponding study carried out simultaneously, beech and chestnut leaf litter placed in the beech site showed weight losses of 58.0 and 75.0 percent, respectively, within a similar time period. Shanks and Olson (1961) also using litter-bag method, found that *Quercus alba* leaf litter decomposed faster than beech (*Fagus grandifolia*).

Jenny et al. (1949) showed that decomposition rates can be quite rapid, with a turnover rate ranging from a few months to a year in tropical forests, and very slow with turnover rates of tens of years in high mountain regions in California. This effect is also modified by the plant species effect. For example, Edwards (1977) examined the decomposition of leaf litter of seven plant species (six tree species and a bamboo) in both ridge and valley sites

and found no significant differences between the two sites. However, differences in the rate of disappearance of leaf litter were found between species. Ewel (1976) measured the decomposition rates of leaf litter of five plant species in a tropical forest succession in eastern Guatemala. The associated effects of stands of different age vegetation and a stand cleared of all vegetation on two different soil types (alluvial and upland) were examined. Decomposition rates did not differ significantly between the two soil types, under all ages of vegetation, and were lower in the cleared stand. Leaves of four successional species generally decomposed more rapidly than the one from the mature-forest species.

### 2.3.3 Decomposition of Litter Components

Generally, coniferous litter is more resistant to decomposition than deciduous litter. According to Mälkönen (1974) coniferous litter undergoes slower decomposition since such litter is usually poor in N and relatively rich in wax and resin. An indication of the rate of decomposition of coniferous litter was given by Mikola (1954), who estimated a dry weight loss of between 11 and 30 percent in the first year, and between 25 and 48 percent in the second year from litters of *Pinus sylvestris*, *Picea abies* and *Larix* species. Most of the loss was attributed to cellulose decomposition. In New Zealand, Will (1967) found a gradual decrease in dry weight of *Pinus radiata* needle litter in the first three years, with a 50 percent loss of dry weight in two years. However, Kendrick (1959)

estimated weight loss of 24 percent in two years and 47 percent after seven years in *Pinus sylvestris* litter in England. According to Kendrick (1959), a needle of *Pinus sylvestris* spent an estimated time of 6 months, 2 years and 7 years in the L, F<sub>1</sub> and F<sub>2</sub> layers respectively, before being humified.

Woody components such as twigs and branches, although constituting a substantial proportion of total litter-fall, have generally received very little attention in decomposition studies in comparison to leaf litter. These components, high in lignocellulosic and low in N content, vary in their decomposition rates. Gosz et al. (1973) reported that in New Hampshire, the decomposition rate for hardwood branches was greater than that for conifer branches, but differences between hardwoods were not significant. Harris et al. (1972) found that the decay rate of wood was dependent on diameter, and doubling the diameter approximately doubled the turnover time.

Bark component, which averages 9 to 15 percent of the trunk volume (Käärik, 1974), generally undergoes slow decomposition. The high content of polyphenolic substances and fats, waxes and terpenes in bark tend to inhibit the growth of micro-organisms, thus hindering decomposition. Fogel and Cromack (1977) found that the decomposition rates of Douglas-fir needles, cones, bark and branches were in the order of needles > branches  $\approx$  cones > bark.

The lack of extensive research on root decomposition does not imply the unimportance of root contribution in an

ecosystem . Root biomass may constitute a considerable proportion of the total biomass in an ecosystem. In addition, decomposing root tissues provide energy substrate and nutrients to micro-organisms and earthworms. Literature on root decomposition has been reviewed by Waid (1974).

#### 2.3.4 Factors Governing the Rate of Decomposition of Litter

The rate of decomposition of litter is controlled by numerous factors, of which chemical composition of litter and environmental conditions represent the major factors. Extensive coverage of literature on litter decomposition and factors affecting decomposition is also given by Dickinson and Pugh (1974), and Singh and Gupta (1977).

##### 2.3.4.1 Chemical Composition of Litter

Litter of different tree species do not usually decompose at similar rates even under similar environmental conditions. Decomposition rates are often influenced by chemical composition and structure of the litter, which includes the amounts of water-soluble compounds, polyphenol content, N content and certain litter organic constituents.

##### 2.3.4.1.1 Water-soluble Constituents

Water-soluble substances are easily leached out and readily metabolised by micro-organisms (Alexander, 1977). The loss is usually very rapid, such that it is often difficult to determine appreciable quantities of these water-soluble substances in litter within a short time. Loss of this fraction has often been ascribed to account for

the rapid initial rate of litter decomposition (Gilbert and Bock, 1960; Bock et al. 1960; Jenny et al. 1949; Boyd, 1970; Melin, 1930).

The amount of water-soluble substances vary according to species. Gilbert and Bock (1960) reported that the contents of water-soluble substances in *Fraxinus excelsior* and *Quercus petraea* leaves were 32 and 18 percent respectively. After 1 month in the field, the amount in *Fraxinus* was reduced to 1.5 percent, while in *Quercus* the decline was more gradual. Nykvist (1963) compared the total amount of water-soluble substances leached from seven different leaf and needle litter. After one day of leaching, the values obtained were: ash 25%, birch 16%, spruce 14%, alder 13%, pine 11% and beech 18%. From the data obtained by Nykvist (1963) the ease of leaching appears to decrease in the order: alder  $\approx$  ash  $\approx$  birch > beech  $\approx$  oak > pine  $\approx$  spruce.

Anderson (1973a) concluded, from results obtained from field and laboratory experiments on litter decomposition, that after one year, most of the weight loss in beech leaf litter and up to 75 percent of that in chestnut leaf litter resulted from the leaching of water-soluble materials.

#### 2.3.4.1.2 Polyphenol Content

There is increasing evidence that the initial loss of polyphenolic compounds (Section 2.2.2) is important in the breakdown of litter in later stages. King and Heath (1967) found that litter became more palatable to soil

organisms after some weeks of weathering, when much of the water-soluble polyphenols were removed (see also Section 2.3.4.2). Kowal (1969) and Nykvist (1961) found that the initial leaching of freshly fallen litter led to an increased decomposition rate.

There appears to be an inverse relationship between polyphenol content and the rate at which leaves are broken down due to the feeding activities of soil animals (Heath and King, 1964; King and Heath, 1967; Satchell and Lowe, 1967). However, Anderson (1973b) did not obtain a good correlation between polyphenol content and soil animal activity. In addition, Feeny (1970) reported that insects were discouraged from attacking canopy litter by the presence of tannins. There is also evidence that the high polyphenolic content of oak and beech leaves appear to inhibit the growth of many fungi (Harrison, 1971).

Evidently, polyphenols play a role in determining differential rates of litter decomposition by influencing the decomposition of a variety of substrates. The degree of inhibition by tannins on decomposition of a number of substrates is given by Williams and Gray (1974). Handley (1954, 1961) reported that leaf proteins combined with polyphenols of the leaves to produce precipitates that resisted decomposition. In addition, Handley (1954, 1961) observed that the protein-polyphenol precipitates also impregnated decomposable substances such as cellulose and hemicelluloses, thereby possibly rendering these structural carbohydrates less susceptible to microbial attack. These polyphenolic-protein complexes are considerably more resistant



to decomposition than the separate constituents (Basaraba and Starkey, 1966).

The extent of inhibition of decomposition of protein through protein-tannin complexing depends on one, or possibly a combination, of several factors. More resistant compounds are produced where the amount of tannin is equal to or greater than the amount of protein in the combination. Basaraba and Starkey (1966) reported that the inhibitive effect increased with increase in the ratio of tannin to protein from 1:4 to 4:1. Also, tannins and protein-tannin complexes vary in their susceptibility to microbial attack. According to Lewis and Starkey (1968), there was considerable variation in the susceptibility to microbial attack of the different protein-tannin complexes of any one tannin, with complexes of high molecular weight tannins generally showing greater resistance to microbial decomposition. Inhibitive effects are also dependent on pH conditions. For example, it has been shown that such inhibition of protein decomposition was considerably greater at pH 4.0 than at pH 7.0 (Basaraba and Starkey, 1966; Benoit et al. 1968). Apparently, this effect is the result of pH influence in the dissociation of the tannin-protein complexes which is low at acid reactions and increases with increase in pH (Gustavson, 1956).

Tannins and related phenolic compounds have also been implicated in many ecological processes (see also Sections 2.3.4.3 and 2.4.4). One of these processes includes the condensation reactions with amino-acids to form humic substances which is exemplified by the reaction

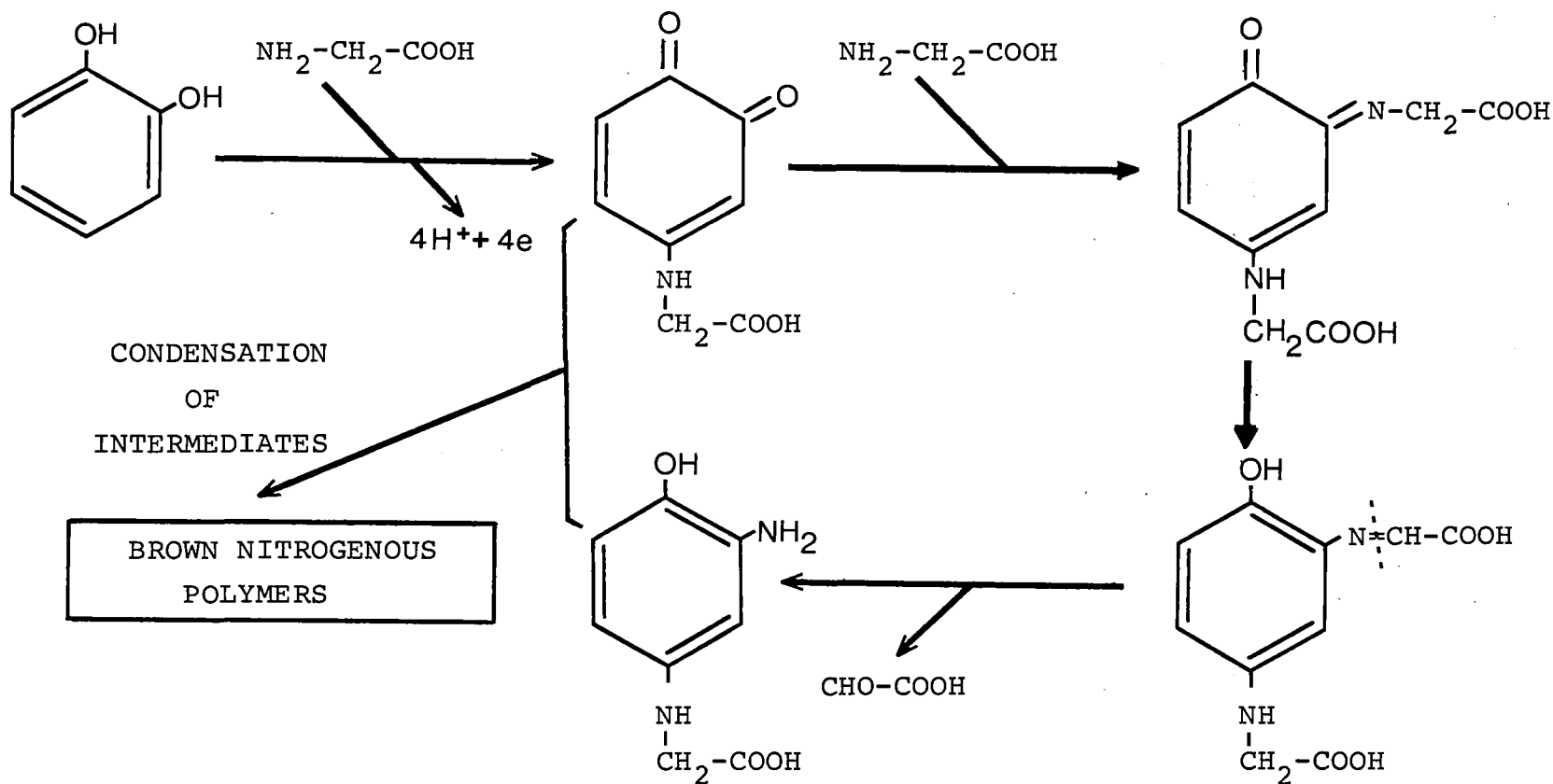


FIGURE 2.3.4.1.2 Formation of humic substances by condensation of amino acids and polyphenols, as exemplified by the reaction between glycine and catechol

between glycine and catechol (Figure 2.3.4.1.2). This effect is significant in decomposition processes since these humic substances are resistant to microbial attack (Parsons and Tinsley, 1975).

#### 2.3.4.1.3 Nitrogen Content

It is generally observed that litter rich in N decomposed more rapidly than those with low N content (Bocock, 1964), with protein-rich substrates being metabolised most readily (Alexander, 1977). In a series of experiments, Satchell and Lowe (1967) and Satchell (1967) found that N content was one of the factors contributing to litter palatability to soil animals.

The C:N ratio of microbial cells is approximately 10:1 (Alexander, 1977). Accordingly, litter with low N content or wide C:N ratio does not promote decomposition through increased microbial population as such litter has insufficient N for meeting the requirements of micro-organisms. In such a situation N becomes the limiting factor in controlling the rate of decomposition. However, Melin (1930) and Daubenmire and Prusso (1963) found poor correlation between N content and decomposition rates.

Many studies use total N values. However, total N estimates do not necessarily provide a good indication of the amount of N available to micro-organisms since most of this N may be strongly immobilised by complexation with lignin (Waksman and Iyer, 1932, 1933; Parsons and Tinsley, 1975; Section 2.3.4.1.2). Therefore, it may be useful to study the interactions between N and the polyphenolic compounds,

and their effects on decomposition of litter as this could lead to more accurate predictions of litter decomposition patterns.

#### 2.3.4.1.4 Organic Constituents

The influence on the overall litter decomposition rates by the structural components of the litter such as cellulose, hemicelluloses, lignin, fats and waxes can often be reasonably predicted. Decomposition rates of litter tend to vary according to the proportion of each component and is generally slow where lignin, fats and waxes constitute a large proportion. Lignin is chemically more variable (Figure 2.2.2.2) and is consequently more resistant to decomposition.

Commonly, hemicelluloses and cellulose are found to accumulate in relatively large amounts in organic matter, not because such components are resistant to decomposition, but because they are added in larger quantities than other components (Section 2.2.1). Waksman and Gerretsen (1931) found that under controlled conditions, hemicelluloses and cellulose were decomposed in a relatively short time. Decomposition rates of cellulose under field conditions have also been reported by other workers. Minderman (1968) found a 55 percent loss of cellulose in one year in an oak forest, this increased to 80 percent after 2 to 3 years. Sowden and Ivarson (1962) reported that 75 and 83 percent of the cellulose in coniferous and deciduous litter respectively, were lost under field conditions within a period of 3 years.

The decomposition of hemicelluloses and cellulose is also affected by the amount of N. Alexander (1977) quoted evidence indicating that the slow rates of decomposition could be enhanced by the addition of inorganic N.

Waxes are found in plants often as epidermal coatings on leaves and fruits, where their function is to prevent excessive water loss by transpiration. Consequently, fats and waxes have been found to affect the rate of wettability of litter surfaces to water (Holloway, 1971; Baker, 1971). Such actions delay the rate at which polyphenolic substances are removed, thereby delaying the onset of decomposer colonization. Minyard and Driver (1972) hypothesised that during the initial stages of decomposition of Douglas-fir needles, fungi are required to break down the waxes on the surface of the needles before the cellular component could be acted upon. Waksman and Tenney (1928) also found that the removal of ether-extractable fraction hastened slightly the decomposition of *Pinus strobus* needles.

The microbial degradation of lignin is generally slow relative to that observed for hemicelluloses or cellulose (Alexander, 1977). Consequently, the lignin content of senescing litter may be observed to increase as decomposition proceeds (Daubenmire and Prusso, 1963; Katagiri and Tsutsumi, 1972). Nevertheless, lignin does disappear under field conditions. Much of the lignin content of plant residues may be metabolised under optimum conditions. Waksman and Gerretsen (1931) found that at 37°C, as much as 50 to 60 percent of the lignin content of oat straw was decomposed in 9 months. Lignin generally retards overall decomposition

because of its own, even more resistant, products (e.g. condensed polymers of lignin degradation products, Figure 2.3.4.1.4) and its hindrance to enzymic hydrolysis of structural polysaccharides, such as the lignin encrustation of cellulose fibres (Bailey, 1973).

The relationship between lignin content of litter and the subsequent rate of decomposition was demonstrated by Cromack (1973) and Fogel and Cromack (1977). A better correlation was observed between leaf litter decomposition rates and lignin content than between decomposition rates and C:N ratio. These authors concluded that the lignin content of leaf litter excels over C:N ratio in predicting decomposition rates.

However, one of the major difficulties encountered in decomposition studies of the separate organic constituents of litter is the suitability of methods used in isolating these plant constituents. During the intermediate and later stages of decomposition, much of the plant residue remaining would generally bear no resemblance to its original constitution in fresh litter. It then becomes difficult to delineate between what had been originally plant substrates and chemical products synthesised by the associated microbial population. There is increasing evidence that humus materials are being formed from simple degradation products of plant constituents (Flaig, 1966; Goh, 1981; Goh and Stevenson, 1971; Stout et al., 1980). These simple degradation products condense into high molecular weight, brown-coloured polymers. The pathways through which this transformation could occur are shown in Figure 2.3.4.1.4 .

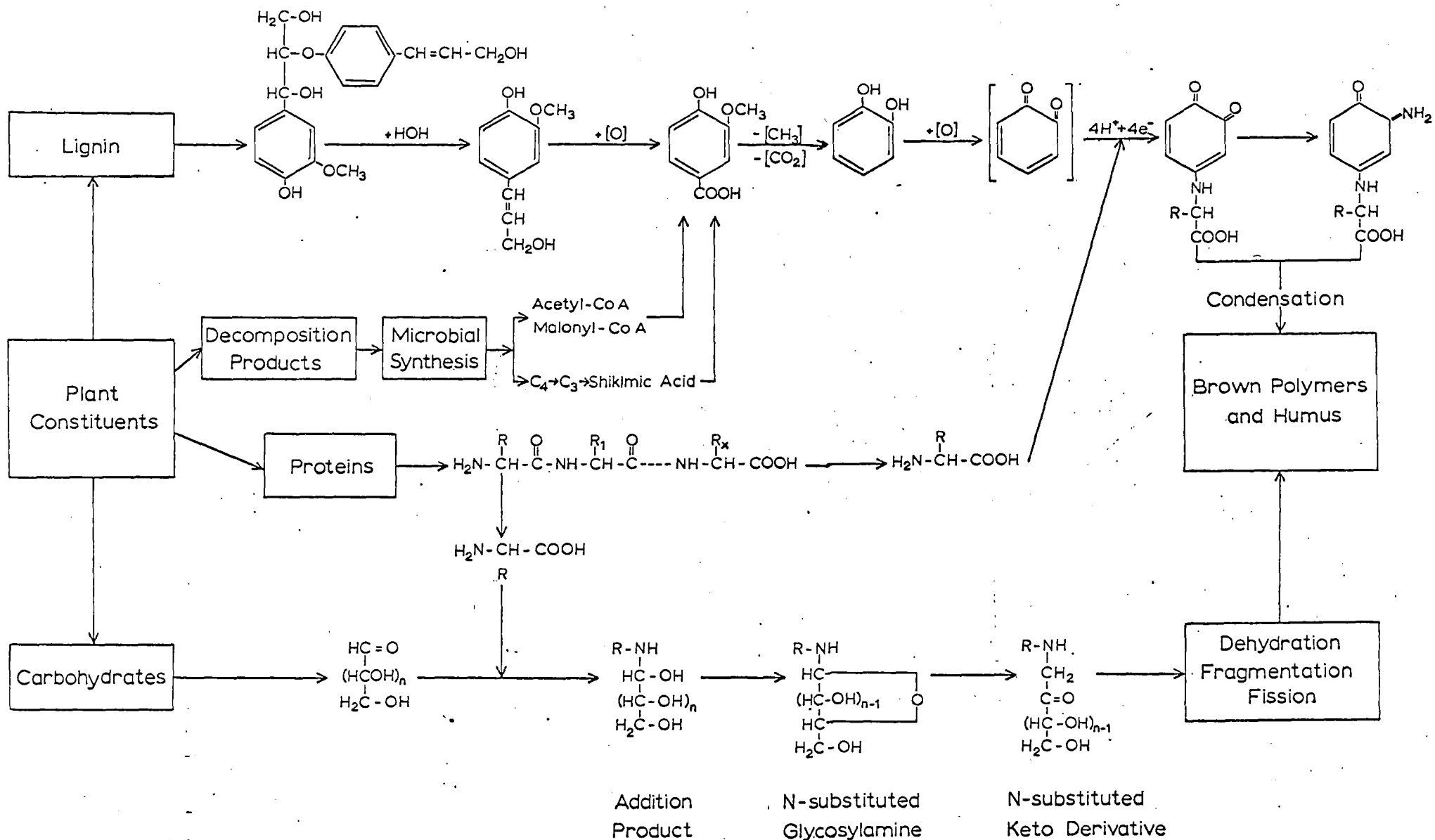


FIGURE 2.3.4.1.4 FORMATION OF HUMIC SUBSTANCES (Goh, 1981)

#### 2.3.4.2 Abiotic Environmental Factors

Major abiotic environmental factors affecting the rate of litter decomposition include temperature, moisture and aeration. Under conditions of adequate moisture, litter decomposition is controlled primarily by temperature (Witkamp, 1966b, 1971).

Olson (1963) reported that in northern and sub-alpine forests, temperature tends to retard biological activity. Consequently, in temperate forests, organic matter accumulation in the forest floor is usually greater than those of tropical forests (Olson, 1963; Rodin and Bazilevich, 1967). This dissimilarity in accumulation is attributed primarily to the more rapid decomposition rates of litter under tropical conditions than those under the cooler conditions of the temperate regions. For example, Jenny et al. (1949) found that alfalfa leaves placed in wire cages on the tropical soils of Colombia decomposed faster than those placed on the temperate soils of California. In Finland, Mikola (1960) found that the rates of decomposition of *Pinus sylvestris* and *Picea abies* litter increased with increase in mean summer temperature.

In a laboratory study with grass litter, Floate (1970b) found that 40 percent and 12 percent of the carbon content of the litter was lost at 30°C and 5°C respectively over the same experimental period. Waksman and Gerretsen (1931) found that increasing temperature hastened the decomposition of plant material, including the ether-extractable constituents, hemicelluloses, cellulose and lignin. The influence of temperature was most dramatic on lignin.

It is evident that the role played by the moisture



regime, interacting with temperature, in influencing litter decomposition rates, cannot be ignored. This has been frequently demonstrated (Witkamp 1963; Witkamp and van der Drift, 1961). Witkamp (1963) found a correlation between moisture content and weight losses of *Quercus alba*, *Fagus grandifolia* and *Morus rubra*, L. litters. In a tropical grassland, decomposition rates of mixed grass litter were found to be greater during the wetter periods than those in the following drier periods (Gupta and Singh, 1977 ). Effects of moisture on decomposition rates were also noted by Bocock et al. (1960) and Edwards and Heath (1963). Crossley and Hoglund (1962) and Madge (1965) associated the rate of weight loss of litter with the effect of moisture on soil animal populations.

The effect of moisture and temperature on litter decomposition rates is closely associated with their effect on microbial activity. Excessive moisture reduces soil aeration and hinders the movement of air, thus reducing the supply of oxygen to micro-organisms. Oxygen is required in the metabolism of carbonaceous matter by aerobic organisms. An extreme of such a situation of reduced aeration is when waterlogging occurs.

The quantitative release of  $\text{CO}_2$  (e.g. from forest floor) is commonly regarded as an indicator of the level of microbial activity. The measurement of  $\text{CO}_2$  evolution is frequently used as a technique to estimate organic matter decomposition rate (see Section 2.5.2). Witkamp (1963, 1966 a, b) obtained correlations of temperature with  $\text{CO}_2$  evolution from litters of *Pinus echinata* Mill., *Quercus alba*, L.

and *Acer rubrum*, L. Maximum CO<sub>2</sub> evolution was observed to occur in the afternoons when temperature was increased. Correlations of moisture with CO<sub>2</sub> evolution were also obtained.

#### 2.3.4.3 Soil Environment

Soil animals and soil organisms have a profound influence on litter decomposition. Soil animals facilitate litter decomposition in two effective ways. Firstly, by breaking down large litter into smaller fragments thereby exposing greater surface area for colonization and attack by micro-organisms. The second method relates to the mixing of organic debris into the upper horizon of the mineral soil during migration, thereby increasing contact between organic debris and micro-organisms inhabiting in the soil horizon. Extensive work on the role of soil animals (invertebrates and vertebrates) have been documented (Edwards and Heath, 1963; Witkamp and Crossley, 1966; Edwards et al., 1970; Anderson, 1975; Wood, 1976).

One usual approach used in evaluating the role of soil animals involve the use of nylon net bags of different mesh sizes to effectively exclude certain sections of the soil populations. Several workers (Edwards and Heath, 1963; Heath et al., 1964, 1966; Madge, 1965; Will, 1967; Anderson, 1973a) found differences in the rate of litter decomposition between litter in coarse and fine mesh bags. Greater losses of litter were generally observed in coarse mesh litter bags. Will (1967) examining decomposition of *Pinus radiata* needles in New Zealand, suggested that soil animals could become important in the litter decomposition

process after the third year of decomposition.

According to Grossbard (1969) litter decomposition was not accelerated by the enrichment from animal faeces. It was found that oribatid faecal pellets persisted in the litter for a long period of time.

The chemical content of litter appears to influence the palatability of litter to soil animals. Satchell and Lowe (1967) and Satchell (1967) found that the nitrogen, carbohydrate and polyphenolic content contributed towards litter palatability. According to Edwards and Heath (1963) litter became more palatable to anthropods as the water-soluble polyphenols were removed by weathering. The dissimilarity in decomposition rates of leaves were reported by Heath and Arnold (1966) to be dependent on the palatability of leaves as a result of their spatial position on the tree. Soft "shade" leaves were preferred by worms over the harder "sun" leaves. Higher polyphenolic content was also associated with hard "sun" leaves.

Undoubtedly, earthworms can consume a considerable amount of litter, thus facilitating the breakdown of litter. Raw (1962) found that in an arable orchard, earthworms consumed over 90 percent of the annual leaf-fall of 2000 kg/ha within a period of 5 months. In both beech and oak sites, earthworms consumed more leaf litter than the rest of the soil invertebrates altogether (Edwards and Heath, 1963).

In New Zealand, Styles (1967) found a change in the pattern of microfauna species as decomposition of *Pinus radiata* needle litter progressed, with a decrease in the micro-fauna population by the fourth year of litter decomposition.

It is useful to mention that insect consumption of forest canopy can be considerable. According to Gosz et al. (1972) insects consumed between 1.8 percent to 10.7 percent of the total leaf production of Hubbard Brook forests. In addition, species of insects collected from both sugar maple and beech foliage showed a marked preference for fresh beech leaves over leaves of sugar maple. Bray (1964) found that insect consumption ranged between 3.1 percent and 14.3 percent of forest canopies.

A comprehensive review of the role of various soil organisms on litter breakdown has been given by Dickinson and Pugh (1974).

#### 2.3.5 Methods of Measurement of Litter

##### Decomposition Rates

Numerous methods have been used to determine rates of litter decomposition and these are discussed here under the broad groupings of direct and indirect methods.

##### 2.3.5.1 Direct Methods

The direct methods involve essentially the initial placement of a known quantity of litter out in the field and the measurement of the periodic weight loss of the litter. This weight loss recorded over a period of time represents the decomposition rate.

The initial amount of litter is kept in account throughout the study period by one of several methods:

#### 2.3.5.1.1 Tethered-Leaf Technique

In this method, whole leaves are tethered by threads attached to the petioles (Witkamp and Olson, 1963; Lang 1973; Anderson, 1973a). Weight loss from each leaf is directly measured. Anderson (1973a) used this suspended tethered-leaf technique to measure the contribution by leaching to the total weight loss of litter. A disadvantage of this method is that fragmentation can frequently result in an over-estimation of the overall decomposition rate.

#### 2.3.5.1.2 Tracer Technique

This method makes use of radio-isotope tagging on the litter. The method is relatively specific in its use, and hence is a convenient way of measuring elemental losses during decomposition (Olson and Crossley, 1963; Witkamp and Frank, 1967; Thomas, 1969). This technique offers many advantages. For example, litter is maintained in a natural environment. The tracer technique can be used to examine the role of invertebrates in the decomposition process (Crossley and Witkamp, 1964; Witkamp and Crossley, 1966). One of the disadvantages is the difficulty involved in the incorporation of the radio-isotope into the study sample.

#### 2.3.5.1.3 Enclosure Technique

The enclosure technique involves the containment of litter under study in some form of netting material enclosure. In the early period wire-screening containers were used (Falconer et al., 1933; Gustafson, 1943). Due to the rigidity of the material, it was soon replaced by more

flexible plastic wires (Yamane and Sato, 1971), nylon netting (Bocock and Gilbert, 1957; Bocock et al., 1960) and fly-wire baskets (Ashton, 1975).

The use of litter-bags of varying mesh sizes has become increasingly popular, particularly as a means of estimating the role of the soil habitat in the breakdown of litter and nutrient release (Edwards and Heath, 1963; Heath et al., 1964, 1966; Anderson, 1973a; see also Section 2.3.4.3).

#### 2.3.5.1.4 Specific Substrate Technique

In this method, strips of pure substrates are buried in the forest floor. The amount of decomposition in a certain length of time is determined by the loss in surface area of the strips or the difference in tensile strength between new strips and the exposed strips. Substrates used in this technique includes cellulose strips (Golley, 1960; Lädhe, 1966) and calico strips (Springett, 1971). However, this technique is useful only in providing a way of estimating relative rates of decomposition and cannot be used to estimate the true rate of decomposition of natural plant tissues, since the method does not take into account interacting effects of other natural substrates such as lignin, poly-phenols and nutrients (see Section 2.3.4.1) which occurs in decomposition of natural plant tissues.

#### 2.3.5.2 Indirect Methods

One of the more common indirect methods used in connection with litter decomposition and organic matter

turnover is the procedure used in the determination of the decomposition constant,  $k$ , from litter addition and organic matter accumulation data (Attiwill, 1968; Reiners and Reiners, 1970; Edwards 1977; Redmann, 1975; Nye, 1961). The process of decomposition is described by mathematical models (Jenny et al., 1949; Olson, 1963; Witkamp and Olson, 1963).

Olson (1963) has examined the relationship between litter addition, decomposition and accumulated organic matter. In general, the instantaneous nett rate of change in the amount of accumulated organic matter,  $dx/dt$ , can be estimated by:

$$\frac{dx}{dt} = \text{input} - \text{loss} \quad (1)$$

With steady input of litter  $L$ ,

$$\frac{dx}{dt} = L - kX \quad (2)$$

where  $k$  is the decomposition constant,  $X$  is the amount of accumulated organic matter.

Assuming a steady state prevailed, which is frequently the case with mature forests, then the decomposition constant  $k$  can be estimated by the ratio of annual litter addition  $L$ , and the amount of accumulated organic matter at steady state  $X_{ss}$ , i.e.

$$k = \frac{L}{X_{ss}} \quad (3)$$

since at steady state, the amount of accumulated organic matter does not change (i.e.  $dx/dt = 0$ ) and hence

$$L = kX_{ss} \quad (4)$$

In a special case where there is no litter addition,  $L = 0$ , then Equation 2 becomes,

$$\frac{dx}{dt} = -kX \quad \text{or} \quad \frac{dx}{X} = -k dt. \quad (5)$$

On integration,

$$\ln \frac{X}{X_0} = -kt \quad (6)$$

$$\frac{X}{X_0} = e^{-kt} \quad (7)$$

where  $X_0$  = initial amount of litter (in litter-bag) and  $X$  = amount of litter remaining (in litter-bag) at time  $t$ .

This situation approximates decomposition of litter enclosed in litter-bags. The exponential model also permits the calculation of litter half-lives ( $0.693/k$ ) and time to reach 95 percent loss ( $3/k$ ). One of the disadvantages of this approach is the difficulty in determining with precision both  $L$  and  $X$  (Section 2.4.2).

Some other indirect methods have also been used in decomposition studies. The harvest method (Golley, 1965; Tyler, 1971; Singh and Yadava, 1974) estimates the rate of decomposition,  $D$ , by the equation

$$D = (A_i + L) - A_f$$

where  $A_i$  and  $A_f$  are the initial and final standing crop of litter,  $L$  is the litter production.

The paired-plots technique (Wiegert and Evans, 1964;



Lauenroth, 1970; Wiegert and McGinnis, 1975) represents another approach. In this method, two quadrats of similar areas with relatively homogeneous vegetation are selected. All living vegetation is removed from both quadrats and then dead litter is removed from only one quadrat. After a time interval, the dead litter from the second quadrat is removed. The weight of litter decomposed during the time interval is given by the weight of dead litter on the first plot minus that of the second plot.

As it would appear, there seems to be no perfect method for determining the rate of decomposition under natural conditions; most methods offer some advantages but also suffer some disadvantages. Some comparisons of the decomposition rates derived from various methods have been reported; between litterbags and paired plots (Wiegert and Evans, 1964; Wiegert and McGinnis, 1975), between litterbag and tethered leaves (Witkamp and Olson, 1963; Woodwell and Marples, 1968; Anderson, 1973a) and between litterbag and decomposition constant (litterfall-accumulation) (Edwards 1977).

## 2.4 ORGANIC MATTER OF FOREST FLOOR

### 2.4.1 Introduction

Forest floor accumulation, largely the result of litter production and litter decomposition, is also influenced by the age of the floor and the elapsed time since the last fire or other disturbances. The importance of organic matter lies in its storage of large resources of nutrients and energy substrates. It is also often suggested that soil

organic matter represents the most important factor in the creation of good soil structure by influencing the physico-chemical properties of the soil. It also appears to be a factor in soil stability.

The present review discusses briefly some of the features of organic matter mentioned above.

#### 2.4.2 Accumulation of Organic Matter

There is often a difficulty in obtaining a quantitative estimation of the accumulation of organic matter of the forest floor. The thickness of accumulation is often unpredictably variable although a greater degree of accumulation is generally found around tree boles (Ovington, 1968). Various other factors are also known to influence the accumulation of organic matter. The uprooting of trees by wind-throw during storms can give rise to an uneven distribution of falling litter, and thus in the collection of fallen litter. Commonly, pits formed from the uprooting cause litter to accumulate to considerable depths (Lyford, 1973). Variability in thickness of organic matter layer is not uncommon in mountainous forest sites where a terracing type of topography has developed. Data by Hart et al., (1962) indicate the relationship between the amount of accumulated litter and surface topography of site. Considerably larger accumulations of leaf fall was found in depressions than in mounds. Leaf litter accumulated on slopes were intermediate. Mean annual accumulations, determined for three years, ranged from 4.69 to 7.33 tonnes/ha in depressions; from 2.83 to 2.98 tonnes/ha on slopes; and from 1.06 to 2.08 tonnes/ha on mounds.

Forest fires can drastically alter the organic matter status in a short time. Armson et al., (1973) studying the effect of fire on the organic layer in the boreal forests of Canada found a loss of about 50 percent of the surface organic matter. Generally, the extent of loss will depend on the intensity of the fire. Under controlled conditions, Sweeny and Biswell (1961) found that 76 percent of the litter and 23 percent of the duff layer in a ponderosa pine stand was destroyed. Besides reducing organic matter, fire also increases the base content and pH of the organic layer (Viro, 1974).

Increase in organic matter accumulation can be brought about by tree pruning and thinning. However, generally under natural conditions, forest development accounts for most of the increase. Foster and Morrison (1976) found a build-up of forest floor organic matter with stand age.

Some figures of the amount of organic matter on forest floor were reported by Remezov and Pogrebnyak (1969). The amounts varied from 22 to 35 tonnes/ha conifers, 27 to 77 tonnes/ha for mixed conifer-hardwoods and 35 to 95 tonnes/ha under hardwood forests in Russia. Greater accumulations than the above have also been reported under coniferous stands (Gessel and Balci, 1965) and under yellow birch-red spruce stands (McFee and Stone, 1965).

Frequently, due to dissimilar chemical composition of different species, the nutrient budget of forest floor may form a different picture to that given by dry weight data. For example, Tarrant and Miller (1963) found an accumulation of organic matter of 27.5 tonnes/ha for a 30-year-old Douglas-

fir stand, and where a red alder had been introduced the accumulation was 32.1 tonnes/ha. Although the weight difference was not great, quite a contrasting situation was clearly evident when nitrogen status was considered. In the Douglas-fir stand the total nitrogen amounted to 158 kg/ha as compared to the Douglas-fir - red alder accumulation of 462 kg/ha.

A comparison of organic matter accumulation and nutrient contents in stands of aspen and birch in Alaska was reported by Van Cleve and Noonan (1971). They found that although no significant difference exists between forest types in mass of the forest floor, the chemical status and chemical properties were quite different.

#### 2.4.3 Source of Nutrients

The organic matter on the forest floor is the habitat and centre of life activities of various communities like the fauna, microflora and root systems of higher plants. It comprises of a diverse range of groups of constituents and represents a reservoir of most nutrients involved in the cycling processes. Generally, nutrients such N, P, and Mg tend to accumulate on the forest floor at a greater rate than other elements (Foster and Morrison, 1976).

While the greater proportion of organic matter is of plant origin, considerable amounts of it are also derived from microbial synthesis. Organic matter contains significant quantities of both living and dead microbial cells, animal tissues and faeces, and products synthesised by micro-organisms. Some of these products such as faeces may persist

for long periods of time (Grossbard 1969) and therefore, may be present in increasing proportion in organic matter as time progresses.

The microbial population is important, if not essential to the decomposition of organic residue and hence the availability of nutrients strongly bound in organic residue. Boyle et al., (1974) reported that acids formed in the transformation of soil organic matter, and also those excreted from living organisms, can contribute to the solubilization of nutrients from mineral components of soil or parent material. However, in some situations, such as during population build-up, the microbial population may actually pose as competitors for the supply of nutrients.

Generally, as much as 5.0 to 5.5 percent of the total weight of organic matter comprises of N. Almost all of this N is held in organic combination such as bound amino-acids and amino sugars, and thus, is not available for plant use (Alexander, 1977). Weetman and Webber (1972) reported that organic matter accumulation due to the slow rate of decomposition in soils of the boreal forests and other cool climate areas sometimes result in nitrogen deficiencies. The release of N from these N sources are brought about by mineralization to ammonium and nitrate by the microbial populations (Alexander 1977).

Micro-organisms also have a marked influence on the availability of phosphates from organic matter. It appears that a number of species are capable of solubilising phosphates, making available for plant uptake and utilization. Some organic acids, particularly citric acid, produced in soil by

micro-organisms can effectively prevent the precipitation of phosphate by iron and aluminium (Struthers and Sieling, 1950). Also, similar action was found with humus substances (Williams, 1960; Domaar, 1963), phenolics (Appelt et al., 1975) and several sugars (Bradley and Sieling, 1953). In examining the origin of released phosphorus, Van Diest and Black (1959 a,b) concluded that a considerable quantity of organic phosphorus was released to growing plants during a growing season.

There appears to be ample evidence indicating that biological factors influence, directly or indirectly, the availability of various nutrients. Microbial influence on K availability may not be as significant as with other more strongly bound cations, mainly because K is not in organic form in plants as is the case with P, N, Ca and Mg. Thus this makes K more mobile and readily released for plant use or leaching. Magnesium and calcium, which are involved in plant structural functions are more dependent on the decomposition of the organic residues for their release.

#### 2.4.4 Effects on Mineral Soil

Organic matter has been established as the main contributing factor in the development of soil physical and chemical properties. Even by its mere existence on the forest floor, it affects such properties as soil moisture and temperature. It also buffers the soil from the sun and wind thereby reducing losses of moisture from evaporation. Organic matter particulates mixed with the mineral soil may improve the water infiltration rate and reduces losses from run-off (Wischmeier and Manning, 1965). This is particularly

notable and effective with steepland soils. Organic matter increases filtration by checking and retaining the flow of water on the surface sufficiently long enough for seepage to occur into the soil. Generally, crusting of the soil surface has a greater likelihood of keeping out filtration than when soil aggregates are in place. However, it has been suggested that permeability of soils heavily mixed with organic matter may be reduced as a result of waterproofing by products of microbial metabolism (Russell, 1973).

It is not uncommon to find that some soils are water repellent and difficult to wet because of the presence of certain hydrophobic organic substances (Wander, 1949; Fink, 1970; Giesecking, 1975). Although the lipids (fats, waxes) of organic matter are seldom considered as having an important influence on soil properties, because of their distinctly hydrophobic nature, they are often suggested as responsible for such a phenomenon. Apparently, certain substances produced by micro-organisms can generate similar occurrences (Savage et al., 1969a, b). On the other hand, lipids can stabilise soil aggregates through waterproofing the aggregates.

The mechanism of soil aggregation has commonly been associated with polysaccharides (Greenland et al., 1961, 1962; Martin et al., 1965; Harris et al., 1963; Mehta et al., 1960). Polysaccharide is a constituent of plant matter and is also a product of micro-organisms. The stabilization of soil aggregates is most likely produced by polymer molecule bridging particles forming the aggregate. Soil aggregation is especially important due to the ability to generate a

continuity of pores in the soil to allow adequate air and water movement.

Organic matter also contributes to the increase in cation exchange capacity of soils. Carboxyl and phenolic groups function as additional exchange sites for cations, retaining them against leaching losses. The chelating ability of organic matter is important in the supply of trace elements (e.g. Zn, Cu, Mn, Fe) to plants.

Tannins and related polyphenols constitute one of the major groups of active chemical compounds in organic matter, and have frequently been implicated in the process of soil development (Bloomfield, 1957; Coulson et al., 1960a, b; Hingston, 1963; King and Bloomfield, 1966; Davies, 1971). The solution and transport of iron in soil is apparently caused by the joint action of carboxylic acids and polyphenols. In addition, polyphenols are suspected of promoting the development of a horizon of clay accumulation.

Polyphenolic compounds have also been implicated in many other ecological processes associated with soil organic matter such as: the development of mor-type organic matter (Davies et al., 1964a, b; Handley, 1954, 1961); the protection of litter against decomposition by micro-organisms (Nykqvist, 1961; Harborne, 1964; Kowal 1969; Harrison, 1971; Williams and Gray, 1974) and by macro-organisms (King and Heath, 1967; Heath and King, 1964; Satchell and Lowe, 1967; Feeny, 1970); the inhibition of nitrification (Basaraba, 1964; Rice, 1965, 1969; Rice and Pancholy, 1973, 1974), and the inhibited degradation of some specific plant substrates such as cellulose, hemicelluloses and



nitrogenous substances (Benoit and Starkey, 1968; Lewis and Starkey, 1968; Benoit et al., 1968; Verma and Martin, 1976). Very little information is available on the relationship between plant phenolics and ammonification.

## 2.5 CARBON AND NITROGEN MINERALIZATION

### 2.5.1 Introduction

During the process of organic matter decomposition, the decomposers utilize the organic substrates as energy source and supply of carbon for cell synthesis. This assimilation of carbon requires a concomitant uptake of some nutrients such as N, P, K and S. Nitrogen, which is essential to plant and microbial growth, is present in only a small proportion as the plant available forms of ammonium and nitrate ions. The availability of ammonium and nitrate is dependent on the rate of mineralization which is brought about by micro-organisms.

### 2.5.2 Carbon Mineralization

Organic matter constitutes a pool of highly diverse carbon substrates under constant utilization by the soil microbial population. Thus, the evolution of carbon dioxide from the litter-soil sub-system, often referred to as soil respiration, is commonly regarded as an index of microbial activity; as a measure of forest floor metabolism. However, it is important to indicate that several processes contribute to the release of carbon dioxide from the forest floor.

These are microbial respiration (Gray and Wallace, 1957; Witkamp, 1966a; Clark, 1967; Anderson and Domsch, 1973, 1975; Minderman and Vulto, 1973), root respiration (Monteith et al., 1964; Kucera and Kirkham, 1971; Harris and Bavel, 1957; Crapo and Bowmer, 1973; Odum et al., 1970; Coleman, 1973), fauna respiration (Macfadyen, 1963; Kitazawa, 1967; Reichle et al., 1975; Edwards and Sollins, 1973) and chemical oxidation (Bunt and Rovira, 1954, 1955; Hilger, 1963).

#### 2.5.2.1 Factors Influencing Carbon Mineralization

Several factors are known to influence the rate of soil respiration. The major factor among these is temperature. Voluminous literature has been written on the effect of temperature on soil respiration (e.g. Lundegarth, 1927; Elkan and Moore, 1960; Monteith et al., 1964; Reiners, 1968; Kucera and Kirkham, 1971; Boois, 1974; Witkamp, 1966a, b; Wiant, 1967a; Edwards, 1975).

Witkamp (1966a, b) obtained a correlation of temperature with  $\text{CO}_2$  evolution from litter. He reported a predawn minimum and an afternoon maximum in the rates of  $\text{CO}_2$  released. His result, therefore, indicates a diurnal effect on  $\text{CO}_2$  production, and suggests the need to measure  $\text{CO}_2$  evolution over 24-hour periods to overcome this effect.

Under controlled laboratory conditions, Wiant (1967a) found a logarithmic increase in  $\text{CO}_2$  production with increase in temperature. Between  $20^\circ$  and  $40^\circ\text{C}$ , soil respiration followed a  $Q_{10} \approx 2$ . Witkamp and Frank (1969) examined the effect of temperature on  $\text{CO}_2$  evolution from litter-bags,

litter layers and entire soil profile, and recorded  $Q_{10}$  values of approximately 2.5, 3 and  $>1.5$  respectively. Logarithmic increases in soil respiration rates with increasing soil temperature have also been observed in temperate woodland soils (Anderson, 1973c) and in tropical plant communities (Medina and Zelwer, 1972).

Generally, moisture has a positive effect on rates of soil respiration (Wiant, 1967b; Clark and Coleman, 1972; Medina and Zelwer, 1972; De Jong et al., 1974). Drying-rewetting cycles, which are more frequent in exposed places (e.g. clear-cut, grasslands or burned sites) or areas with low rainfall, has significant effects on  $CO_2$  production. Birch (1958) has demonstrated that  $CO_2$  production is stimulated by the drying-rewetting cycle. The degree of stimulation was dependent on the drying conditions. Working with labelled cellulose incubated in various soils, Sørensen (1974) found that the effect of drying-rewetting decreased with time. Birch (1958) attributed the decline to a decrease in microbial activity rather than substrate exhaustion.

In general, the effect of moisture on soil respiration is not as dramatic as that of temperature except, perhaps, in extreme situations. Boois (1974) reported that in the litter layer of an oak forest, moisture contents below 20 percent resulted in virtual cessation of respiration while above 27 percent, increasing moisture content had no influence on respiration. Edwards and Sollins (1973) correlated daily fluctuations in  $CO_2$  evolution to litter moisture and found no marked variation when the moisture was

more than 50 percent of the dry weight. Waterlogging conditions were found to depress the rates of  $\text{CO}_2$  evolution (Kucera and Kirkham, 1971).

Numerous studies have indicated that there is a general decrease in respiration rate with increase in the depth of the soil profile. (Lundegardh, 1924; Makarov, 1960; Jorgensen and Wells, 1973). According to Clark and Coleman (1972), the top 5cm and the next 5 to 10cm layer of the soil profile contributed 75 percent and 10 percent respectively, of the daily output of  $\text{CO}_2$ . However, De Jong and Schappert (1972) observed that under certain conditions when there was an increase in soil temperature with depth and decrease in moisture content in upper layers due to evapo-transpiration, lower  $\text{CO}_2$  evolution rates at the top layer occurred.

Although several studies on soil respiration rates have been reported in the literature, very few investigations have actually estimated the varying contributions made by the total carbon lost through respiration from various soil horizons. One such study, by Edwards and Harris (1977), indicated that of the total carbon lost annually as  $\text{CO}_2$  from the forest floor ( $1,065 \text{ gcm}^{-2}$ ), 42.2%, 35.0%, 19.0%, 9.7%, and 2.2% was derived from root decay, living root respiration, 01 litter, 02 litter, and catabolism of root exudates and soil organic detritus, respectively.

The importance of light intensity is illustrated by the results of De Santo and Alfani (1971) which showed that the degree of light intensity influences soil metabolism. Soil respiration rates were found to decrease with increasing

shading over time. In addition, the density of bacterial and fungal populations were much higher in plots at greater light intensities.

Respiration rates, as obtained in tropical and temperate regions, have been presented in a review by Singh and Gupta (1977). Maximum soil respiration rates reported for temperate forests using alkali absorption techniques range from 100 to 2340 mg CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup>, with most values falling in the range 100 to 500 mg CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup>. The method used and the measurement period appear to account for some of the variability between values reported by Singh and Gupta (1977). For example, in comparison the air current technique generally gives higher values than the static alkali absorption technique.

#### 2.5.2.2 Method of Quantification

A wide range of methods and procedures have been used for respiration rate measurement, either in the laboratory or under field conditions. These methods include infra-red gas analysis (IRGA), gas chromatography (GC) and alkali absorption methods (BA).

Results of respiration rates as obtained by the various methods have been examined, for example, between IRGA and BA (Witkamp, 1969; Kucera and Kirkham, 1971; Edwards and Sollins, 1973) and also between IRGA, GC, BA and Gilson respirometry (Van Cleve et al., 1979). Generally, BA tends to give an underestimation of the CO<sub>2</sub> production than that measured by IRGA. For example, Edwards and Sollins (1973) found that under similar field conditions,

respiration measurements with BA were 63 percent of IRGA values at 20°C and 90 percent at 12°C. However, under laboratory conditions, Ino and Monsi (1969) obtained similar CO<sub>2</sub> evolution rates by both methods. Van Cleve et al., (1979) found that both IRGA and BA gave greater estimates than GC and Gilson respirometry. In general, methods measuring CO<sub>2</sub> production employing free diffusion movement through the soil could give more reliable estimates than those which employed enforced flow through the soil (Wiant, 1967c).

According to Kirita and Hozumi (1966) and Kirita (1971a, b), the alkali absorption method is dependent on, among other factors, the effective absorption surface area of the alkali solution, and also the height of this absorption surface above the forest floor. In addition, to achieve an absorption rate greater than 90 percent of the potential rate, at least 80 percent of the initial amount of alkali must remain unused at the end of the measurement period.

The alkali absorption method, nevertheless, has found popularity among many workers and is observed to be widely used (Singh and Gupta, 1977). The method is simple, cheap and enables extensive replications under field conditions. These features are especially important in field studies when considering the variability of soil respiration. Moreover, many of the more sophisticated methods that are found to offer greater precision in laboratory studies prove cumbersome and impractical for field studies.

### 2.5.3 Nitrogen Mineralization

Organic matter of the forest floor represents a large potential supply of N, but not necessarily one of readily plant-available form of N (e.g. ammonium and nitrate). The status of the latter pool of N is very much governed by the nett outcome of the continuously and simultaneously occurring processes of mineralization and immobilization of N (Alexander, 1977). In addition, this small pool of inorganic N is also affected by a number of biotic and abiotic factors.

#### 2.5.3.1 Factors Affecting Nitrogen Mineralization

Several factors affect soil N mineralization rates and these have been discussed in detail in a number of reviews (e.g. Haynes and Goh, 1978).

##### 2.5.3.1.1 Temperature and Moisture

The process of ammonification and nitrification are temperature dependent. Generally, both processes are limited by low temperatures, with nitrification suppressed more than ammonification. Optimum ammonification occurs between the temperature range of 50° to 70°C while optimum nitrification is generally found between 25° to 35°C (Harmsen and Kolenbrander, 1965). Below the optimum temperature (25° to 35°C), nitrification decreases gradually down to the freezing point.

From a laboratory study, Myers (1975) found that in a tropical soil, the optimum temperatures for nitrification and ammonification are about 35° and 50°C respectively. Tyler et al. (1959), however, found that nitrification

proceeded at a moderate rate even below  $8^{\circ}\text{C}$  and occurred at temperatures as low as  $3^{\circ}\text{C}$ . Anderson (1960) found considerable nitrification above  $6^{\circ}$  to  $7^{\circ}\text{C}$  and Frederick (1956) reported formation of nitrates from ammonium at all temperatures between  $2^{\circ}\text{C}$  and  $35^{\circ}\text{C}$ .

It appears that the relationships describing temperature and N mineralization may vary between climatic zones. Optimum nitrification was found to take place at a lower temperature for soils of northern areas of United States than it did for soils from more southerly areas (Mahendrappa et al., 1966). Although nitrification above  $45^{\circ}\text{C}$  is rare (Harmsen and Kolenbrander, 1965), Myers (1975) found measurable nitrification occurring even at  $60^{\circ}\text{C}$  in tropical soils. This suggests a possibility that nitrifiers in tropical soils may build up a greater tolerance level of temperature extremes.

However, according to Kowalenko and Cameron (1976) neither ammonification nor nitrification showed a quantitative relationship with temperature since there is a significant interaction between temperature and moisture.

In soils under water-logged conditions, and hence reduced aeration, nitrification is suppressed. Ammonification is less affected. Generally, although nitrification and ammonification are affected by low moisture contents, appreciable nitrification has been found at 4 percent moisture (Greenland, 1958). Robinson (1957) detected nitrification even at the wilting point (of  $pF = 4.2$ ). Ammonification has also been reported to occur at low moisture contents, sometimes under air-dry conditions



(Robinson, 1957; Greenland, 1958; Dommergues, 1959).

#### 2.5.3.1.2 Soil pH

Nitrogen mineralization is influenced by the pH of the soil environment. Acidity tends to depress but does not eliminate mineralization. Alexander (1977) indicated that nitrification usually decreases below pH 6.0 and becomes negligible at pH 5.0. Usually the soil environment with a pH range of 5 to 8 favours nitrification. The more complex ammonifying micro-organisms are, however, less sensitive to the pH effect.

Nitrite accumulation seldom occurs under average soil conditions because of the rapid oxidation of nitrite to nitrate by *Nitrobacter* organisms as compared to the formation of nitrite from ammonium by *Nitrosomonas* species. However, temporary accumulation of nitrite can occur at around pH 7.5 to 8.0 when oxidation of nitrite to nitrate is retarded while nitrite formation from ammonium continues (Chapman and Lieberg, 1952; Soulides and Clark, 1958; Broadbent et al., 1958).

Although nitrification is expected to become negligible below pH 5.0, populations of nitrifiers have been found even at a relatively lower pH. Boswell (1955) detected nitrifiers in soils with a pH as low as 3.8. Also, considerable populations of nitrifiers were found in cut-over forest soils at pH 4.0 (Smith et al., 1968). Weber and Gainey (1962) found high levels of nitrate in soils of pH less than 4.0.

According to Gray and Williams (1975), certain strains

of nitrifiers may exist with different pH requirements, but these have not been isolated. Furthermore, it is also possible that nitrification observed may actually occur in small pockets of soils of high pH conditions than that determined from bulk soil samples (Smith et al., 1968; Gray and Williams, 1975). Generally, low nitrification is associated with low pH (Ross, 1958; Ross and McNeilly, 1975), which appears to be the dominant factor governing patterns of nitrification in many soils (Morrill and Dawson, 1967; Russell, 1973).

#### 2.5.3.1.3 Chemical Properties of Soil Environment

There is increasing evidence that some of the chemical constituents of overlying tree litter play a role in influencing mineralization (Basaraba, 1964; Rice, 1965, 1969; Munro, 1966b). Polyphenolic compounds, in particular, have been implicated as a major factor contributing to inhibition of nitrification (Rice and Pancholy, 1973, 1974). The compounds appear to be strongly inhibitory to nitrification even at low concentrations. This phenomenon of nitrification inhibition by polyphenolic compounds has often been associated with climax vegetation (Rice and Pancholy, 1972; Munro, 1966b).

Nitrification was found to increase greatly after clearing of the above ground vegetation (Berlier et al., 1956; Dominski, 1972). Upon clear-cutting a Connecticut forest, Smith et al. (1968) found an 18-fold increase in *Nitrosomonas* and a 34-fold increase in *Nitrobacter* populations. Nitrate concentration in the stream water was also found to increase

subsequent to clear-cutting (Likens et al., 1969).

It is also possible that variable tree litter under different species play an important role in controlling pH, nitrification and mineralization (Lodhi, 1977). Generally, low rates of N mineralization are found in most grassland. This phenomenon has been variously attributed to the ability of grassroots to inhibit mineralization (Theron, 1963; Robinson, 1963; Neal, 1969; Rice, 1965). Certain species of grass have been shown to secrete substances which inhibit the growth of nitrifying bacteria (Boughney et al., 1964). Water extracts of roots were also found to have a similar effect on nitrification (Munro, 1966b).

In a laboratory study of N mineralization in soil, Fenton (1958) found that additions of litter produced a marked decrease in the rate of release of mineralized N from soil columns. The inhibition was observed to be greater with *Pinus radiata* litter than with *Betula* spp. (birch). Release of nitrate was found with *Betula* spp. but not with *Pinus radiata*.

Ivarson and Sowden (1959) suggested that nitrate formation which occurred in deciduous litter but not in coniferous litter may be related to the higher initial N content of deciduous litter. During the decomposition of grassland litters, Floate (1970a) found that 13.9 percent of the original N (1.39%) of *Agrostis-Fetisca* litter was mineralized compared with 6.8 percent from *Nardus* litter (0.89% original N) during the same period.

In temperate regions, mineralization of N appears to follow a seasonal pattern (Ellis, 1974) with low ammonifi-

cation and nitrification in winter months and high levels during summer (Gasser, 1961). Sometimes nitrification may occur for a short period during spring and autumn (Davy and Taylor, 1974). Usually, in temperate regions very low nitrification occurs in many acid soils while in the tropical regions, rapid nitrification often occurs throughout the year even in strongly acid soils (DeRham, 1970).

It is evident that mineralization-immobilization of N is affected by many factors and their complex interactions, thus making possible only broad generalizations on the available N supply. Essentially, mineralization of organic N generally requires a favourable biological environment.

CHAPTER 3

LITTER PRODUCTION

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## CHAPTER 3

### LITTER PRODUCTION

#### 3.1 INTRODUCTION

In a forest ecosystem, the organic matter in the forest floor is an important source of nutrients and energy substrates for both soil organisms and trees. The major supply of this organic matter is litter. Thus, measurements of litter-fall occurring in a forest ecosystem provide information on the productivity of the ecosystem.

The objectives of the present study were to quantify the litter-fall in selected beech forests and *Pinus radiata* plantations, and to carry out chemical analyses of litter in order to obtain information on the regulation of chemical budgets within and between these forest ecosystems.

#### 3.2 MATERIALS AND METHODS

##### 3.2.1 Study Areas

Litter-fall in a beech stand and in an adjacent *Pinus radiata* stand in each of three forests located in the South Island (Figure 3.2.1) was measured in order to provide a more

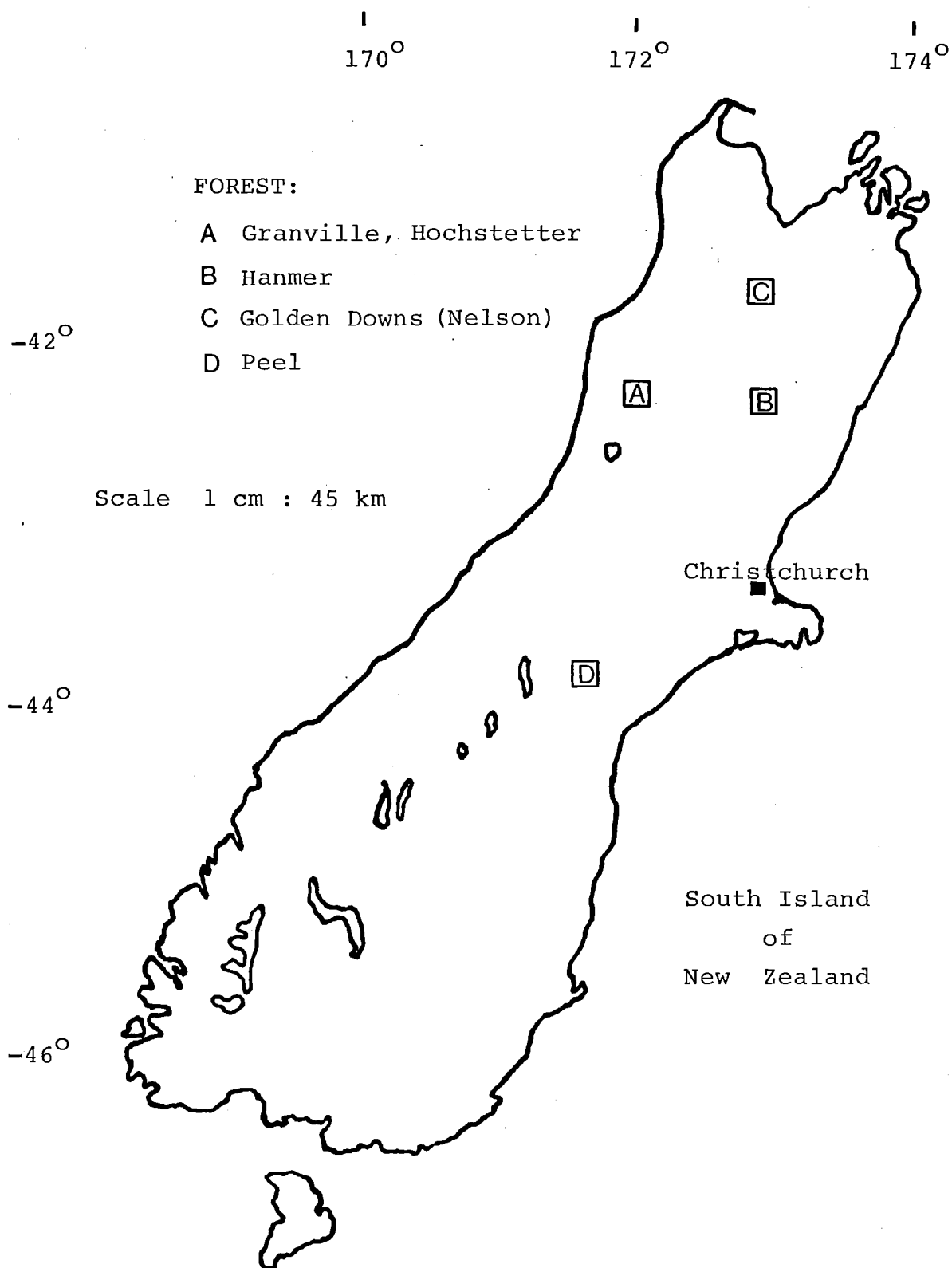


FIGURE 3.2.1 Location of the forest areas used in the present study.



TABLE 3.2.1 Climatic conditions, forest species, topography and soil types for forest stands at Granville, Hanmer and Nelson.

Forest	Climatic Conditions <sup>‡</sup>				Forest Species <sup>‡‡</sup>		Topography			Soil Type <sup>#</sup>
	Rainfall (mm)	Air Temperature (°C)	Mean	Max.	Min.	in Stands Used	Slope <sup>@</sup>	Aspect	Altitude	
Granville	2630	11.7	24.2	-1.9	<i>Nothofagus truncata</i>		25°	S-W	210	Mahoney Steepland
					1955-planted	<i>P. radiata</i>	25°	S	170	Granville Steepland
Hanmer	1380	10.0	32.5	-7.9	<i>Nothofagus solandri</i> var <i>cliffortioides</i>		10°	S-W	450	Tekoa Hill
					1960-planted	<i>P. radiata</i>	25°	S-W	580	Tekoa Hill
Nelson	840	12.3	27.3	-3.8	<i>Nothofagus solandri</i> var <i>solandri</i> and <i>Nothofagus solandri</i> var <i>cliffortioides</i>		10°	S	570	Spooner Hill
					1956-planted	<i>P. radiata</i>	15°	S-W	430	Spooner Hill
					1956-regen.	<i>P. radiata</i>	25°	S-W	460	Spooner Hill

‡ provided by New Zealand Meteorological Service, data refer to mean annual values for 1977 and 1978  
 ‡‡ dominant forest species  
 @ predominant slope  
 # see also Appendix I

accurate quantification of litter-fall occurring in beech and *Pinus radiata* forest stands under a wider range of environmental conditions. These forests and stands were:

(a) Granville forest: situated on the west coast and located approximately 300 km north-west of Christchurch; a *Nothofagus truncata* stand and a 1955-planted *Pinus radiata* stand were selected,

(b) Hanmer forest: located about 160 km north of Christchurch; a *Nothofagus solandri* var *cliffortioides* and a 1960-planted *Pinus radiata* were selected,

(c) Golden Downs forest: near Nelson, located about 400 km north of Christchurch; a mixed-beech stand (main species: see Table 3.2.1) and a 1956-planted *Pinus radiata* stand were selected. In addition to these two stands, a 1956-regenerated *Pinus radiata* stand was used.

Effort was made to keep the stands at each forest as close to each other as possible and on similar soils. Aspect of all stands chosen were also kept similar. Detail descriptions of these forest stands are given in Table 3.2.1 .

To facilitate statistical analysis and comparison of experimental data obtained, the experimental area of 50m x 30m in each forest stand was divided into 5 identical experimental plots (10m x 30m)

### 3.2.2 Experimental Procedure

The trap used in the collections of litter-fall consists of an open-ended cylindrical-shaped polypropylene bag stitched open onto a circular metal hoop (Figure 3.2.2). The bottom of this bag was tied closed with a nylon string.

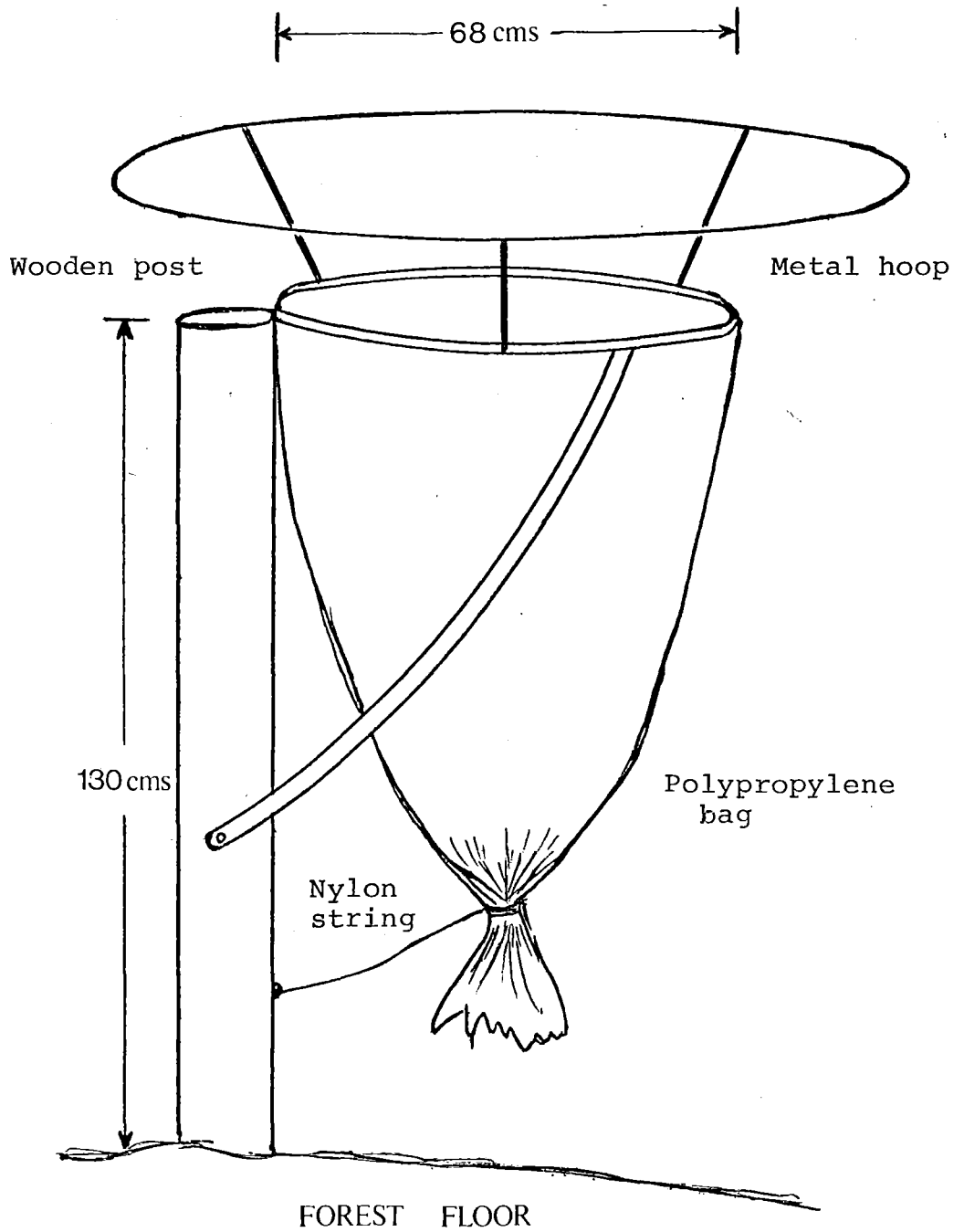


FIGURE 3.2.2 DIAGRAM OF LITTER-TRAP

About 30 cm above the mouth of the bag was constructed another larger parallel hoop to deter birds from perching on the mouth of the bag. This trap was held in place in the forest stand by a wooden post such that the mouth of the bag was kept at a height of 1.3 m above the forest floor. Regular inspections were made throughout the study period to ensure that the hoop holding the bag was maintained in a horizontal position, in order to provide a uniform collection area between traps. The mean collection area determined from 30 traps was  $0.380 \text{ m}^2$ .

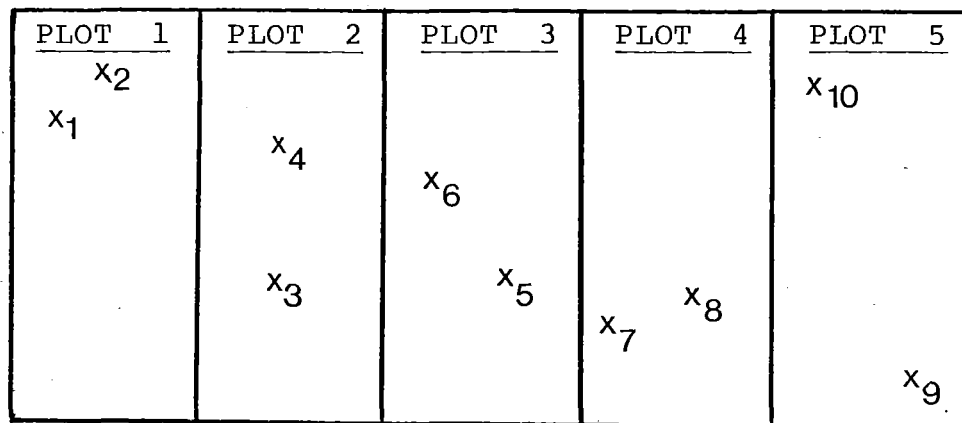
A total of 10 litter-traps were installed in each forest stand, with 2 litter-traps randomly assigned within the boundaries of each experimental plot. Litter-traps were emptied at the beginning of each month.

### 3.2.3 Sample Preparation

Litter samples collected were air-dried at  $30^{\circ}\text{C}$  until constant weight. Total litter weights were determined on an individual trap basis (see Figure 3.2.3). Litter components were separated, on a plot basis, into leaves, twigs and stems ( $< 1 \text{ cm}$  diameter), branchwood ( $> 1 \text{ cm}$  diameter) and "others" fraction for beech litter, and needles, pollen-cones, female cones and branchwood for radiata pine. Materials classified under "others" include seeds, bark, flowers, wood-rot, insect frass, faeces, non-recognizable materials and all fragments passing through a 2mm sieve. After separation and weighing, sub-samples, obtained by the method of quartering, were oven-dried at  $105^{\circ}\text{C}$  for 24 hours. All respective air-dried weights were then corrected to an oven-dried basis.

In each plot, litter components from 3 monthly

### A. Layout Plan



x litter-traps

### B. Sampling Procedure

(using Plot 1 as an example)

Month of sampling      January 1977      February 1977      March 1977

Litter-trap No.

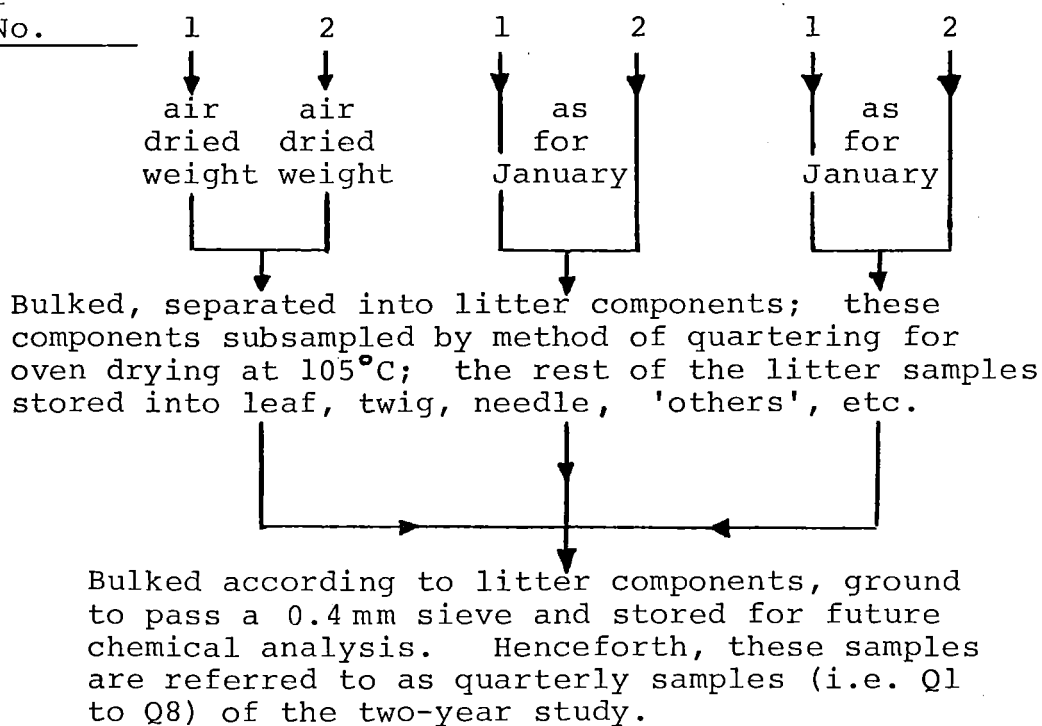


FIGURE 3.2.3 EXPERIMENTAL DESIGN AND SAMPLING PROCEDURE USED IN THE MEASUREMENT OF LITTER PRODUCTION

collections were bulked, finely ground to pass through a 0.4 mm sieve and stored in air-tight containers for future chemical analysis.

#### 3.2.4 Chemical Analysis

The general scheme used in the chemical analysis of litter tissues (elemental and proximate analyses) is shown in Figure 2.2.3.1 .

##### 3.2.4.1 General Procedure

Prior to any chemical analysis of the litter samples, preliminary tests were usually carried out using plant standards. These plant standards consist of large quantities of air-dried beech leaves, beech twigs and radiata pine needles (ground to pass through a 0.4 mm sieve and stored in air-tight containers). These three plant standards were used throughout the study to test the reproducibility of the chemical methods used and as a mean of detecting irregularities and contaminations. The plant standards did not deteriorate after two and a half years in storage.

##### 3.2.4.2 Total Carbon

Total carbon contents of litter samples were determined by the method using the Thomas Micro-Carbon Hydrogen Analyser (Model 35). In this method, carbon in the litter sample was oxidized to  $\text{CO}_2$  by combusting the litter sample at  $900^\circ\text{C}$  in a stream of  $\text{O}_2$  .

A modification was made on the original method. In the modification,  $\text{CO}_2$  produced was absorbed in 50.0 ml of 0.2M NaOH

solution and quantified by titration with 0.2M HCl. This procedure replaced the original gravimetric determination of CO<sub>2</sub> absorbed in ascarite in absorption tubes. The titrimetric method provided good accuracy and reproducibility; results for glucose (A.R. Grade) did not deviate greater than 1 percent from the theoretical value. Turnover of samples by this modified procedure was 14 samples per hour, and sample sizes used ranged from 10 to 30 mg.

#### 3.2.4.3 Total Nitrogen

Total nitrogen was determined by the semi-micro Kjeldahl method, according to the procedure given by Goh (1972) for soils. A combined potassium sulphate:copper sulphate:selenium powder catalyst of the ratio 100:10:1 was used.

#### 3.2.4.4 Total Cations (K, Mg, Ca) and Phosphorus

Sample solutions for the determinations of these elements were prepared by way of dry ashing, as described by Metson (1972)

Determinations of potassium, magnesium and calcium were made by atomic absorption using a Varian Model 1100. Strontium chloride, a releasing agent for magnesium and calcium was added to give a final concentration of 1000 parts per million of strontium.

Phosphorus was determined colorimetrically using the procedure described by Blakemore et al. (1977). Absorbance was measured at 880 nm using a Shimadzu Spectrophotometer UV - 210A.

### 3.2.4.5 Simple Carbohydrates, Polyphenols and Total Hot Water-soluble Extracts

Sample solutions for the colorimetric determinations of water-soluble simple carbohydrates and polyphenols were prepared by hot water extraction according to the procedure described by Allen (1974).

Simple carbohydrates were measured at 625 nm using anthrone reagent. The colour was developed in a boiling water bath in darkened fume cupboard for 10 minutes. Glucose (A.R.) was used for calibration.

Polyphenols were determined at 725 nm using Folin-Ciocalteu reagent. For each determination an aliquot (10.0 ml) of sample solution, which had been appropriately diluted, was used. Folin-Ciocalteu reagent (0.5 ml) was added with shaking. The solution was let stand for 3 minutes before 1 ml of saturated  $\text{Na}_2\text{CO}_3$  was added and the solution again shaken. The solution was left to stand for 1 hour before determination. Catechin (Koch-Light Laboratories Ltd) was used as a polyphenol standard.

Total hot water-soluble extracts were determined gravimetrically by evaporating suitably large aliquots (30 ml) of sample solutions to dryness at  $70^\circ\text{C}$ , and on reaching dryness, to a further 24 hours drying at  $105^\circ\text{C}$ .

### 3.2.4.6 Petroleum Ether Extracts and Ethanol Extracts (75% aqueous)

Petroleum ether ( $40^\circ - 60^\circ$ ) and 75% aqueous ethanol were used as the respective solvents. A method of extraction was developed to facilitate the turnover of large numbers



(>1000) of samples, and this method is described in Chapter 8.

#### 3.2.4.7 Holocellulose

Following the exhaustive extractions with petroleum ether and aqueous ethanol, the residual tissues were oven-dried at  $105^{\circ}\text{C}$  for 24 hours. Holocellulose in these tissues were determined by delignification with  $\text{NaClO}_2$  and  $\text{CH}_3\text{COOH}$  at  $75^{\circ}\text{C}$ , following the procedure described by Allen (1974).

For each determination, the tissue (about 0.6g) was placed in a conical flask with 30 ml of water; 1 ml of 10%  $\text{CH}_3\text{COOH}$  and 0.3g of  $\text{NaClO}_2$  were then added, mixed well, and the solution let stand with intermittent shaking in a hot water bath at  $75^{\circ}\text{C}$ . A total of six treatments of  $\text{CH}_3\text{COOH}$  and  $\text{NaClO}_2$ , carried out at hourly intervals, were used for each sample. After cooling the solution, the residual tissue was filtered, washed with cold water, followed by acetone and finally ether. The weight of holocellulose was determined after oven-drying at  $105^{\circ}\text{C}$  for 1 hour.

#### 3.2.4.8 Residual Lignin

Residual lignin, as appropriately named, was estimated by subtracting from the initial weight of litter sample used, the weights of petroleum ether extract, aqueous ethanol extract and holocellulose.

#### 3.2.5 Statistical Computations

Analysis of variance, Duncan's test, correlation coefficients and regression analysis were performed using the Teddybear programme (Wilson, 1976) on the Burroughs B6700 computer at the University of Canterbury.

### 3.3 RESULTS AND DISCUSSION

#### 3.3.1 Annual Total Litter Production

Annual total litter production (or litter-fall) for beech forests and radiata plantations at Granville, Hanmer and Nelson are given in Table 3.3.1.1 and also in Appendix II. Different litter components that made up the total litter in each site are also included.

Annual total litter-fall in all the beech stands studied ranged from 3915kg/ha to 7471 kg/ha, averaging 5921 kg/ha. For *Pinus radiata* (or radiata) annual total litter-fall ranged from 1445 kg/ha to 5532 kg/ha, averaging 3932 kg/ha. The lower limit for the range of litter-fall in radiata stands was from the 17-year-old radiata stand at Hanmer which had been thinned in 1974. Consequently, lower litter was deposited. On exclusion of these figures, annual litter production in the radiata stands ranged from 3334 kg/ha to 5532 kg/ha, averaging 4742 kg/ha.

These figures of litter production are well within the range of reported litter-fall for warm temperate forests (Bray and Gorham, 1964). A comparison of litter-fall data recorded for similar and different species of forests in New Zealand (Table 3.3.1.2) indicate that litter-fall values for beech and radiata stands in the three forests used in the present study were not greatly different from those of similar species in other regions. However, it is difficult to compare accurately between the air-dried weights of radiata litter-fall reported by Will (1959) and oven-dried weights used in the present study. In addition, results from only

TABLE 3.3.1.1 Annual litter production of beech and radiata stands in Granville, Hanmer and Nelson forests (Values given in kg/ha)

Forest & Stand	Leaves	Needles	Twig/stem	"Others"	Pollen-cones	Branchwood	Female-cones	TOTAL
GRANVILLE								
Beech 1 <sup>#</sup>	2575( 378) <sup>@</sup>		1872( 936)	1222( 492)		1073(2757)		6742(2153)
2 <sup>#</sup>	2493( 297)		832( 252)	1416( 427)		2730(5021)		7471(3007)
Radiata 1		4085( 377)			390( 77)	28( 37)		4503( 391)
2		3026( 453)			308( 65)			3334( 379)
HANMER								
Beech 1	2650( 291)		707( 111)	656( 254)				4013( 592)
2	2637( 246)		724( 129)	554( 64)				3915( 390)
Radiata 1		1379( 309)			66( 37)			1445( 592)
2		1503( 397)			60( 13)			1563( 398)
NELSON								
Beech 1	3702( 355)		1282( 377)	1001( 104)				5985( 592)
2	2998( 635)		1366( 459)	1335( 289)		1702(2422)		7401(2563)
Radiata 1		4215( 313)			838(156)	126( 156)	153( 34)	5332( 556)
2		4372( 491)			208( 20)	322( 421)	630(1621)	5532(1204)
Radiata 1		3661( 300)			623(120)	57( 79)	585(1504)	4926(1354)
2		3465( 580)			369( 63)	61( 95)	929(1463)	4824(1578)

# First and second year; @ Mean( $\pm$  95 percent confidence intervals)

TABLE 3.3.1.2 Comparison of mean annual litter production# of some New Zealand forests

FOREST TYPE	LOCATION	SPECIES, AGE	ALTITUDE,m	LEAF	WOOD	TOTAL	REFERENCE
BEECH	SILVER STREAM	<i>Nothofagus truncata</i>	240	4320	1720	6040	Miller (1963)
	CRAIGIEBURN	<i>Nothofagus solandri</i> var <i>cliffortioides</i>	850	2751	959	3710	Wardle (1970)
		"	1340	2012	1050	3062	" "
	KAWEKA	"	1340	2624	944	3568	" "
	WAIRARAPA	<i>Nothofagus solandri</i> var <i>solandri</i>	60			5335	Bagnall (1972)
	GRANVILLE	<i>Nothofagus truncata</i>	210	4132	2995	7127	Levet+ (1978)
	GRANVILLE	" "	"	3853	3254	7107	Present Study
	HANMER	<i>Nothofagus solandri</i> <i>cliffortioides</i>	450	3249	715	3964	" "
	GOLDEN DOWNS	<i>Nothofagus</i> species	570	4518	2175	6693	" "
RADIATA	WHAKAREWAREWA	<i>Pinus radiata</i> , 39	270	3110	3520	6630 <sup>@</sup>	Will (1959)
	KAINGAROA	<i>Pinus radiata</i> , 28	430	3790	1790	5580 <sup>@</sup>	" "
	GRANVILLE	<i>Pinus radiata</i> , 17	170	3863	82	3945	Levet+ (1978)
	GRANVILLE	<i>Pinus radiata</i> , 21	170	3556	363	3919	Present Study
	HANMER	<i>Pinus radiata</i> , 17	580	1504	-	1504	" "
	GOLDEN DOWNS	<i>Pinus radiata</i> , 21	430	4294	1138	5432	" "
		<i>P. radiata</i> reg. 21	460	3563	1312	4875	" "
	MAWHERA	<i>Pinus radiata</i> , 11	290	1465	47	1512	Levet+ (1978)

# Values of litter production given in kg/ha; @ refer to air-dried weights

two years data may not be adequate enough to allow a good comparison. Large year to year variations in the total litter-fall tend to mask any real dissimilarities, especially since Miller and Hurst (1957) have reported annual variation in total litter-fall of hard beech, as given by the maximum annual litter production/minimum annual litter production ratio, could be as high as 2.7. Higher ratios for other species and other regions have been reported (Bray and Gorham, 1964).

Results of the present study show some notable features. For example, the Granville beech forest site had a comparatively higher litter-fall than those of other native forests (Table 3.3.1.2). Low value of litter-fall for the radiata stand at Hanmer was closely similar to that recorded for an 11-year-old radiata stand in Mawhera forest which also had been thinned previously (Levett, 1978). The amount of total litter-fall in the radiata stands were between 36% and 92% of those in the adjacent beech stands. Despite closed canopy in both radiata stands at Nelson, needle-fall was evidently lower for the regenerated stand. The trees in the latter stand had not been pruned before and consequently had extensive branches down to low levels which, as observed, tend to intercept falling needles and retain them on the branches for long periods. It is probable that considerable decomposition and loss in weight had occurred before such needles were dislodged into the traps. The interception of falling needles had also been reported by Will (1959) in radiata stands at Rotorua.

It would appear that litter production in the beech

and radiata stands at Granville have reached a stage of slow long term change. Previous annual litter-fall data (Levett, 1978) and those recorded in the present study did not differ significantly (Table 3.3.1.3).

#### 3.3.1.1 Statistical Comparison of Experimental Data

In order to validate statistical comparisons of experimental data obtained from the two adjacent beech and radiata stands of each forest at Granville, Hanmer and Nelson, it was necessary to carry out a preliminary analysis of variance to test the homogeneity of variances of the plot and sample means between the two stands of each forest. This is essential since the experimental design used in the present study (see Section 3.2.1) was not based on a completely randomized design. Annual litter-fall was used in the analysis of variance, based on the procedure given by Steel and Torrie (1960), because litter-fall constitutes an important factor associated with litter decomposition and other transformation processes.

Results from statistical analysis (Table 3.3.1.4) showed that plot and sample variances between adjacent beech and radiata stands of each forest were homogeneous. Except for sample variances at Hanmer, there were no significant differences in the variances between samples or plots. These results therefore validate the pooling of data obtained in beech and radiata stands for comparisons of mean values.

TABLE 3.3.1.3 Annual litter production in beech and radiata stands at Granville

STAND	1973/74 <sup>@</sup>	1974/75 <sup>@</sup>	1976/77	1977/78
Beech	7109 ± 2285 <sup>#</sup>	7394 ± 3671	6742 ± 2153	7471 ± 3007
Radiata	4515 ± 1191	3376 ± 801	4503 ± 391	3334 ± 379

# refer to mean litter production ± 95 percent confidence intervals

@ data obtained from Levett (1978)

TABLE 3.3.1.4    Ratio of variances in annual litter-fall in adjacent beech and radiata sites on sample and plot basis

	GRANVILLE	HANMER	NELSON		
	(B) vs (R)†	(B) vs (R)	(B) vs (R)	(B) vs (R <sub>r</sub> )	(R) vs (R <sub>r</sub> )
First Year					
SAMPLE	3.69 #	5.37	1.06	1.54	1.64
PLOT	6.06	1.56	3.45	5.17	1.50
Second Year					
SAMPLE	2.70	1.07	1.50	1.72	2.58
PLOT	1.63	1.33	4.70	4.27	1.10

# equals larger variance/smaller variance,  
for SAMPLE, ratio > 4.03, significantly different at 5%  
PLOT, ratio > 9.60, significantly different at 5%

† (B) = beech; (R) = radiata; (R<sub>r</sub>) = radiata<sub>reg</sub>.



### 3.3.2 Seasonal Litter-fall

Monthly litter-fall results (Figure 3.3.2) indicate that litter deposition occurred throughout the year in all the forest stands studied although there were periods of high and low litter-fall. These periods, however, were not always sharply distinct and frequently the peak litter-fall varied in relative magnitude between years. For example, in Granville forest, peak litter-fall in autumn (about May) and spring (about October) in the first year were not clearly repeated or equalled in magnitude in the second year.

In general, the present results show a definite peak litter-fall occurred in late spring-early summer months of October, November and December for beech stands. This is in agreement with the peak litter-fall periods reported by Miller and Hurst (1957) for beech forests in the North Island. Wardle (1970) also found a summer maximum leaf-fall for mountain beech. In the present study, there are indications that a secondary period of high litter-fall occurred in the autumn months of April and May in the beech forest stands studied. However, this is not entirely in contrast to seasonal litter-fall patterns reported by Bagnall (1972) where a major peak litter-fall in early winter was followed by a secondary maximum in late spring.

Excluding branch litter, which was observed to be extremely erratic in its litter-fall pattern, the major components of leaf, twig and miscellaneous (or "others") litter deposited in October, November and December averaged 38, 41 and 54 percent respectively, of the annual litter-fall in beech stands at Granville, Hanmer and Nelson.

The pattern of litter-fall was less regular in radiata stands, the irregularity being more pronounced in Nelson where periods of high litter input occurred throughout the year. As with the beech forests, two main periods of litter-fall were generally evident in Granville and Hanmer, in late autumn-early winter and in late spring-early summer. Litter-fall collected in the first period (late autumn) amounted to a mean of 37, 22 and 34 percent of the annual total litter-fall in the radiata stands at Granville, Hanmer and Nelson respectively. In the second period (late spring) the corresponding values were 30, 41 and 28 percent. This pattern was relatively similar to that reported by Will (1959) for radiata stands in the North Island where a comparatively larger proportion of litter fell in autumn followed by a smaller peak during spring-early summer. Gosz et al. (1972) have also reported two peak periods of needle-fall for spruce, with a definite autumn peak.

### 3.3.3 Litter-fall Components

Apart from the occasional fall of large branch litter, leaf and needle constituted the largest proportion of the annual total litter collected in their respective stands in the three forests at Granville, Hanmer and Nelson (Figures 3.3.3.1 to 3.3.3.4).

#### 3.3.3.1 Leaf Litter

Leaf litter made up 36, 67 and 52 percent of the annual total litter-fall at Granville, Hanmer and Nelson respectively. Data for Granville and Nelson were much lower than

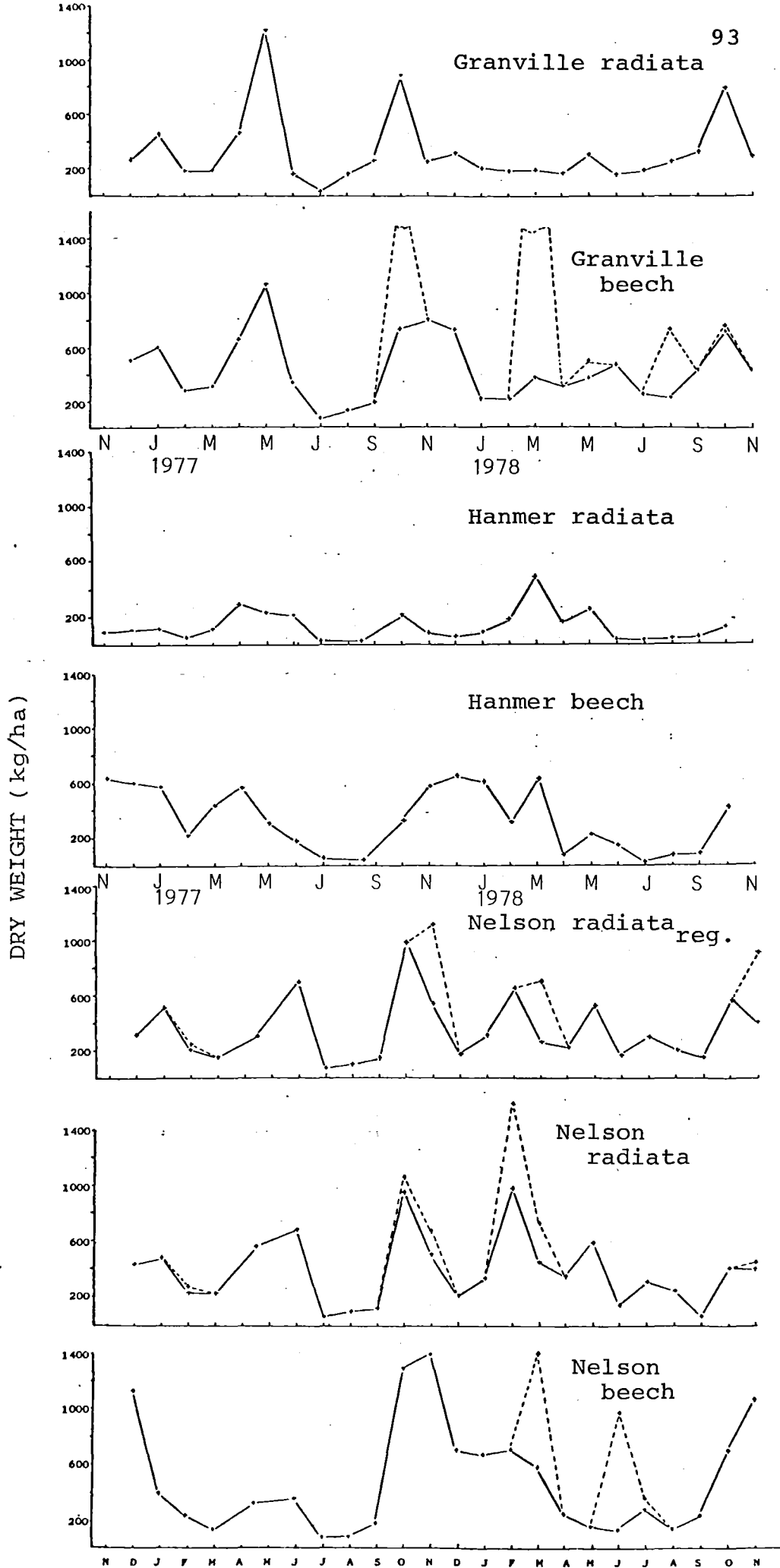


FIGURE 3.3.2 Monthly total litter-fall in Granville, Hanmer and Nelson forest stands (Broken line denotes inclusion of branchwood)

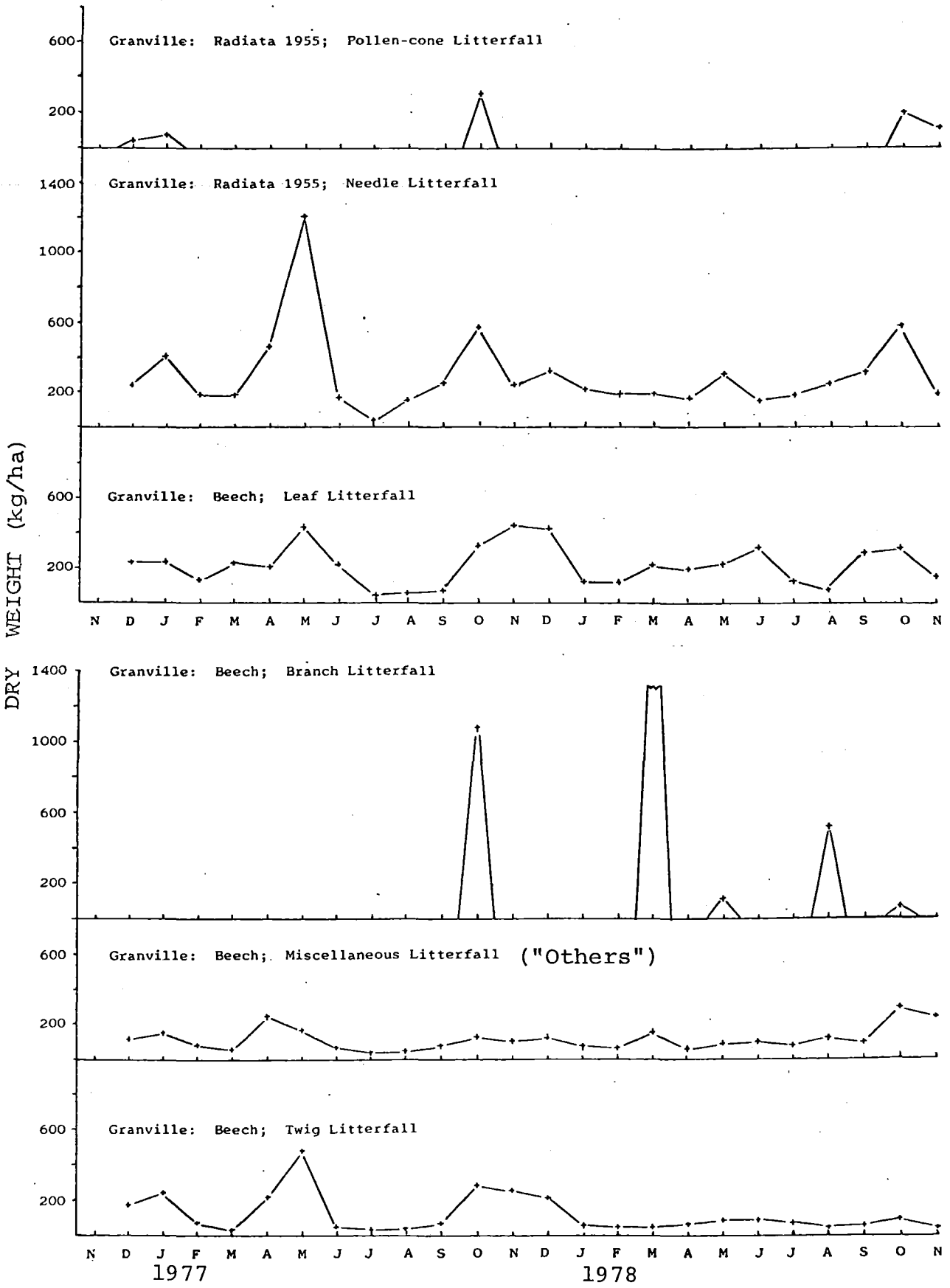


FIGURE 3.3.3.1 Monthly litter-fall in beech and radiata pine forest stands at Granville

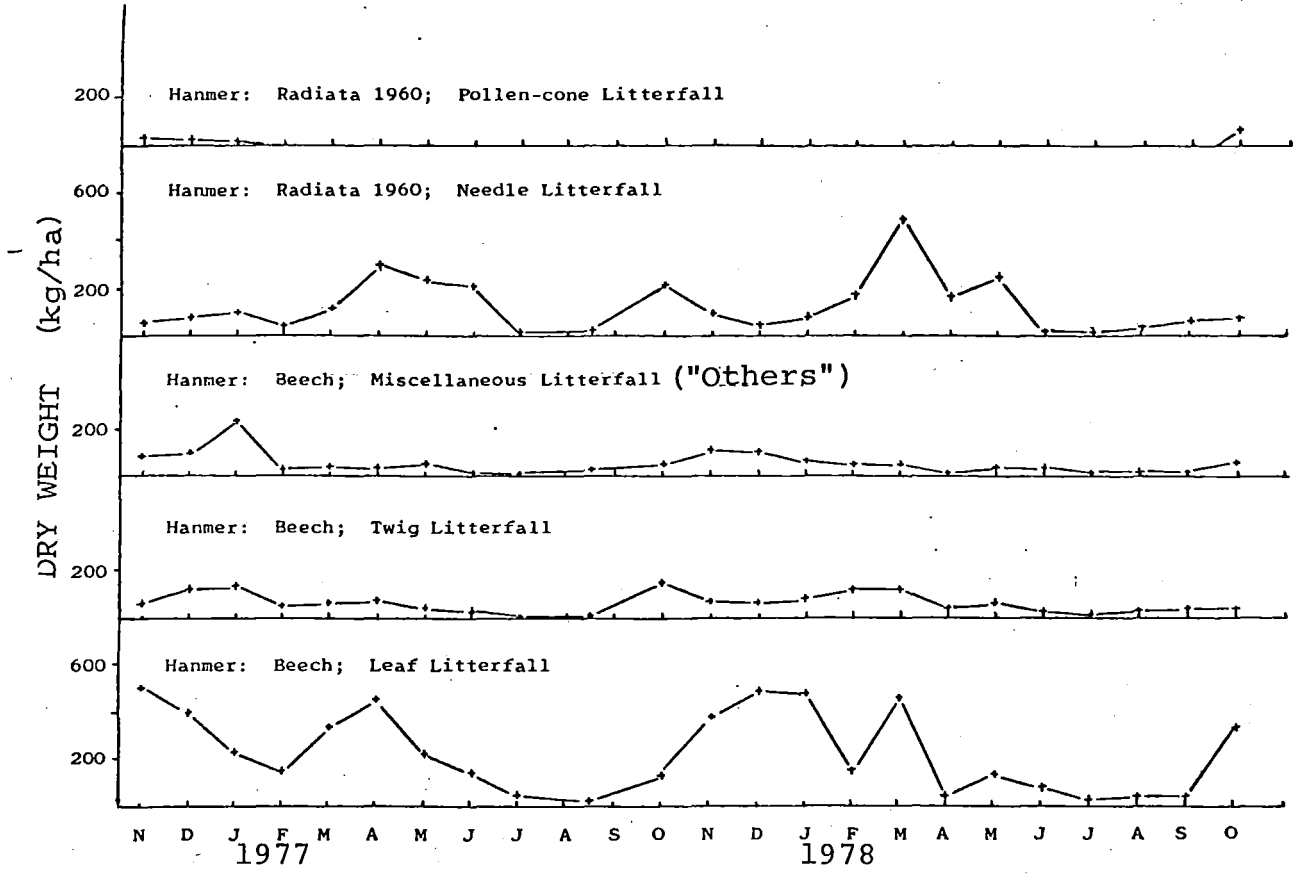


FIGURE 3.3.3.2 Monthly litter-fall in beech and radiata pine forest stands at Hanmer

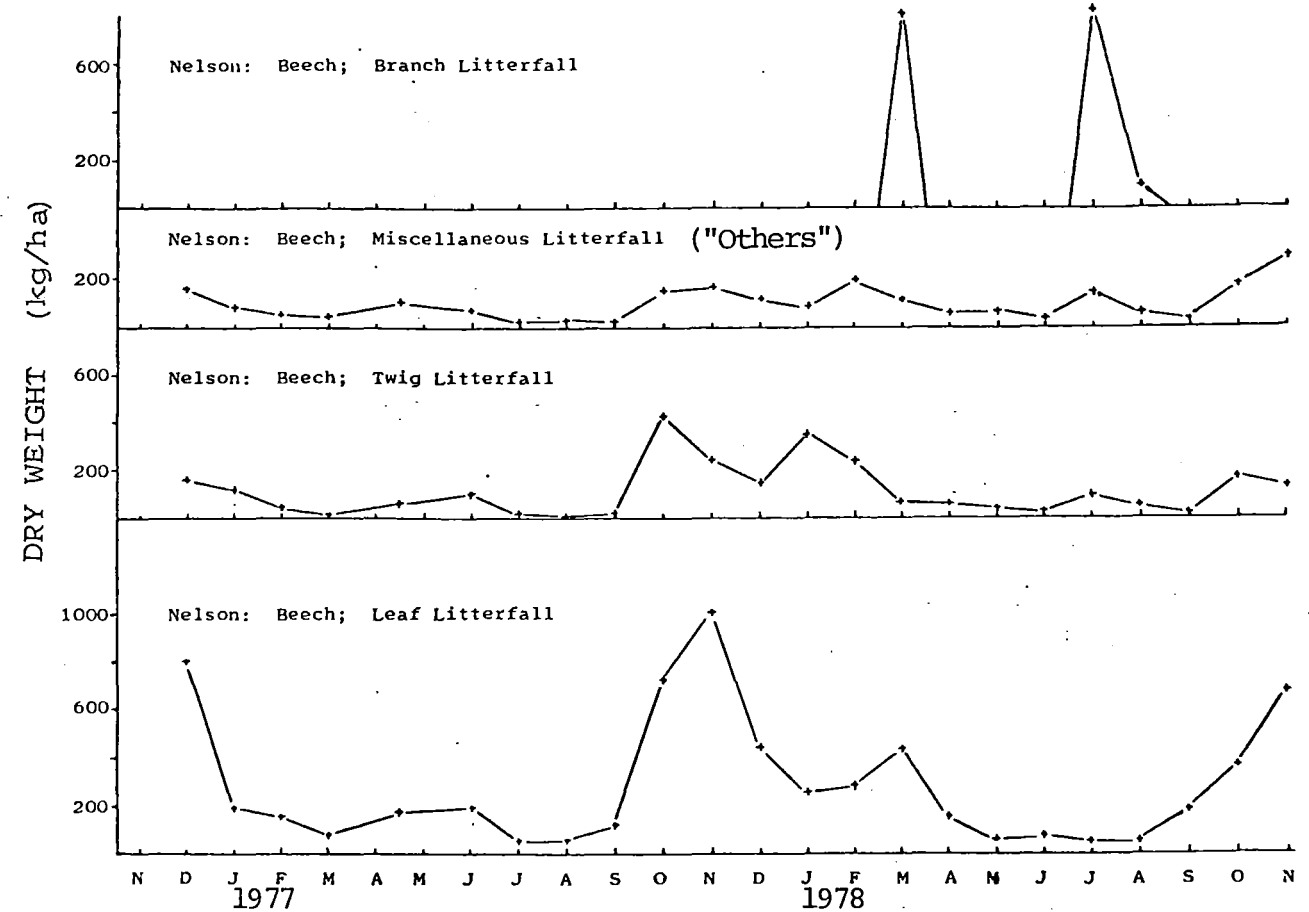


FIGURE 3.3.3.3 Monthly litter-fall in beech forest stand at Nelson

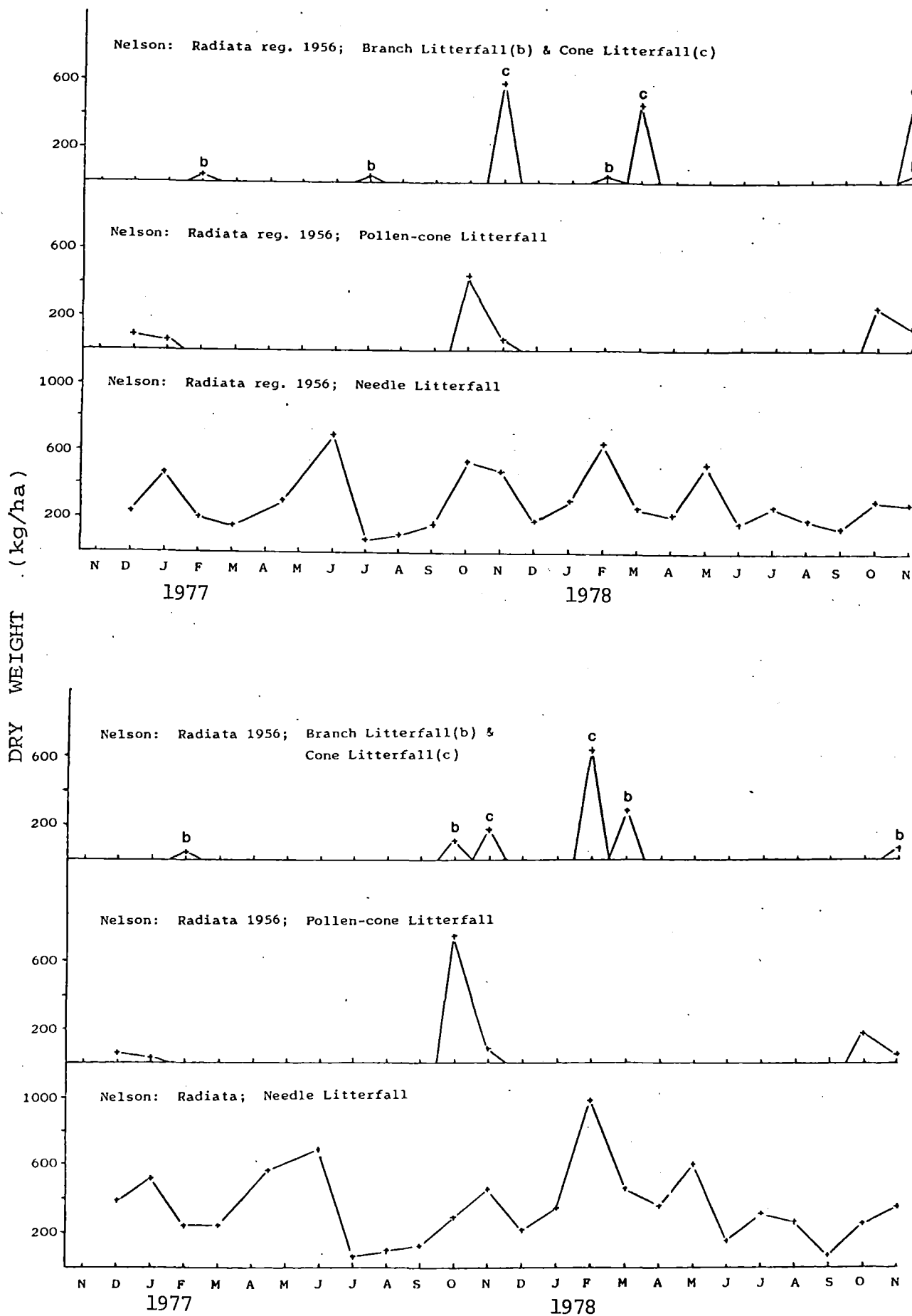


FIGURE 3.3.3.4 Monthly litter-fall in radiata pine stands at Nelson

those summarized by Bray and Gorham (1964) of 60 to 76 percent. This deviation may be attributed to the method of litter separation used in the present study. Due to the difficulty in identifying small fragments of litter, all materials passing through a 2mm sieve were inadvertently classified into the "others" litter fraction. Thus, it was inevitable that some fragmented leaf materials were inappropriately classified. Furthermore, the inclusion of branch material reduced the percentage composition of leaf litter in total litter-fall in Granville and Nelson.

Leaf-fall patterns were relatively similar in all three beech forests, with a moderately defined peak leaf-fall during October, November and December. Leaf tissue of these three months amounted to a mean of 37, 42 and 52 percent of the annual leaf-fall in the beech forests of Granville, Hanmer and Nelson respectively. Leaf-fall was lowest during the months of July, August and September, and constituted a mean of only 12, 3 and 8 percent of the annual leaf-fall in the respective forests. Miller and Hurst (1957) observed similar peak leaf-fall in October and November for hard beech forests at Silverstream, and attributed this peak fall to the development of new leaves during these months. This period between mid-September and mid-November accounted for nearly half of the annual leaf-fall in Miller's (1963) study. Leaf-fall patterns were relatively similar to those observed for other beech forests in New Zealand (Bagnall, 1972; Wardle, 1970).

### 3.3.3.2 Needle Litter

Needle litter constituted between 72 and 96 percent of the annual total litter-fall recorded for the radiata stands. Although the figure of 96 percent recorded for the 17-year-old radiata stand at Hanmer appears unusually high, the proportion was very similar to that found for an 11-year-old radiata stand of 97 percent reported by Levett (1978). The stand also had been thinned previously. Other studies have shown similar results. For example, Cromack (1973) found that needle litter made up 98 percent of the annual litter-fall in a 14-year-old white pine stand in North Carolina.

It is probable that very little wood litter such as twig, branch or female cone was reaching the forest floor in these younger conifer forest stands. It is unlikely that the high proportion of needle litter collected in the 17-year-old radiata stand at Hanmer was mainly the result of inadequate litter-traps in estimating the fall of wood litter. Regular surveys of the forest floor in this stand revealed a lack of fresh wood litter being deposited.

Needle-fall patterns at Granville, Hanmer and Nelson showed few similarities. Nevertheless, there are indications of two periods of major needle-fall in late spring (about October) and late autumn (about May). At Granville, a large peak in May followed by a smaller peak in October was observed in the first year. However, in the following year, this peak in May was only weakly evident although that of October remained relatively similar. Needle-fall at Hanmer was definitely greater in autumn than spring, while at Nelson, in addition to the peak needle-fall at these two periods, others



were observed about January or February. Obviously, this emphasizes the difficulty in predicting litter-fall patterns in general.

Other workers have also reported two periods of peak needle-fall. For example, Gosz et al. (1972) for red spruce and Van Lear and Goebel (1976) for loblolly pine.

### 3.3.3.3 Miscellaneous Litter ("Others")

This litter fraction included insect frass, buds, bark, fruits, wood-rot and other fragmented materials. Miscellaneous litter-fall did not appear to follow any strong seasonal pattern in all three beech forests. The amounts collected were relative constant throughout most of the year, despite possibility of peak falls associated with the various fractions like bud scales and flowers (Gosz et al., 1972). This was not observed because the inclusion of large amounts of fragmented materials may have masked such peak effect. Annual miscellaneous litter amounted to 1319, 605 and 1168 kg/ha, which corresponded to 19, 15 and 18 percent of the annual total litter-fall at Granville, Hanmer and Nelson respectively.

In the *radiata* plantations, it was also notable that a considerable amount of pollen cones fell during spring occurring from October through to as late as January. On some occasions, pollen cones comprised as much as 63 percent of the total litter collected in a single month (e.g. Nelson, in the *Pinus radiata* 1956 stand for the month of October 1977). In the North Island, Will (1959) also found that pollen cone-fall occurred in the months of October and November.

#### 3.3.3.4 Wood Litter

Wood Litter (including branchwood, twigs and stems) was a more prominent component of litter collected in beech forests compared to radiata plantations. It was found that wood litter constituted about 45, 18 and 32 percent of the annual litter-fall in the beech forests at Granville, Hanmer and Nelson respectively. Twig litter fell all the year round but occasionally exhibited peaks in autumn and spring. Miller (1963a) also found that twig-fall in a hard beech forest was relatively uniform throughout the year. In the present study, twig litter contributed approximately equal amounts to the annual total litter-fall in all the three beech forests at Granville, Hanmer and Nelson, making up an average of 20, 19 and 20 percent respectively. Contributions from branchwood varied between 0 and 37 percent.

The primary difference between branch and twig litter was the extremely variable nature of the former component. For example, in one year at Granville, branch litter collected in one single month alone accounted for over 58 percent of the total wood-fall and over 27 percent of the total litter-fall of that year. Such an erratic nature is not uncommon, since branch-fall is generally influenced by the fall of trees (Nye, 1961) and greatly affected by storm events. Gosz et al. (1972) found that the fall of branch litter depended on the severity of the storm and also the time of occurrence.

In the present study, while it was generally not possible to ascertain the exact cause of branch-fall, there are indications that the heavy fall of branch litter in the

one month reported in Granville was associated with storm events. Most of the branch litter collected were freshly severed, in contrast to those collected for the most part of the year. In the two-year litter-fall measurements, branch litter was found in only 3 monthly periods in the beech stand at Nelson, compared to 5 at Granville. No branch litter was collected at Hanmer, probably because the beech stand was located in a gully, thus sheltered from prevailing strong winds.

#### 3.3.4 Variations in Litter-fall Measurements

Results of coefficients of variation (C.V.) for litter-fall weights recorded are reported in Table 3.3.4.1. The C.V. of the months of commonly highest and lowest litter-fall, which were observed to be about October and July respectively, were relatively similar for all the forests studied. The amount of litter-fall did not appear to influence the degree of variability since there was no obvious relationship between the ratios  $R$  (amount of litter-fall in October/amount of litter-fall in July) and the coefficients of variation. As far as the author is aware, no similar determinations of variation in such months have been reported in New Zealand to allow a comparison, but it may be reasonable to expect that, on the basis of our results, there should not be any great dissimilarity in the other regions.

In general, the C.V. of annual litter-fall (excluding branch litter) averaged 18 percent (range 12 to 30 percent) for the first year and 20 percent (range 14 to 36 percent) in the second year of measurements. These results, therefore,

TABLE 3.3.4.1 Coefficients of variation for dry weights of litter-fall

	GRANVILLE		HANMER		NELSON		
	Beech	Radiata	Beech	Radiata	Beech	Radiata	Radiata <sub>reg.</sub>
Total litter-fall in July	(31,49) <sup>#</sup>	(45,39)	(42,35)	(67,94)	(28,70)	(25,38)	(27,36)
Total litter-fall in October	(45,29)	(22,20)	(31,26)	(71,88)	(29,33)	(24,29)	(20,23)
Annual total litter-fall (excl. branchwood)	(21,14)	(12,16)	(21,14)	(30,36)	(14,21)	(14,22)	(13,19)
Annual total litter-fall (incl. branchwood)	(45,89)	(12, -)	( -, -)	( -, -)	( -,49)	(15,31)	(39,46)
Ratio of total litter- fall (October/July)	(24, 3)	(28, 4)	( 6,15)	(35, 8)	(15, 2)	(18, 1)	(15, 2)

# (first year, second year)

obtained using 10 replications

TABLE 3.3.4.2 Coefficients of variation for dry weights of litter-fall components

Litter-fall Components	GRANVILLE		HANMER		NELSON		
	Beech	Radiata	Beech	Radiata	Beech	Radiata	Radiata <sub>reg.</sub>
Leaf/Needle	(13,10) #	( 8,13)	(10, 8)	(20,23)	(10,18)	( 6,10)	( 7,15)
Twig/stem	(43,26)		(14,15)		(26,29)		
"Others"	(35,26)		(34,10)		( 9,19)		
Branchwood	(223,160)	(114, -)	( -, -)	( -, -)	( -,124)	(103,114)	(121,136)
Pollen-cone		(17,19)		(48,18)		(16, 8)	(17,15)
Female-cone		( -, -)		( -, -)		(223,223)	(223,137)

# (first year, second year) obtained using 5 replications



branch-fall. In the present study, despite a larger litter-trap collection area, a similar difficulty was encountered.

By our estimates, the C.V. of female cone litter-fall was greater than 137 percent (Table 3.3.4.2). This value is reconcilable with that estimated for cones on the forest floor as reported by Van Lear and Goebel (1976) for a loblolly pine plantation. Although their estimates were based on forest floor measurements, it nevertheless clearly indicates the sporadic nature of cone-fall.

Spatial variation appears to influence litter-fall collection. This is supported by the relatively high C.V. of needle-fall recorded in the Hanmer radiata stand. This is attributed to a more open canopy as a result of stand thinning. Traps positioned directly below open areas would consequently collect the smallest amount of litter especially during calm weather conditions. On the other hand, windy conditions which happen throughout the year should promote a more even distribution of litter. Such a reasoning is consistent with results showing a much lower C.V. for the annual litter-fall in this radiata stand. The above view is also supported by the results of Gosz et al. (1972) which indicated that the litter-fall in each trap was reflective of the species immediately above or adjacent to the trap.

### 3.3.5 Nutrient Concentrations of Litter

Concentrations of nutrients in the separate litter components are shown in Table 3.3.5.1. These concentration values shown for a stand represent the mean nutrient concentrations in the litter collected in each quarter (see Figure

3.2.3) for a total of 2 years (i.e. 8 quarters altogether viz Q1 to Q8). Mean concentrations of nutrients in the separated litter components of each quarter ( $\pm$  95 percent confidence intervals) in Granville, Hanmer and Nelson are given in Appendix II.

The distribution of the nutrient elements of N, P, K, Mg and Ca varied substantially between most litter components in each forest (Table 3.3.5.1). However, lesser differences between litter components and between forests were observed to occur in Mg concentrations, compared to those of the other elements. Calcium, on the other hand, showed the greatest differences between litter components within each forest. Generally, for all forests, the concentrations of the nutrients decreased in the order:

$$\text{Ca} \leq \text{N} > \text{K} > \text{Mg} > \text{P}$$

For certain litter components (e.g. pollen cones), the concentration of nutrients were relatively similar between forests. This effect is believed to be due to the similarity in age of pollen cones and the time of cone-fall. Unlike other litter components, pollen cones are deposited within a period of 2 to 3 months during spring (Will, 1959; Section 3.3.3.3).

Generally, in the three forests studied, "others" litter showed the highest N concentrations, and possibly also phosphorus. The high content of N, P and K in "others" litter is attributed to the inclusion of large proportions of productive materials such as flowers, buds, seeds and insect frass. Other workers (e.g. Cromack, 1973; Woodwell et al., 1975) have also reported results showing comparatively



TABLE 3.3.5.1 Mean nutrient concentrations (mg/g) in  
litter-fall components of beech and radiata  
pine forests at Granville, Hanmer and Nelson

Forest/Litter component		N	P	K	Mg	Ca
GRANVILLE						
Beech	Leaf	6.1	0.34	1.7	1.6	8.0
	Twig	4.9	0.27	1.5	1.7	11.5
	"Others"	11.3	0.96	2.6	1.4	7.6
	Branchwood	1.7	0.10	0.5	0.8	6.4
Radiata	Needle	8.3	0.53	2.1	1.2	4.5
	Pollen cone	6.3	0.75	2.7	1.3	3.7
HANMER						
Beech	Leaf	4.8	0.96	2.8	1.3	10.2
	Twig	4.9	0.79	2.2	2.0	13.2
	"Others"	7.8	1.13	2.6	1.5	8.5
Radiata	Needle	5.7	1.20	4.6	1.1	6.6
	Pollen cone	6.3	0.58	3.1	1.1	2.1
NELSON						
Beech	Leaf	6.9	0.92	3.7	1.2	12.6
	Twig	5.7	0.74	2.7	1.8	14.2
	"Others"	9.0	1.08	3.6	1.2	13.3
	Branchwood	4.4	0.34	0.9	0.8	0.8
Radiata	Needle	7.6	1.10	3.8	1.4	7.7
	Pollen cone	7.1	0.68	2.8	1.2	2.1
Radiata reg.	Needle	7.8	1.21	3.6	1.5	9.3
	Pollen cone	6.9	0.71	2.6	1.1	2.2

high levels of N, P and K in flowers and fruits.

Branchwood contained the lowest concentration in all nutrients studied, while twig litter showed highest concentrations in Ca, and to a lesser degree Mg. This difference in Ca concentration between twig and branch litters is attributed mainly to the smaller proportion of bark component in branch than in twig litter. Nutrient concentrations of various current plant components reported by Woodwell et al. (1975) showed a comparatively high Ca content in bark. As Ca is relatively immobile and is not involved in translocation (Mälkönen, 1974) its concentrations should remain high during senescence.

Levels of nutrients in the major litter components of beech leaves and radiata needles were generally similar to those reported in other studies in New Zealand and elsewhere (see Table 3.3.5.2). However, direct comparisons between nutrient concentrations in the different species of litter reported in other studies are not valid because of site and location differences (see Review Section 2.2.4). Some of these factors which complicate comparison of nutrient concentrations in litter between studies and forests are discussed in a later section.

In order to overcome this problem, the present study was carried out using adjacent beech and radiata stands with identical site properties (see Appendix I). Furthermore, sampling was maintained in phase and within a similar time period.

Results from the present study (Table 3.3.5.1) showed some notable differences within and between forests. For

TABLE 3.3.5.2 Macro-nutrient concentrations (%) of leaf and needle litter-fall of some beech and pine forests

REFERENCE	SPECIES, AGE	N	P	K	Mg	Ca
Miller (1963b)	<i>Nothofagus truncata</i>	0.53-0.76	0.04-0.06	0.09-0.19	0.14-0.19	0.98-1.08
Lutz and Chandler (1946)	<i>Fagus grandifolia</i>	0.67	0.10	0.65	0.22	0.99
Heine (1973)	<i>Nothofagus fusca</i>	0.7		0.19	0.14	0.90
	<i>Nothofagus menzesii</i>	1.0		0.14	0.09	0.55
	<i>Nothofagus cliffortioides</i>	0.7		0.08	0.08	0.58
Gosz <i>et al.</i> (1972)	<i>Fagus grandifolia</i>	0.84-0.86	0.04-0.06	0.38-0.42	0.11-0.12	0.72-0.78
Levett (1978)	<i>Nothofagus truncata</i> ‡	0.55 <sup>@</sup>	0.051	0.22	0.17	0.81
Present Study	<i>Nothofagus truncata</i> ‡	0.61	0.034	0.17	0.16	0.80
	<i>Nothofagus solandri</i> var <i>cliffortioides</i>	0.48	0.096	0.28	0.13	1.02
	<i>Nothofagus</i> spp.	0.69	0.092	0.37	0.12	1.26
Will (1959)	<i>Pinus radiata</i> , 27	0.67	0.065	0.30	0.11	0.54
Spain (1973)	<i>Pinus nigra</i>	0.64-1.45	0.03-0.08	0.18-0.22	0.07-0.08	0.70-0.88
Mälikönen (1974)	<i>Pinus sylvestris</i> , 28	0.48	0.04	0.10		0.57
Miller <i>et al.</i> (1976)	<i>Pinus nigra</i> , 39		0.09	0.20	0.08	0.59
Levett (1978)	<i>Pinus radiata</i> , 11	1.12 <sup>@</sup>	0.058	0.24	0.10	0.38
	<i>Pinus radiata</i> , 20 ‡‡	0.77 <sup>@</sup>	0.055	0.21	0.13	0.46
Present Study	<i>Pinus radiata</i> , 22 ‡‡	0.83	0.053	0.21	0.12	0.45
	" , 17	0.57	0.120	0.46	0.11	0.66
	" , 21	0.76	0.110	0.38	0.14	0.77
	<i>Pinus radiata</i> reg., 21	0.78	0.121	0.36	0.15	0.93

@ refer to total litter-fall

‡, ‡‡ refer to the same stand

example, N and P concentrations were consistently higher in radiata needles than in beech leaves (i.e. 35, 19 and 11 percent higher N, and 56, 25 and 26 percent higher P in Granville, Hanmer and Nelson, respectively). In addition, beech leaves and radiata needles in the respective stands at Granville had much lower P concentrations than those found in the corresponding litters in either Hanmer or Nelson.

In the present study, data obtained show an apparently closer relationship between leaf and needle litter P concentrations and the levels of Bray-P than that between leaf and needle P concentrations and total-P levels in the top-soils (0-20cm) of each forest stand (Table 3.3.5.3). The low leaf and needle litter P levels found in Granville forest as compared to those of the other two forests was probably a reflection of the lower Bray-P levels in Granville. However, no firm conclusion could be drawn from these results without analysing the P levels in green intact foliage and determining P uptake by the plants in each stand.

The results of the present study appear to be compatible with those of Fisher and Stone (1969) which suggested increased N and P availability in the top-soil, and plant uptake beneath conifers over those in adjacent open fields. These workers attributed the effect to increased mineralization of N and P in the rhizosphere of conifers.

### 3.3.6 Seasonal Variation in Nutrient Concentrations

Concentrations of N, P, Mg and Ca of the separated litter components showed no definite seasonal variation

TABLE 3.3.5.3 Concentration values of total phosphorus and Bray-phosphorus in litter and top-soil (0-20cm) of beech and radiata forest stands at Granville, Hanmer and Nelson

	GRANVILLE		HANMER		NELSON		
	Beech	Radiata	Beech	Radiata	Beech	Radiata	Radiata <sub>reg.</sub>
Total P in leaf or needle litter ( $\mu\text{g/g}$ )	340 <sup>#</sup>	530	960	1200	920	1100	1210
Total P in top-soil ( $\mu\text{g/cm}^3$ )	104 <sup>@</sup>	214	444	612	250	319	247
Bray-P in top-soil ( $\mu\text{g/cm}^3$ )	0.2 <sup>@</sup>	2.1	1.5	18.3	1.9	4.1	2.5

@ Mean of 5 replicate samples

# Value given represents the average of quarterly litter P concentrations

( Appendix II ). Even though the differences in nutrient concentrations between seasons were large, they were not significant statistically. Generally, the trend in nutrient concentrations observed in the first year was not repeated in the following year.

In contrast, K concentrations in certain litter components showed definite seasonal patterns in both years (Figures 3.3.6.1 to 3.3.6.3). For example, in the Granville forest, K levels in the miscellaneous litter were relatively high in the winter quarters (June, July and August) of both years. At Hanmer, K levels in leaf, twig and needle litter followed a much similar pattern, but high K levels occurred in the autumn quarters (February, March and May). The seasonal pattern showed by twig litter was expressed less clearly, however. At Nelson, only leaf and needle litters showed seasonal variation in K concentrations which was similar to that at Hanmer.

A closer examination of Figures 3.3.6.1 to 3.3.6.3 revealed that, except for twig litter, the different litter components in Granville forest showed K concentration trends opposite to those found for corresponding litter components in the other two forests. For example, "others" litter only showed seasonal variation at Granville but not at Hanmer or Nelson, while leaf and needle litter only showed seasonal variation at Hanmer and Nelson but not at Granville. The reasons underlying these results are unknown, and will be difficult to uncover unless a more detailed separation of the "others" fractions is undertaken to allow an examination of its constitution (e.g. flowers, seeds, insect frass, etc.).

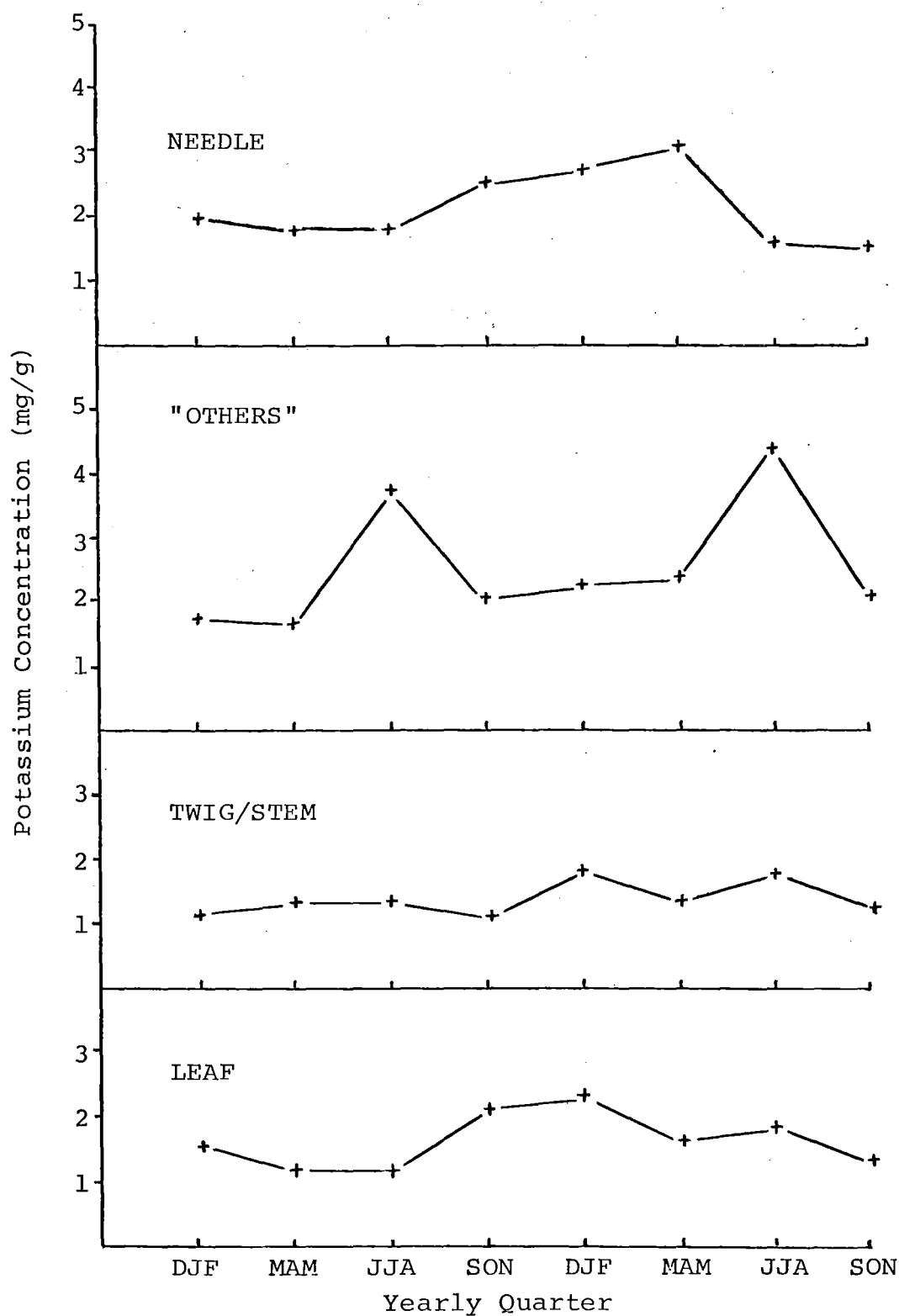


FIGURE 3.3.6.1 Seasonal variation in potassium concentration of litter-fall components for Granville forest

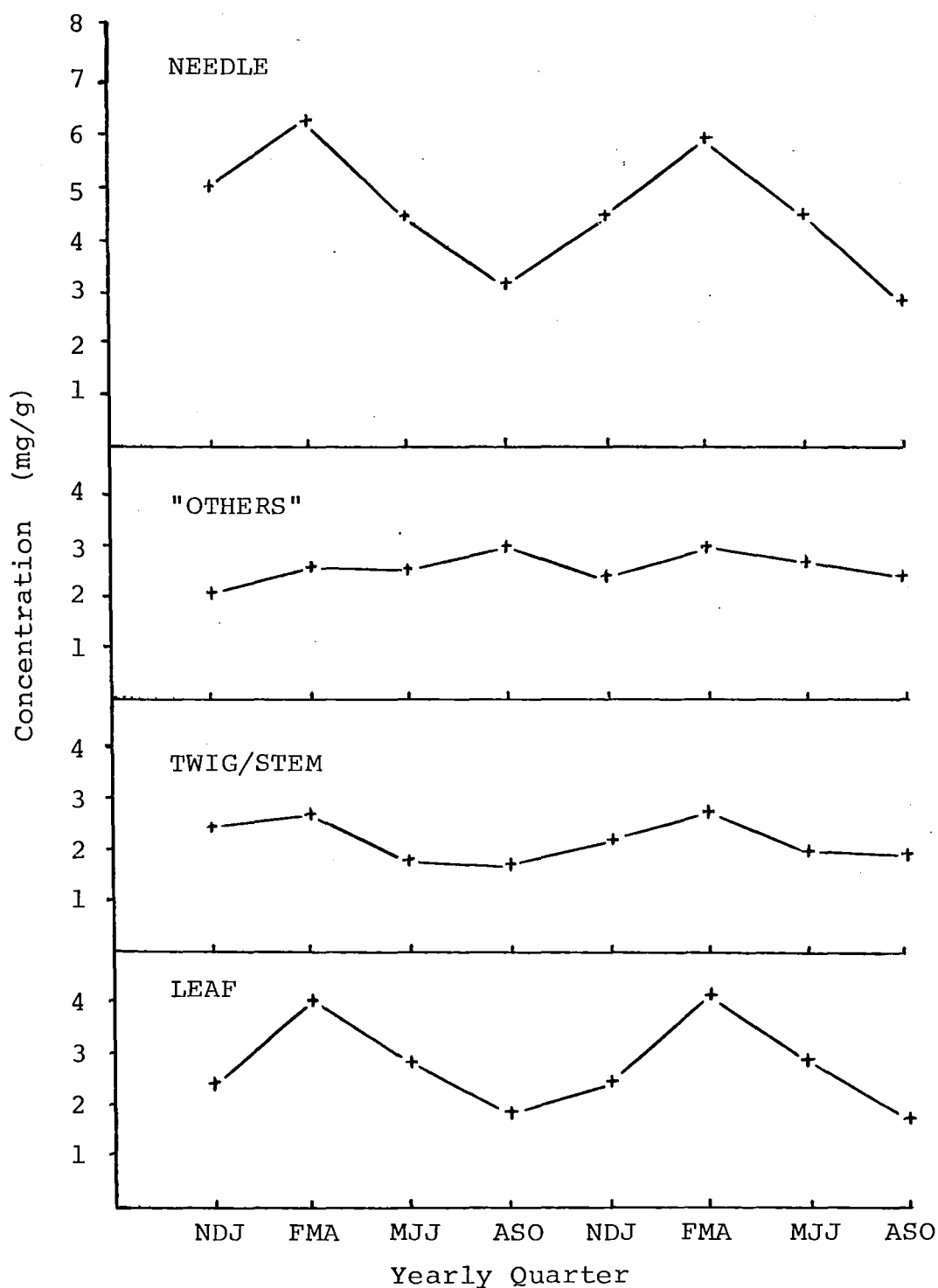


FIGURE 3.3.6.2 Seasonal variation in potassium concentration of litter-fall components for Hanmer forest



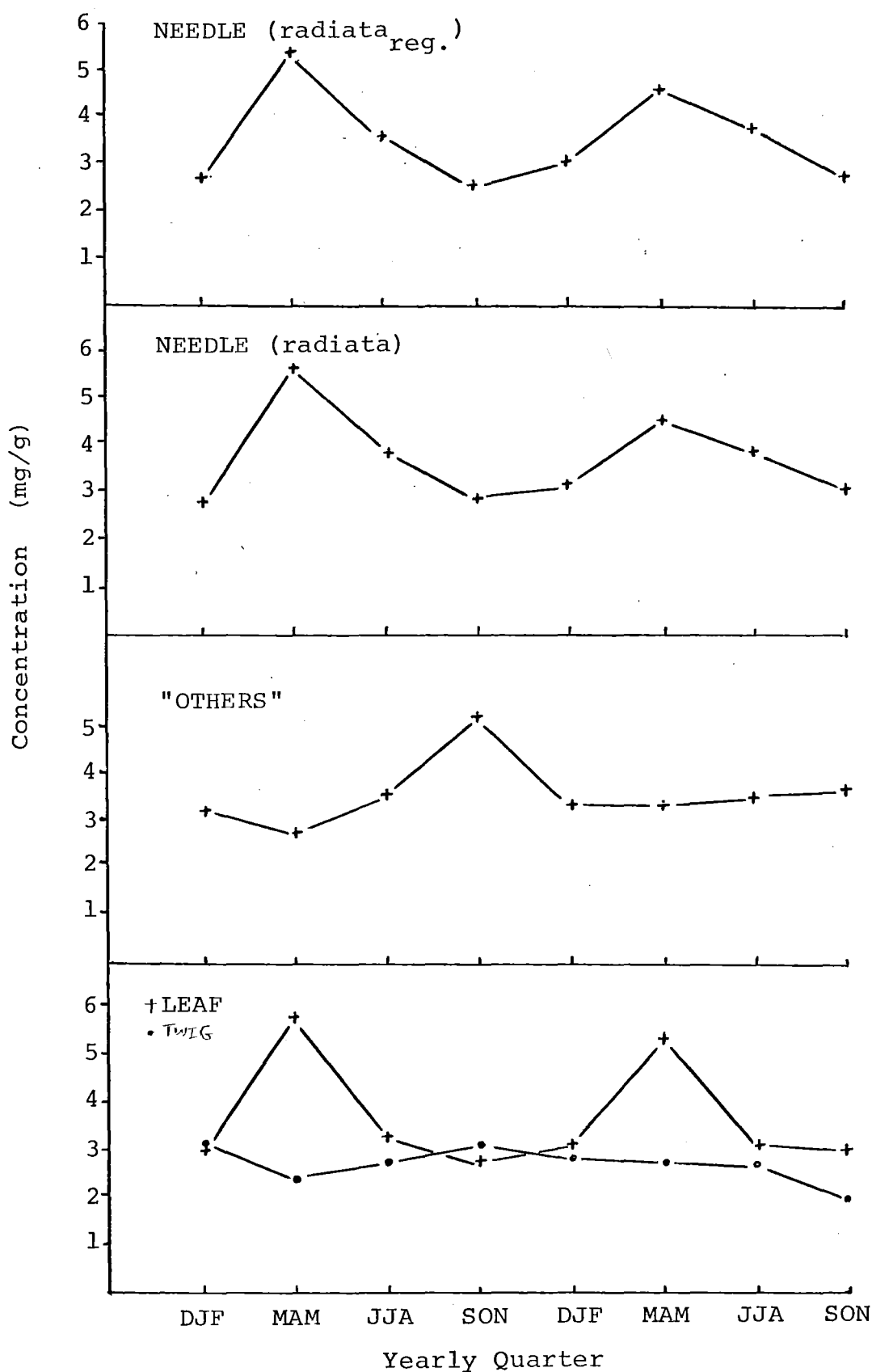


FIGURE 3.3.6.3 Seasonal variation in potassium concentration of litter-fall components for Nelson forest

Low K concentrations of leaves and needles observed in early spring at Hanmer and Nelson may be associated with internal transfers of K from older plant tissues into new productive structures such as flowers, seeds, and also new leaves. Potassium is readily translocated by the phloem from older leaves to young growing ones (Epstein, 1972). Potassium is also a nutrient element most susceptible to leaching (Tukey, 1970) and therefore its concentration in litter may depend on the extent of precipitation penetrating the tree canopy and leaching from the litter. This possibility is partly supported by the recent finding of Levett (1978) which showed a negative correlation between K concentration of needle litter and precipitation. The forest stand used by Levett (1978) was younger and had a more open canopy than those used in the present study. Thus, the leaching effect is less pronounced in our study as compared to that of Levett's (1978). The interception by the litter in litter-traps of K leached from canopy foliage is considered to be unimportant because the "others" and twig litter components which were relatively low in K did not show corresponding marked peaks in K level.

Seasonal variation in nutrient concentrations in both litter and intact foliage in New Zealand and elsewhere have been reported by many workers (e.g. Will, 1959; Miller, 1963a; Katagiri and Tsutsumi, 1973; Spain, 1973; Mälkönen, 1974; Mead and Will, 1976; Levett, 1978). Frequently, seasonal patterns in nutrient concentrations are found not to be consistently repeated on a yearly basis. Thus, no advantage is to be gained by comparing seasonal patterns of

nutrient concentrations between different studies. Instead, it is more useful to discuss possible reasons underlying such observations. The many factors which affect seasonal variation in nutrient concentrations or its absence, as shown by some nutrient elements, have been reviewed previously (Section 2.2.4) and will be additionally discussed in Section 3.3.12.

### 3.3.7 Distribution of Water-soluble and Organic Constituents in Litter

The distribution (or concentration) of the following constituents, water-soluble carbohydrates (WSC), water-soluble polyphenols (WSP), total water-soluble fraction (WSF), petroleum ether-extractable fraction (EE), holocellulose (HOL) and residual lignin (RLIG) in the separated litter components are given in Tables 3.3.7.1 and 3.3.7.2. The values shown represent the average values of the mean concentrations of these constituents found in quarterly (Q1 to Q8) litter samples (see Section 3.2.3) which are given in Appendix II.

#### 3.3.7.1 Water-soluble Constituents

Data obtained indicate that of the different litter components, beech leaf litter showed the largest amounts of water-soluble constituents of WSC, WSP and WSF (Table 3.3.7.1). The overall mean values for WSC, WSP and WSF concentrations in leaf litter of the beech forests studied were 6.4, 13.6 and 30.1 percent of the dry weight of litter respectively. The values for WSC, WSP and WSF in radiata

TABLE 3.3.7.1 Distribution (%) of water-soluble carbohydrates, polyphenols and total water-soluble materials<sup>#</sup> in litter-fall components of beech and radiata pine forests at Granville, Hanmer and Nelson

Forest/Litter component		WSC	WSP	WSF
GRANVILLE				
Beech	Leaf	6.8	14.8	31.8
	Twig	4.4	7.6	18.3
	"Others"	4.8	5.5	17.6
	Branchwood	0.8	1.4	7.6
Radiata	Needle	3.8	4.1	16.9
	Pollen-cone	4.9	7.2	23.9
HANMER				
Beech	Leaf	6.4	13.5	30.2
	Twig	3.5	6.6	15.6
	"Others"	4.4	7.9	20.7
Radiata	Needle	6.6	7.8	28.6
	Pollen-cone	5.0	7.3	22.0
NELSON				
Beech	Leaf	6.0	12.5	28.4
	Twig	3.6	7.7	17.3
	"Others"	5.5	5.3	17.3
	Branchwood	1.7	1.1	8.3
Radiata	Needle	4.5	4.9	20.1
	Pollen-cone	2.7	3.8	9.2
Radiata reg.	Needle	4.4	4.4	18.9
	Pollen-cone	2.7	3.8	9.4

<sup>#</sup> WSC = water-soluble carbohydrates; WSP = water-soluble polyphenols; WSF = total water-soluble materials

needles were 4.8, 5.3 and 21.1 percent respectively. Branchwood contained the lowest amount of water-soluble constituents while twig, "others" and pollen cones showed intermediate values. Comparatively, the concentration of the water-soluble constituents in radiata needles were about the same as those found in twig and "others" litter. It is most notable that the concentrations of the water-soluble constituents in needles of both radiata stands at Nelson were closely similar. This result suggests that the distribution of the water-soluble constituents may be influenced by climatic conditions and site properties.

The largest difference in the amounts of the different water-soluble constituents between beech leaves and radiata needles was found in the WSP fraction. Using the procedures and standards for estimating WSC and WSP described in the present study (Section 3.2.4.5), it was determined that the amount of WSP was about equal to that of WSC in radiata needles, while the amount of WSP was more than double that of WSC in beech leaf litter. Since these two litter components constitute the major litter deposited in the respective stands, this result therefore has significant implications concerning the possible chemical effects on certain ecological processes associated with changes in the kind of forest vegetation (see Review Sections 2.3.4.1.2 and 2.4.4). The effects of WSC and WSP fractions on soil carbon and nitrogen mineralization are examined in the present study (Chapter 7).

Alike tissues from the different stands studied contained similar amounts of the water-soluble constituents, except for the relatively high concentrations of all three

water-soluble fractions in radiata needles at Hanmer. The causative factors underlying this deviation are unknown, but the result was probably due partly to the return of a large proportion of green needles in the litter-fall in this stand, possibly as a result of recent stand thinning.

Compared with results reported in the literature which are summarized in Table 3.3.7.1.1, WSF values found in the present study were generally higher than those reported by other workers. Our WSF values for pine needles are compatible with those reported by Daubenmire and Prusso (1963) for a number of species of pine needles, but are about four times higher than those reported by Waksman and Tenney (1928) for *Pinus strobus*. Our results also show that beech leaves contained higher amounts of WSF than pine needles. This is supported by the data of Katagiri and Tsutsumi (1972) but not by those of Marten and Pohlman (1942) and Nykvist (1963). However, it is extremely difficult to compare data from different workers because of different methods and conditions of extraction used.

Concentration values for WSC, WSP and WSF in all the separated litter components studied showed no definite seasonal pattern (Appendix II). This is not unusual because the water-soluble fractions have been shown to be easily leached from senescent litter (Nykvist, 1963) or rapidly metabolized by micro-organisms (Alexander, 1977). Nykvist (1963) reported that water-soluble substances amounting to between 8 and 25 percent of the dry weights were leached from leaf and needle litters within one day at 25°C. In the present study, litter was collected once a month, which is

TABLE 3.3.7.1.1 Comparison of percentage composition of water-soluble fractions in some species of leaf and needle litter (Values given as % of dry weight of litter)

Litter Species	Amount obtained by:		Total <sup>#</sup>	Reference
	Cold Water	Hot Water		
<i>Pinus strobus</i>	4.4	2.9	7.3	Waksman and Tenney (1928)
<i>Pinus pungens</i>			~ 18	Marten and Pohlman (1942)
<i>Fagus grandifolia</i>			~ 10	
<i>Pinus sylvestris</i>	10.7 <sup>@</sup>			Nykvist (1963)
<i>Fagus sylvatica</i>	7.6 <sup>@</sup>			
<i>Pinus ponderosa</i>	13.3	8.2	21.4	Daubenmire and Prusso (1963)
<i>Pinus contorta</i>	18.5	9.8	28.3	
<i>Pinus albicaulis</i>	16.7	8.2	24.9	
<i>Pinus monticola</i>	16.3			
<i>Fagus crenata</i>			8.2 - 16.4	Katagiri and Tsutsumi (1972)
<i>Pinus densiflora</i>			5.2 - 10.7	
<i>Nothofagus truncata</i>			28.3 - 38.4	Present Study
<i>Nothofagus solandri</i> var <i>cliffortioides</i>			24.9 - 37.5	
<i>Nothofagus</i> spp.			24.5 - 36.4	
<i>Pinus radiata</i>			10.2 - 34.7	

# refer to amounts removed by hot water or those removed by cold and hot water

@ litter leached at 25°C

observed to be a similar procedure in many other studies. This raises the possibility that leaching could be a major contributing factor underlying the irregularities which were observed in the concentrations of the water-soluble constituents. Additionally, several other factors such as temperature, insolation and diurnal changes have been known to influence the amount of water-soluble carbohydrates in plant tissue (Smith, 1973).

### 3.3.7.2 Organic Constituents

The distribution (or concentration) of organic constituents in litter, except in the "others" litter component, are shown in Table 3.3.7.2. The "others" litter component was not analysed for these organic constituents because of its extremely variable composition since it included insect frass, buds, seeds and wood-rot.

No marked differences were observed between the EE fraction in beech leaves and radiata needles, and also between those in similar kind of tissues from the different forests studied. Mean EE concentration values for the quarterly litter collected ranged from 4.0 to 4.9 percent in beech leaves and 4.5 to 5.5 percent in pine needles. In general, EE concentrations in the different litter components decreased in the order:

needles  $\approx$  leaves > pollen cones > twigs > branchwood

Concentration of EE in radiata needles found in the present study were comparatively lower than those reported for a range of pine needles by other workers (e.g. Waksman and Tenney, 1928; Marten and Pohlman, 1942; Daubenmire and



TABLE 3.3.7.2 Distribution (%) of organic constituents<sup>#</sup> in litter-fall components of beech and radiata pine forests at Granville, Hanmer and Nelson

Forest/Litter components		EE	AE	HOL	RLIG
GRANVILLE					
Beech	Leaf	4.9	23.0	45.4	26.7
	Twig	2.2	10.3	49.4	38.1
	Branchwood	0.6	6.3	71.8	21.3
Radiata	Needle	4.5	11.6	49.7	34.2
	Pollen-cone	3.4	8.5	50.3	37.8
HANMER					
Beech	Leaf	4.8	24.3	53.3	17.6
	Twig	3.6	13.6	50.3	32.5
Radiata	Needle	5.3	21.3	49.6	23.8
	Pollen-cone	4.1	11.7	47.1	37.1
NELSON					
Beech	Leaf	4.0	20.9	50.9	24.2
	Twig	2.8	12.0	50.0	35.2
	Branchwood	0.5	5.3	76.3	16.9
Radiata	Needle	5.3	15.0	51.5	28.2
	Pollen-cone	3.8	8.6	50.1	37.5
Radiata reg.	Needle	5.5	14.2	50.1	30.2
	Pollen-cone	4.2	8.2	50.7	36.9

<sup>#</sup> EE = ether-extractable materials; AE = aqueous ethanol-extractable materials; HOL = holocellulose; and RLIG = residual lignin

TABLE 3.3.7.2.1 Comparison of distribution (%) of organic constituents in leaf and needle litter

Litter Species	EE <sup>#</sup>	HOL(=Hemi+Cell) <sup>@</sup>	LIGNIN	Reference
<i>Pinus strobus</i>	11.4	31.6	21.9	Waksman and Tenney (1928)
<i>Pinus pungens</i>	7	27	48	Marten and Pohlman (1942)
<i>Fagus grandifolia</i>	4	32	35	
<i>Quercus rubra</i> , L.			40	
<i>Pinus ponderosa</i>	8.1	28.2	23.8	Daubenmire and Prusso (1963)
<i>Pinus contorta</i>	5.6	22.4	23.3	
<i>Pinus albicaulis</i>	11.6	19.7	27.5	
<i>Pinus monticola</i>	5.9	22.8	25.7	
<i>Pinus strobus</i>			31.0	Cromack (1973)
<i>Quercus prinus</i>			25.5	
<i>Quercus alba</i>			17.2	
<i>Nothofagus truncata</i>	4.2 - 5.5	42.3 - 46.9	22.1 - 31.9	Present Study
<i>Nothofagus solandri</i> var <i>cliffortioides</i>	4.0 - 5.5	52.5 - 54.7	13.9 - 23.1	
<i>Nothofagus</i> spp.	3.4 - 4.5	48.3 - 53.1	18.8 - 28.2	
<i>Pinus radiata</i>	3.9 - 8.3	46.0 - 53.7	20.9 - 39.1	

@ HOL, estimated from results of other studies by summing hemicellulose and cellulose values given

# EE = ether-extractable fraction

Prusso, 1963) shown in Table 3.3.7.2.1. However, EE concentration values for beech leaves were similar to those of Marten and Pohlman (1942). These discrepancies in EE concentration values for pine needles were probably due to the different degree of weathering of the waxes in the needles during the later stages of their life. It was observed that the older and yellowing needles in the radiata stands studied lacked the thick waxy appearance of green intact needles.

The AE fraction of plant litter was extracted only to facilitate the analysis of holocellulose. However, the ratios of AE fraction to WSF fraction as found for the separated litter components ranged from 0.3 to 0.9. Lower amounts of AE compared to WSF probably resulted from the removal of certain amounts of EE previously.

Distribution values for HOL in leaf, twig, needle and pollen cone litters showed no marked differences, but they differed substantially from that of branchwood (Table 3.3.7.2). Branchwood contained a larger amount of holocellulose because of the greater proportion of heartwood. Comparison of HOL values with those of other studies is difficult as such comparison is frequently complicated by the dissimilar methods of isolation of HOL used. This difficulty is clearly demonstrated by the diverse distribution values of HOL shown in Table 3.3.7.2.1.

Results in Table 3.3.7.2 show that beech leaf litter contained lower residual lignin (RLIG) content than radiata needle litter at the time of litter-fall. However, larger differences were observed in RLIG values between twig and leaves of beech than between beech leaves and pine needles.

This is due primarily to the high bark content of twig which usually has a greater lignin content than wood (Kerr, 1976). This view is supported by our result of a lower RLIG content in branchwood than twig litter. Cromack (1973) has also reported higher lignin percentages in oak stems than in green and senescent oak leaves, although he studied stems of  $< 2.5\text{cm}$  diameter and not  $< 1\text{cm}$  as used in the present study. Furthermore, most twigs presumably could have undergone a greater degree of decomposition than leaf litter before abscission. This reasoning is supported by results of Edwards (1977) which showed that the density of healthy twigs were much greater than twigs at litter-fall.

In general, RLIG values obtained for radiata needles as determined according to the procedure described in the present study (Section 3.2.4.8) were not markedly different from those reported by other workers (e.g. Daubenmire and Prusso, 1963) for different species of pine needles (Table 3.3.7.2.1), in spite of the different methods of determination used. This suggests that the RLIG values as defined in this study closely approximate normal lignin concentration values.

### 3.3.8 Total Annual Budgets of Macro-nutrient and Carbon

Total annual budgets for macro-nutrients (N, P, K, Mg, Ca) and carbon in the beech and radiata stands studied are shown in Table 3.3.8.1. Further data for nutrient and carbon budgets in each quarter, and in the two years (1976/79 and 1977/78) are given in Appendix II. Contributions

TABLE 3.3.8.1 Total annual budgets (kg/ha) of macro-nutrients in beech and radiata stands at Granville, Hanmer and Nelson forests

Forest/Stand	N	P	K	Mg	Ca	Total Nutrients	Carbon
GRANVILLE							
Beech	39.95 <sup>@</sup>	2.71	10.88	10.31	62.48	126.33	3693
Radiata	31.12	2.26	8.75	4.82	18.02	64.97	2166
HANMER							
Beech	20.70	3.78	10.95	5.75	41.36	82.54	1983
Radiata	9.07	1.84	7.43	1.74	9.21	29.29	755
NELSON							
Beech	46.45	5.31	19.38	8.16	80.56	159.86	3147
Radiata	37.33	5.32	18.86	6.99	34.74	103.24	2564
Radiata <sub>reg.</sub>	31.11	4.52	13.64	5.87	33.24	88.38	2044

@ values given represent average of annual budgets of 2 years

by branch litter to the annual returns are shown separately because branch litter, as discussed previously (Section 3.3.4) was an extremely variable component of total litter deposited in these stands studied. In addition, branch litter collected fluctuates markedly from year to year (Section 3.3.3.4).

The annual total nutrient returns in beech forests studied were comparably similar to those found by other workers (Table 3.3.8.2), and were closely similar to that reported by Miller (1963b) for hard beech in New Zealand. Relatively low total nutrients found for beech at Hanmer is attributed to a much lower total litter-fall, since total nutrient content expressed as a percentage of total litter-fall (given as R in Table 3.3.8.2) was not different from those estimated for other forests.

Data on total nutrient returns obtained for radiata plantations agree reasonably well with results of Will (1959) for radiata pines in Whakarewarewa forest in the North Island of New Zealand. The small return of total nutrients found for the radiata stand at Hanmer was primarily the result of low litter-fall brought about by stand thinning. The R value of the Hanmer radiata stand was within the range calculated for other pine forests.

Comparison of the annual total nutrient content of litter deposited in both beech and radiata stands leads to the conclusion that the beech stands were returning, but not necessarily recycling, larger amounts of nutrients, including carbon, than their adjacent radiata stands in the three forests studied. Excluding contributions by branch and

TABLE 3.3.8.2 Comparison of annual macro-nutrient budgets (kg/ha) of some beech and pine forests

REFERENCE	SPECIES	DRY MATTER	N	P	K	Mg	Ca	Total M/ Nutrient	R <sup>@</sup>
Present Study	<i>Nothofagus truncata</i>	7107	40.0	2.7	10.9	10.3	62.4	126.3	1.8
	<i>Nothofagus solandri</i> var <i>cliffortioides</i>	3964	20.7	3.8	11.0	5.7	41.4	82.6	2.1
	<i>Nothofagus</i> spp.	6693	46.4	5.3	19.4	8.2	80.6	159.9	2.4
Miller (1963b)	<i>Nothofagus truncata</i>	6026	31.4	2.5	9.0	11.0	71.0	124.9	2.1
Ulrich <i>et al.</i> (1973)	<i>Fagus sylvatica</i>		54.7	4.9	17.3	1.7	22.7	101.3	
Gosz <i>et al.</i> (1972)	<i>Fagus grandifolia</i> <sup>‡</sup>	5613	55.8	3.7	21.1	6.4	45.2	132.2	2.4
Cromack (1973)	<i>Pinus strobus</i>	4250	33.3	4.9	18.0	6.5	43.6	106.3	2.5
Will (1959)	<i>Pinus radiata</i>	7398 <sup>#</sup>	39.8	6.4	15.0	5.7	25.5	92.4	
	<i>Pinus nigra</i>	7933 <sup>#</sup>	36.2	3.4	17.9	7.6	51.1	116.2	
Spain (1973)	<i>Pinus nigra</i>	5196	44.8	2.6	10.2	3.7	38.4	99.7	1.9
	<i>Pinus ponderosa</i>	5642	64.2	4.0	13.0	3.7	17.0	101.9	1.8
Miller <i>et al.</i> (1976)	<i>Pinus nigra</i>	2615	11.1	1.9	3.4	2.2	13.6	32.2	1.2
Tappeiner and Alm (1975)	<i>Pinus resinosa</i>	3290	16.5	3.3	7.2	3.0	16.6	46.6	1.4
Present Study	<i>Pinus radiata</i>	3905	31.1	2.3	8.8	4.8	18.0	65.0	1.7
	"	1504	9.1	1.8	7.4	1.8	9.2	29.3	1.9
	"	4817 <sup>+</sup>	37.3	5.3	18.9	7.0	34.7	103.2	2.1
	"	4059 <sup>+</sup>	31.1	4.5	13.6	5.9	33.3	88.4	2.2

# refer to air-dried weights

+ excluding branchwood and female cones

‡ primary species in a mixed hardwoods stand

@ refer to ratio given by

$$\frac{\text{Total m/nutrients}}{\text{Dry matter}} \times 100 \%$$

female cone litter, the amounts of nutrients returned annually in radiata stands constituted only 60, 35 and 65 percent of those returned in adjacent beech stands in the forests at Granville, Hanmer and Nelson respectively. Such a finding is in agreement with the data for beech obtained by Miller (1963b) and for radiata by Will (1959) although their studies were conducted at different locations. The present results were obtained from adjacent pairs of beech forest and radiata plantations on the same or similar soil. Cromack (1973) also found that a deciduous hardwood stand was returning 85 percent more total nutrients than a white pine stand.

Generally speaking, results of the present study indicate that radiata pines were returning to the forest floor as much P as beech (Table 3.3.8.1). The amounts of P returned annually showed lesser differences between beech and radiata stands, when compared to those of the other nutrients studied. It is notable that in terms of weight of P per unit weight of litter returned, radiata pines were in fact returning much more P than beech (i.e. 50, 28 and 40 percent greater in Granville, Hanmer and Nelson forests respectively). This result may be related to the effects of increased P availability and uptake under pine plantations reported by Fisher and Stone (1969).

The annual budget for Ca in beech and radiata stands showed marked difference. Such a difference is also apparent if the results of Miller (1963b) and Will (1959) for hard beech and radiata respectively in New Zealand, are compared. The same trend is also apparent if data for beech and pines



obtained elsewhere are compared (Table 3.3.8.2).

The order of importance for total annual budgets of the different nutrient elements in terms of weight contribution in beech and radiata stands studied was observed to be:

Beech forests:  $\text{Ca} > \text{N} > \text{K} > \text{Mg} > \text{P}$

Radiata plantations:  $\text{N} \geq \text{Ca} > \text{K} > \text{Mg} \geq \text{P}$

This order of abundance in the different nutrient elements is generally consistent with those found by other workers (see Table 3.3.8.2).

### 3.3.9 Nutrient Returns by Litter-fall Components

In general, leaf and needle litter constitute the major sources of nutrients returned to the forest floor by way of litter-fall in the respective stands studied.

(Appendix II). However, by comparison, it was found that needle litter was more important than leaf litter as a supplier of nutrients, particularly for the elements of N, P and K (Table 3.3.9.1). This result is due primarily to the comparatively larger amounts of pine needles than beech leaves deposited in the respective stands. Nevertheless, substantial amounts of nutrients were also returned by both twig and "others" litter in beech forests (Table 3.3.9.1).

It is most notable that in critical elements such as N, P or K, "others" litter could become as important a source of nutrients as leaf litter. For example, "others" litter supplied substantially large amounts of P and possibly also N in some years (e.g. in Granville forest, Table 3.3.9.2), although this result did not take into account that part of the "others" litter had also included fragmented

TABLE 3.3.9.1 Amount of macro-nutrients returned annually (kg/ha) by leaf and needle litter-fall in beech and radiata pine forests respectively

	N	P	K	Mg	Ca
GRANVILLE					
Beech leaf	15.5 <sup>#</sup>	0.9	4.6	4.4	21.9
Radiata needle	28.9	2.0	7.8	4.4	16.7
HANMER					
Beech leaf	12.4	2.6	7.8	3.5	26.9
Radiata needle	8.8	1.8	7.2	1.7	9.1
NELSON					
Beech leaf	24.1	2.9	11.0	3.9	41.2
Radiata needle	33.6	4.9	17.3	6.3	33.5
Radiata <sub>r</sub> needle	27.7	4.2	12.4	5.3	32.2

# values given represent mean of two years' data

leaves. As discussed previously (Section 3.3.5) much of the N and P in "others" litter were also derived from tissues rich in N and P such as insect frass and flowers. Results of the present study also suggest that twig litter could become a major source of Ca and Mg.

Generally, leaf litter accounts for the greater proportion of most nutrients. Such contributions by leaf litter were found to vary according to the different forests and ranged between 34 and 56 percent, 58 and 72 percent and 48 and 63 percent, according to the element in question in Granville, Hanmer and Nelson forests respectively (Table 3.3.9.2).

The greater nutrient returns in beech stands than in their adjacent radiata stands were not due to greater branchwood litter. The exclusion of branchwood contributions did not alter the relative order in the magnitude of total nutrients returned in beech and radiata stands.

Generally speaking, although branchwood makes up a substantial proportion of the total annual litter deposited in beech forests, its contribution of nutrients to the total annual return is usually comparatively smaller. For example, in Granville, branchwood accounted for about 16 percent and 37 percent of the total litter deposited on the forest floor of the beech stand in the first and second year respectively. However, its contributions to the total nutrient return in the corresponding years were found to amount to only 8 percent and 21 percent respectively. In comparison, Gosz et al. (1972) found that tree trunk-fall which amounted to 14.1 percent of total litter weight, supplied only 1.5 percent of

TABLE 3.3.9.2 Relative contribution (%) made by the different litter components to the annual nutrient returns in beech forests at Granville, Hanmer and Nelson

Forest	FIRST YEAR			SECOND YEAR		
	Leaf	Twig	"Others"	Leaf	Twig	"Others"
GRANVILLE						
N	43	23	34	41	12	47
P	41	20	39	34	12	54
K	47	30	23	45	15	40
Mg	45	39	16	56	20	24
Ca	41	46	13	48	25	27
HANMER						
N	58	17	25	62	17	21
P	63	16	21	69	16	15
K	70	14	16	72	15	13
Mg	59	24	17	60	26	14
Ca	63	22	15	66	23	11
NELSON						
N	63	17	20	50	20	30
P	62	17	21	53	19	28
K	61	19	20	57	18	25
Mg	54	30	16	48	31	21
Ca	63	22	15	50	24	26

the total nutrients.

The results obtained in the present study clearly show that critical elements such as N, P and K were being utilized more sparingly in wood tissues than leaf or needle tissues in the forests studied. This suggests that the greater proportion of these critical nutrients consequently follows short turnover cycles back to the forest floor while only a small part undergoes larger cycles through the wood.

Total annual carbon budget of beech stand was consistently and substantially greater than those of adjacent radiata stands at each of the three forests (Table 3.3.8.1). This is not unexpected since the distribution values of carbon in the different litter components of beech and radiata pine were comparatively similar (Appendix II). Thus, the trend in annual carbon budgets closely reflected that in the total annual litter-fall.

### 3.3.10 Annual Return of Water-soluble and Organic Constituents

Results of the total annual returns for the water-soluble and organic constituents by litter-fall are shown in Table 3.3.10.1 and 3.3.10.2 respectively. Quarterly returns for these constituents in the two years (1976/77 and 1977/78) are given in Appendix II.

#### 3.3.10.1 Water-soluble Constituents

In the three forests studied, water-soluble constituents made up a substantially large proportion of the annual litter biomass (excluding branch and female cone litter) in

both beech and radiata stands (i.e. ranging from 17.6 to 28.1 percent by weight: Table 3.3.10.1). For beech stands in general, amounts of WSC, WSP and WSF returned amounted to 5.6, 10.8 and 25.3 percent respectively, of the annual litter weight. The corresponding values for radiata stands were 4.9, 5.4 and 22.2 percent.

Other published literature data with which some comparisons on the annual return of these water-soluble constituents can be made, is unavailable. However, the results of the present study were sufficiently consistent to indicate that beech stands were returning larger amounts of water-soluble constituents than their adjacent radiata stands by way of litter-fall annually.

Furthermore, the greatest difference in the amounts of water-soluble constituents returned to the forest floor between beech and radiata pine occurred in the WSP fraction. This is clearly indicated by the ratio R (amount in beech stand/amount in radiata stand) given in Table 3.3.10.1. The R values for WSC and WSF were consistently smaller than those of WSP.

Leaf and needle litter also remained the major litter components responsible for the return of the water-soluble constituents in the respective forests. In beech forests, leaf litter accounted for a greater percentage of the annual return of these constituents when compared to their contributions to the annual litter-fall biomass (Table 3.3.10.1.1).

TABLE 3.3.10.1 Amounts (kg/ha) of the different water-soluble constituents returned in annual litter-fall of beech and radiata stands<sup>†</sup>

Forest/Stand	CARBOHYDRATES	POLYPHENOLS	TOTAL FRACTION
GRANVILLE			
Beech	309 (5.9) <sup>#</sup>	574 (11.1)	1353 (26.2)
Radiata	164 (4.2)	184 ( 4.7)	740 (12.0)
Ratio <sup>@</sup>	1.9	3.1	1.8
HANMER			
Beech	227 (5.7)	474 (11.9)	1065 (26.9)
Radiata	97 (6.4)	117 ( 7.7)	425 (28.1)
Ratio	2.3	4.1	2.5
NELSON			
Beech	306 (5.2)	558 ( 9.5)	1335 (22.8)
Radiata	223 (4.6)	239 ( 5.0)	956 (20.0)
Ratio	1.4	2.3	1.4
Radiata <sub>reg.</sub>	172 (4.3)	174 ( 4.3)	710 (17.6)
Ratio	1.8	3.2	1.9

@ refer to the ratio beech/radiata

† mean of 2 years' data, branchwood and female cone litter contributions were not included

# data in parenthesis refer to percentage of annual litter weight

TABLE 3.3.10.1.1 Contribution (%) by leaf litter to the annual returns of water-soluble constituents and litter-fall biomass in beech<sup>@</sup> forests at Granville, Hanmer and Nelson

Forest	CARBOHY- DRATES	POLY- PHENOLS	TOTAL FRACTION	LITTER-FALL BIOMASS
GRANVILLE	59	64	64	48
HANMER	76	78	77	66
NELSON	64	72	69	57

@ mean of 2 years' data, contribution by branchwood not included

### 3.3.10.2 Organic Constituents

Data in Table 3.3.10.2 show that considerable amounts of ether-extractable (EE) substances were returned to the forest floor in beech and radiata stands by way of litter-fall, amounting to between 150 to 167 kg/ha in the beech stands and 77 to 270 kg/ha in the radiata stands studied. It was difficult to compare between adjacent forest stands since these estimates did not include "others" litter of beech stands. As mentioned previously, no attempt was made to analyse this litter component because it was considered not meaningful to chemically isolate the organic constituents, particularly into HOL or RLIG, on account of the extremely variable range of materials included in "others" component. However, an estimation of the amounts of these organic constituents returned annually by "others" litter component was made. This was done by assuming that for each of the constituents (EE, AE, HOL and RLIG), the concentration value in the "others" litter was equivalent to the annual mean concentration found for leaf litter. This assumption will not be seriously in error since part of "others" litter comprised of fragmented leaf litter (Section 3.3.3.1). These values estimated accordingly are shown in parenthesis in Table 3.3.10.2.

It is evident that, as have been found for total macro-nutrients and water-soluble constituents, larger amounts of the different organic constituents were also returned to the forest floors in beech and radiata stands. The differences between beech and radiata stand in the amounts of EE and RLIG were less marked, however. Much of these differences



TABLE 3.3.10.2 Amounts (kg/ha) of the different organic constituents returned in annual litter-fall of beech and radiata stands at Granville, Hanmer and Nelson<sup>#</sup>

Forest/Stand	Ether Extracts	Aqueous Ethanol Extracts	Holocellulose	Residual Lignin
GRANVILLE				
Beech	166 <sup>‡</sup> (65) <sup>@</sup>	777(303)	1987(599)	1324(351)
Radiata	181	466	2052	1431
HANMER				
Beech	150(29)	749(147)	1757(322)	652(107)
Radiata	77	324	699	349
NELSON				
Beech	167(47)	807(244)	2282(595)	1219(283)
Radiata	260	727	2579	1499
Radiata <sub>reg.</sub>	213	525	2008	1256

# Values given are means of 2 years' data

‡ from leaf + twig litter

@ from "others" litter, estimated using concentration values of leaf litter

were the result of larger biomass of litter-fall in beech stands since it was determined that dissimilarities in concentration values for EE, HOL and RLIG between the major litter components of leaf and needle were generally small, except for those of branchwood (Table 3.3.7.2).

Results of the present study indicate that beech leaves and radiata pine needles represented major sources of EE, HOL and RLIG (Table 3.3.10.2.1). However, substantial contributions were also derived from branchwood for HOL and twig for RLIG. For example, at Granville, branchwood which accounted for 36 percent of the total litter-fall biomass (leaf + twig + branchwood), made up 41 percent of the annual total HOL. Similarly, twig litter accounted for 22 percent and 35 percent of the annual litter-fall biomass and annual total RLIG respectively. Relatively similar patterns were also found at Hanmer and Nelson.

Contributions made by pollen cones to the annual returns of HOL and RLIG in radiata stands ranged from 4 to 14 percent, almost all of which were deposited within two to three months in spring (Will, 1959; Section 3.3.3.3).

### 3.3.11 Comparison of Quarterly Return of Litter

#### Biomass and Chemical Constituents in Beech Forests and Radiata Pine Plantations

Differences in the amounts of chemical constituents returned in quarterly litter-fall between beech and adjacent radiata stands at Granville, Hanmer and Nelson were statistically analysed. No comparison was carried out for the organic constituents as there was incomplete data for beech

TABLE 3.3.10.2.1 Comparison of amounts<sup>‡</sup> (kg/ha) of litter weight, ether extract, holocellulose and residual lignin returned annually by the different litter components in beech and radiata forest stands at Granville, Hanmer and Nelson, together with their relative contributions (%) to respective annual total amount

FOREST/STAND/LITTER COMPONENT			LITTER WEIGHT		ETHER EXTRACT		HOLOCELLULOSE		RESIDUAL LIGNIN	
			Amount†	%	Amount†	%	Amount†	%	Amount†	%
GRANVILLE	Beech	Leaf	2534	42	132	74	1215	36	718	42
		Twig	1352	22	34	19	772	23	607	35
		B/wood	2217	36	12	7	1365	41	404	23
	Radiata	Needle	3556	91	168	93	1865	91	1290	90
		P/cone	349	9	13	7	187	9	141	10
HANMER	Beech	Leaf	2644	79	135	84	1401	80	437	66
		Twig	716	21	25	16	356	20	226	34
	Radiata	Needle	1441	96	74	96	667	95	324	93
		P/cone	63	4	3	4	32	5	25	7
NELSON	Beech	Leaf	3350	61	132	77	1680	57	790	58
		Twig	1324	24	35	20	602	21	429	31
		B/wood	851	15	4	3	650	22	145	11
	Radiata	Needle	4294	89	239	92	2295	89	1287	86
		P/cone	523	11	21	8	284	11	212	14
	Radiata reg.	Needle	3563	88	192	90	1758	88	1074	86
		P/cone	496	12	21	10	250	12	182	14

‡ mean of 2 years' data

stands on account that no chemical analysis was made on "others" litter for these constituents. Results obtained are shown in Tables 3.3.11.1 to 3.3.11.4. All values of amounts found in each quarter are given in Appendix II.

Generally, spring (September to November, Q4 and Q8) and summer (December to February, Q1 and Q5) were the times when largest differences in the amount of nutrients returned were found between the beech and adjacent radiata stands at Granville, Hanmer and Nelson. Smallest differences were found in winter (June to August, Q3 and Q7).

Of the individual nutrient elements, P and K showed the least contrast between beech and adjacent radiata stands in all quarters, while Ca showed the greatest. Nitrogen, K and Mg were intermediate.

Some additional notable points found include greater amounts of litter biomass and nutrients in radiata than beech stands at Nelson in the winter quarters (Table 3.3.11.3), which were not observed to occur at Granville or Hanmer. However, the size of litter-fall biomass collected during the winter quarters were generally very small in comparison to those collected in spring or summer quarters (Appendix II). Therefore, these differences observed may be unimportant. At Hanmer, differences between stands were extremely pronounced in the late spring-early summer quarters (Table 3.3.11.2). Only small differences were found in the autumn and winter quarters, inspite of thinning in the radiata stand. Occasionally, in certain nutrients (e.g. P and K), larger amounts were returned in the radiata stand than in the beech. In Granville, except for P in the summer quarter and K in the

TABLE 3.3.11.1    Ratio values<sup>#</sup> and levels of significance obtained from comparison of quarterly litter-fall budgets for macro-nutrients, carbon and water-soluble constituents between beech and radiata pine forest stands at Granville

Litter constituents	Annual Quarters							
	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
Dry weight	1.58***	1.09	1.48	1.24	1.68***	1.67***	1.67*	1.08
Nitrogen	1.29*	1.01	1.42*	1.01	1.30*	1.16	1.85*	1.13
Carbon	1.60**	1.06	1.48	1.26	1.61*	1.48	1.45	1.09
Carbohydrates	2.21**	1.38	2.42**	1.72*	2.71**	2.08*	2.59**	1.62*
Polyphenols	3.34***	2.37**	4.51***	2.37***	4.79**	4.00***	4.77***	2.61***
Total w/s materials	2.08**	1.32	2.59**	1.52**	2.64**	2.47***	2.52**	1.56**
Phosphorus	1.40**	0.81	1.69	0.93	1.17	1.26	1.75	1.10
Potassium	1.18	0.87	1.54**	0.95	1.35	0.91	2.87	1.00
Magnesium	2.19**	1.51*	2.08*	1.70	2.40*	2.21*	2.11*	1.39*
Calcium	3.52**	2.59**	2.56	2.88***	3.09**	2.96*	3.01*	2.14**

#    Ratio = beech/radiata  
 Levels of significance,    \* p < 0.05  
                                      \*\* p < 0.01  
                                      \*\*\* p < 0.001

TABLE 3.3.11.2 Ratio values<sup>#</sup> and levels of significance obtained from comparison of quarterly litter-fall budgets for macro-nutrients, carbon and water-soluble constituents between beech and radiata pine forest stands at Hanmer

Litter constituents	Q1	Q2	Q3	Annual Quarters		Q6	Q7	Q8
				Q4	Q5			
Dry weight	6.11***	2.60**	1.20	1.71*	8.57***	1.29	1.41	2.79**
Nitrogen	5.88**	2.18**	1.23	1.72	6.54***	0.78	1.78	3.07**
Carbon	6.27***	2.38*	1.25	2.06	8.55***	1.13	1.26	3.89*
Carbohydrates	5.65***	2.29	1.08	1.70	6.82***	1.04	0.99	4.07*
Polyphenols	9.61***	4.08*	1.60	2.45	14.99***	1.73*	1.85	6.11**
Total w/s materials	5.98***	2.23*	1.00	1.77	8.81***	1.15	1.14	4.03*
Phosphorus	6.31***	1.59	1.17	1.85	7.31***	0.96	1.06	3.22*
Potassium	3.27*	1.45	0.81	1.50	4.89**	0.75	0.77	2.33*
Magnesium	9.26***	3.01*	1.63*	4.02*	11.80***	1.41	1.77	5.03**
Calcium	12.57***	5.26*	1.72	3.48*	14.37***	2.08*	2.06	8.58**

# Ratio = beech/radiata

Levels of significance, \* p < 0.05  
 \*\* p < 0.01  
 \*\*\* p < 0.001

TABLE 3.3.11.3 Ratio values<sup>#</sup> and levels of significance obtained from comparison of quarterly litter-fall budgets for macro-nutrients, carbon and water-soluble constituents between beech and radiata pine forest stands at Nelson

Litter constituents	Annual Quarters							
	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
Dry weight	1.50**	0.59***	0.63**	1.78***	1.44*	0.71*	0.82	2.16***
Nitrogen	1.15	0.57**	0.76	1.88***	1.17	0.56**	0.72	2.90***
Carbon	1.28	0.60*	0.58*	1.66***	1.01	0.54*	0.83	1.91*
Carbohydrates	1.97*	0.73	0.57*	2.97***	1.02	0.73	0.79	2.93***
Polyphenols	4.46**	1.16	0.92	4.08***	2.74***	1.29	1.00	3.97**
Total w/s materials	2.43*	0.63*	0.55*	2.80***	1.33	0.73	0.71	2.72**
Phosphorus	1.40	0.50*	0.49**	1.67***	1.08	0.43**	0.74	1.80**
Potassium	1.47	0.49*	0.52*	1.90**	1.02	0.59*	0.70	1.94**
Magnesium	1.36	0.58*	0.54*	1.71***	1.08	0.55*	0.83	1.90*
Calcium	2.49**	1.29	0.96	3.67***	1.84**	1.17	1.54*	3.84**

# as for TABLE 3.3.11.2

TABLE 3.3.11.4 Ratio values<sup>#</sup> and levels of significance obtained from comparison of quarterly litter-fall budgets for macro-nutrients, carbon and water-soluble constituents between beech and radiata<sub>reg.</sub> pine forest stands at Nelson

Litter constituents	Q1	Q2	Q3	Annual Quarters		Q6	Q7	Q8
				Q4	Q5			
Dry weight	1.71**	1.09	0.62**	1.77***	1.95**	1.04	0.93	1.87**
Nitrogen	1.34	0.93	0.68*	2.12***	1.64*	0.67	0.87	2.67**
Carbon	1.55	1.06	0.72	1.66***	1.39*	0.95	0.93	1.74*
Carbohydrates	2.50*	1.66	0.65*	2.92***	1.14	1.73	0.89	2.73***
Polyphenols	5.50**	2.93**	1.22	4.19***	3.33***	3.50**	1.22	3.39**
Total w/s materials	3.53**	1.43	0.60*	2.91***	1.55*	1.77	0.82	2.64**
Phosphorus	1.46	0.86	0.59*	1.69***	1.19	0.51*	0.82	1.63**
Potassium	1.83*	0.85	0.58	2.15**	1.46*	1.05	0.84	1.96**
Magnesium	1.37	0.95	0.71	1.66***	1.36	0.80	0.94	1.81*
Calcium	2.26**	1.88*	0.94	3.07***	2.16**	1.88	1.36	3.28**

# as for TABLE 3.3.11.2



winter quarter of the first year, no significant difference was found between stands in P and K returns (Table 3.3.11.1). Calcium, on the other hand, showed largest differences between adjacent stands among the nutrients. For the same two stands at Granville (beech and radiata), Levett (1978) recorded considerably greater Ca, and to a much lesser degree K, returns in beech than in radiata stand, while that of P was about similar. His results, therefore, were in general agreement with those found in the present study.

Carbon R ratios reflected closely those of litter biomass. This is not unexpected since carbon content of most litter components were consistently similar (Appendix II).

Spring and summer were also found to be important times for differences between stands in the water-soluble constituents, although some significant differences were also found in the other quarters. It is significant that at Granville, the beech and radiata stand differed markedly in the water-soluble constituents throughout the year (Table 3.3.11.1). As observed, the R ratios in WSC and WSF were consistently smaller compared to that of WSP. For example, while the ratios for litter-fall biomass ranged from 1.08 to 1.68, those for WSP ranged from 2.37 to 4.79. The corresponding ranges for WSC and WSF were 1.38 to 2.71 and 1.32 to 2.64 respectively. Large differences in the quarterly returns of the water-soluble constituents between beech and radiata stands were also observed at Hanmer (Table 3.3.11.2) and Nelson (Tables 3.3.11.3 and 3.3.11.4). These large differences in the water-soluble constituents, in particular

WSP, between beech and radiata stands could be important factors in the study of the dynamics of certain ecological processes (Review Sections 2.3.4.1.2 and 2.4.4) occurring in these forested ecosystems.

### 3.4 GENERAL DISCUSSION

As there were only small and irregular seasonal variations in litter nutrient concentrations (Section 3.3.6), and in the distribution of water soluble and organic constituents (Section 3.3.7), it was therefore not unusual to observe that the seasonal (quarterly) return patterns followed closely to that of litter biomass. This effect is illustrated in Figures 3.4.1.1 and 3.4.1.2, using as an example, the nutrient (N, P, K, Mg, Ca) returns in the beech and radiata stands at Granville. There was definitely a closer seasonal relationship between nutrient returns and litter-fall biomass returns than between nutrient returns and nutrient concentrations. This pattern was closely similar for all nutrient elements in both beech and radiata stands. Miller (1963b) also found that seasonal variation in nutrient returns was largely governed by the seasonal litter production since chemical composition varied over a relatively small range. Levett (1978) found that nutrient returns were highly correlated with litter-fall biomass for a number of hardwood and pine stands.

The degree of contrast between quarterly nutrient returns during the first year was definitely more evident

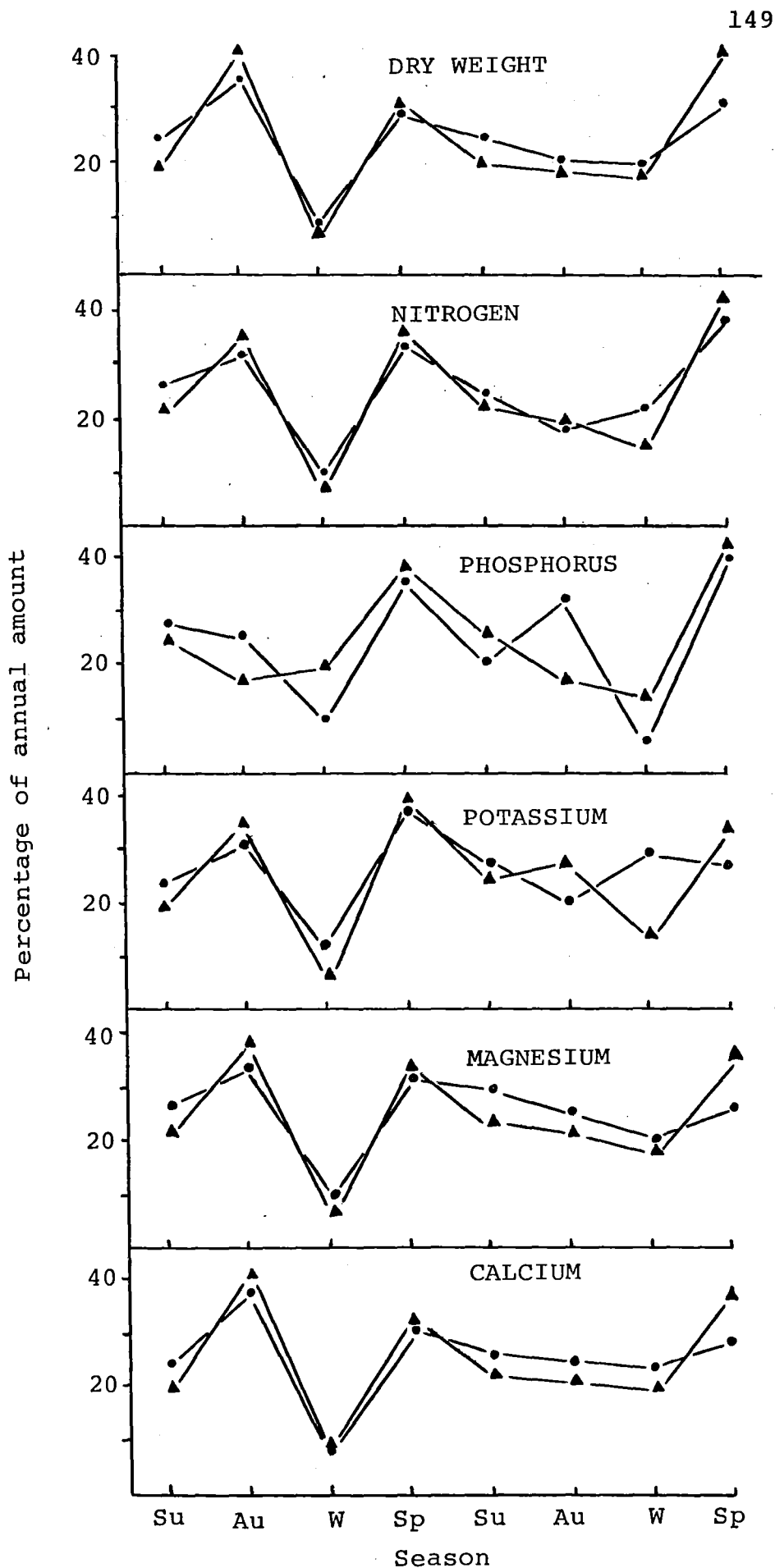


FIGURE 3.4.1.1 Seasonal variation in litter weight and nutrient return in beech and radiata stand at Granville (• beech, ▲ radiata)

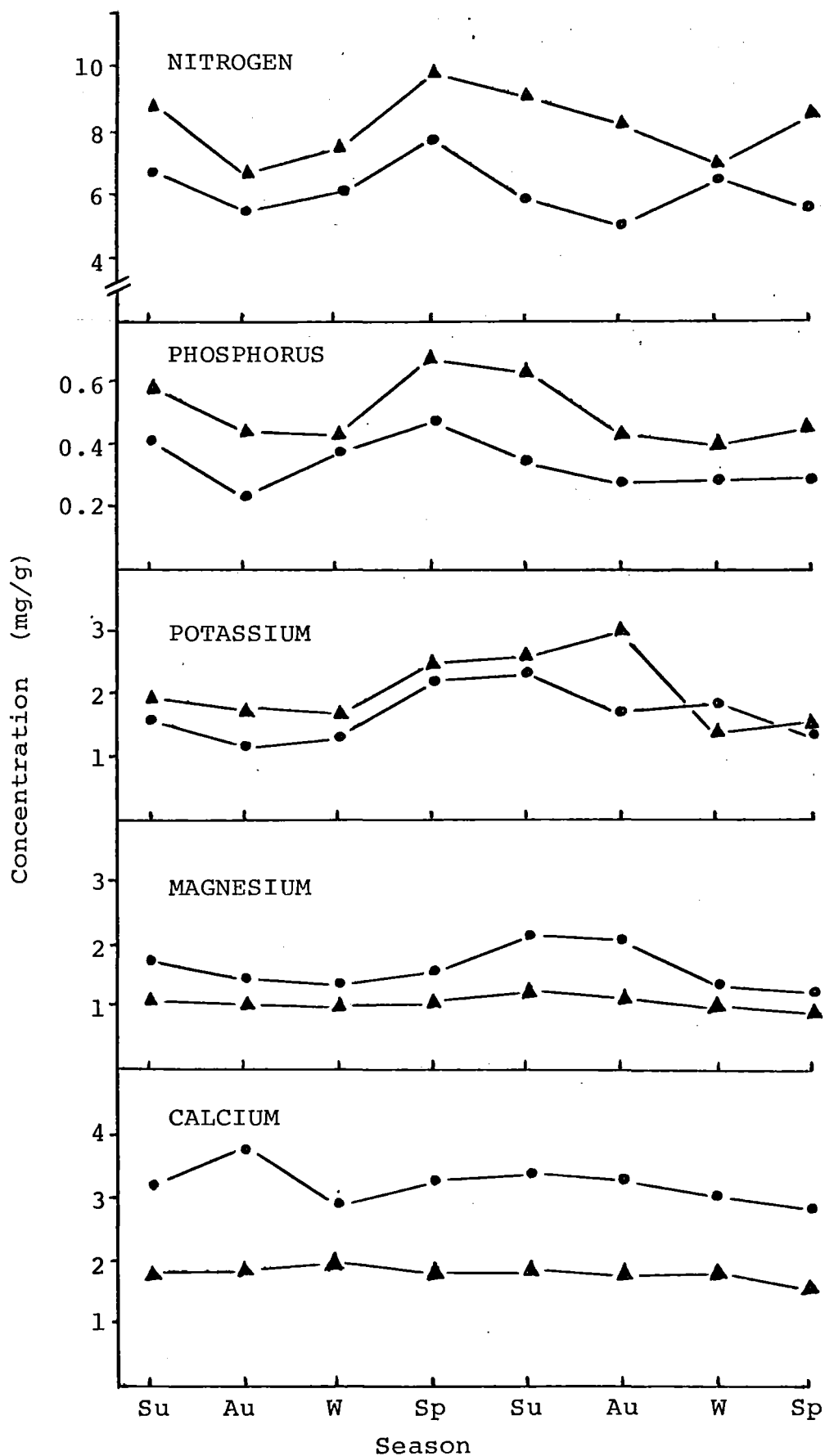


FIGURE 3.4.1.2 Seasonal variation in nutrient concentration of leaf and needle litter ( • leaf, ▲ needle)

than in the following year. However, despite poorly developed pattern in the second year, there was no reason to doubt that returns in autumn and spring accounted for comparatively larger amounts of litter biomass, nutrients and water-soluble and organic constituents (Figure 3.4.1.1.; Appendix II).

In general, many factors interact with normal seasonal variation effects to change the pattern of returns of litter constituents during the year. For example, the premature fall of litter, as caused by storm events, could markedly affect seasonal variations in the nutrient concentrations (e.g. N, P, K) by interrupting the natural process of the translocation of these elements out of tissues which are becoming senescent or dormant (Mälkönen, 1974). This effect could result in seasonal peak levels of N, P, K in periods when litter is expected to have low nutrient concentrations. Spatial and age variations in litter (Will, 1957; Mälkönen, 1974) also contribute to mask seasonal variations. Unlike deciduous litter which falls within a short period of time and comprises of similar age tissues, evergreen litter falls continuously throughout the year and includes litter of different ages. In addition, "sun" and "shade" leaves, which result from their spatial position on the tree, may influence nutrient concentration (Gosz et al., 1972). One of these factors, or perhaps a combination of these factors, may interact to change the chemical composition of the litter tissues at litter-fall.

It is also possible that analyses determined on a quarterly basis may diffuse what would otherwise be sharp

peaks on a monthly basis.

One of the more significant interactions between nutrient levels and the distribution of organic constituents in plant tissues is exemplified by the relationships between N, K and water-soluble carbohydrate concentrations. These relationships are amply demonstrated by the composition of radiata needle litter at Hanmer in comparison to those at other forests studied. At Hanmer, needles had comparatively lower N and higher K and water-soluble carbohydrate concentrations than those from either Granville or Nelson forest.

Results obtained in the present study indicate that in general, the rates of release of K and water-soluble carbohydrates from freshly fallen litter were relatively rapid although that of N was relatively slow (Section 4.3.2). At Hanmer, these effects probably resulted in an increase in the amounts of water-soluble carbohydrates and P, K, Mg, Ca released from the waste cuttings of recent stand thinning and a widening of the C/N ratio of the forest floor in the radiata stand immediately subsequent to thinning. Increased tree growth induced by increased nutrient availability and without a supplementary source of available N to fulfil this additional growth in such a situation would require an increased N redistribution within the foliage in order to maintain regular growth. This translocation of N would consequently result in the premature abscission of the older needles. The premature litter-fall would also lead to higher K and water-soluble carbohydrate concentrations in needles obtained from Hanmer as compared with those at Granville or Nelson.

Turner and Olson (1976) showed that the application of carbohydrate (sugar + sawdust) to a Douglas-fir plantation resulted in decreased needle retention time and increased litter-fall when compared to the corresponding effects found in plots where only N had been applied. However, these workers reported that there was no significant effect from addition of other inorganic nutrients (P, K, Ca, S) in the carbohydrate treatment.

In the present study, an important implication of the results obtained at Hanmer is that although stand thinning increased the availability of most macro-nutrients and usually tree growth, without a source of available N to supplement such increased tree growth, total tree foliage biomass may not increase because of reduced needle retention time. This cycle, further induced by the addition of litter-fall low in N and high in carbohydrate contents, may persist over an extended period of time but with a progressively diminishing degree of severity over time.

This result, and the implications which may be drawn from it, suggests that the time of stand thinning and pruning could have a significant effect on subsequent tree growth. For example, these treatments, when carried out at a time of greatest tree biomass production such as the early stages (5 to 10 years) of stand development of radiata pines (Forrest and Ovington, 1970; Madgwick, 1979), may have a serious effect on normal tree growth.

### 3.5 CONCLUSIONS

Annual litter production was consistently higher in beech than radiata pine stands in all the three forests studied. The three beech stands produced a mean annual litter-fall of 5921 kg/ha compared to 3932 kg/ha in the four radiata pine stands. Thinning reduced considerably the amount of litter-fall.

Seasonal patterns were broadly evident in total litter-fall. A spring peak was common to both species in all forests although additional periods of peak litter-fall were observed during autumn. Leaf and needle litter were the major components of annual total litter-fall although in beech forests branchwood could become important in terms of biomass.

Concentrations of N, P, Mg and Ca in the different quarterly litter components generally did not exhibit seasonal patterns, except for K which showed spring (September to November) low and autumn (March to May) high levels in some of the litter components. Higher N and P concentrations in needles than in beech leaves were evident in the forests at Granville, Hanmer and Nelson.

Among the water-soluble and organic constituents, beech leaf litter contained greater amounts of WSC, WSP and WSF than radiata needles, with WSP showing the largest difference. There was generally no marked difference in the distribution of organic constituents between the separated litter components, except for higher lignin content in twigs and higher holocellulose content in branchwood.



Beech trees were returning larger amounts of individual nutrient elements, and water-soluble and organic constituents than radiata pines (due largely to greater beech litter biomass). The N, P and K contents of beech and radiata litter showed smaller differences than Mg and Ca. For an equal amount of litter-fall biomass, the two stands of beech and radiata at Granville were returning comparatively smaller amounts of P and K than corresponding stands at either Hanmer or Nelson.

The use of ten litter-traps (collection area:  $0.38 \text{ m}^2$  each) per stand (i.e. sampling intensity: 66 traps per hectare) was adequate to provide a reliable estimate (C.V.: range, 12 to 22 percent; mean 17 percent) of major and more uniformly distributed litter components such as leaves, twigs, "others" and needles on an annual basis. The variability of the estimates obtained was not influenced by amounts of litter-fall biomass collected. Higher intensity of sampling is required in forests of discontinuous canopy in order to achieve as good an estimate as that for forests of closed canopy.

It is important to measure litter-fall over extended lengths of time ( $\geq 2$  years) in order to obtain a representative estimate of the litter production occurring in a stand, by overcoming seasonal and annual fluctuations of some seasonal litter components (e.g. pollen cones).

## CHAPTER 4

## LITTER DECOMPOSITION

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## CHAPTER 4

## LITTER DECOMPOSITION

## 4.1 INTRODUCTION

The decomposition process constitutes the main pathway by which nutrients in freshly fallen litter, or immobilised in the accumulated organic residue on the forest floor, are gradually released and exported into the upper soil layers for eventual re-utilization. The process of nutrient transfer is of prime importance to the restoration and maintenance of fertility. Thus the dynamics of this continual nutrient release during the process of decomposition of litter tissues are of particular interest in this study.

This section of the study is concerned with the rates of decomposition of the major litter components of both beech and radiata stands. The objectives were:

- (1) to determine the rates of decomposition of beech and radiata pine litter in their respective stands,
- (2) to examine the relationship between rates of decomposition and the factors which are likely to influence the rates in each stand and,
- (3) to estimate and predict, if possible, the probable long-term effects from any differential rates of decomposition

between beech and radiata pines.

## 4.2 MATERIALS AND METHODS

### 4.2.1 Study Areas

Decomposition dynamics were studied at the various beech and radiata stands in each of the three forests where detailed litter production analyses have been made. These areas have been previously described in Section 3.2.1.

### 4.2.2 Experimental Procedure

The decomposition of beech litter (leaf + twig tissue) and radiata pine litter (needle) was studied by means of the nylon mesh-bag technique (Bocock et al., 1960; Gosz et al., 1973). In the present study nylon bags (25cm x 25cm) with 1mm aperture were used. An additional mesh-size bag of 0.045mm aperture was also used at the Granville sites. One advantage of using larger nylon bags is the greater quantity of litter which can be enclosed with reduced compaction. Larger amounts of litter used also reduce errors associated with smaller weights.

Known quantities of combined beech litter and radiata pine needles were enclosed in the bags and placed on the forest floor. Fresh litter for these bags were previously collected with a large net in each stand for a short period of time (4-6 weeks). To supplement these amounts of litter collected, freshly fallen litter were also taken from the forest floor and mixed together. The use of freshly fallen

litter would provide a better representation of the natural processes occurring within the forest stands than if green living tissues were physically removed from trees.

All litters were air-dried at 20°C for one day to ensure even moisture content. Equal and exact air-dried weights were enclosed in the bags to be placed in each stand. However, the weights used differed between stands, depending upon the amount of litter required to completely form a thin layer of litter across the bag. Air-dried weights of litter used ranged from 15g to 20g, which did not exceed the litter accumulation on the forest floors (recorded minimum > 20g oven-dried litter within an equivalent area of 25cm x 25cm). Although the amounts of litter used in bags were larger than those reported in the literature (e.g. Bockock, 1964; Gosz et al., 1973; Cromack, 1973), they provide a greater proportion of litter-to-litter contact than litter-to-nylon contact; the former situation represents a more natural condition existing in forest floors.

A total of 135 bags (1mm) were prepared from the litter collected in each stand. At the time of placement of bags, 10 bags were randomly removed to establish zero-time values from chemical analyses and total oven-dried weights, thus leaving 125 bags to be distributed in each of the five plots within a respective stand. Placement of the bags was randomized within the confines of the five experimental plots of each stand (see Figure 3.2.3) in the three forests between mid-October and early November 1976. A layer of fresh litter was removed from the forest floor where each bag was subsequently placed.

During retrieval of litter-bags, two bags were picked randomly from each plot and placed in plastic bags, sealed and transported back to the laboratory for analysis. After removing all litter adhering to the outside of the litter-bags, the litter samples were air-dried at 20°C for at least 48 hours before weighing. No attempt was made to remove contaminant litter (e.g. very fine roots) in order to minimize fragmentation and experimental loss. All air-dried weights were determined on per litter-bag basis and corrected to oven-dried weights using subsamples obtained by quartering. The remaining samples from the two litter-bags in each plot of the beech sites were then combined and separated into leaf and twig tissues. The needle litter from the two litter-bags in each plot of the radiata sites were also combined. All samples of leaves, twigs and needle were finely ground (0.4mm) and stored in air-tight containers until chemical analyses were made.

At Granville only, a total of 20 fine mesh (0.045mm) litter-bags were placed on the forest floor in each of the two stands used. Four litter-bags were removed after about every six months. Preparation of the litter samples were carried out as that described for the 1mm litter-bags.

#### 4.2.3 Chemical Analysis

All tissues were analysed for total N, P, K, Mg, Ca, carbon, water-soluble components, and the organic constituents according to the chemical methods described in Section 3.2.3.

## 4.3 RESULTS AND DISCUSSION

### 4.3.1 Dry Weight Loss

The loss of weight over a period of about 25 months in litter of beech forests and radiata plantations in Granville, Hanmer and Nelson are shown in Figure 4.3.1.1.1, 4.3.1.1.2 and 4.3.1.1.3 respectively. Additional data are also given in Appendix III.

In all three forests, beech and radiata litter appear to undergo large weight losses during the first four or five months. These losses were in excess of 20 percent of the original dry weight used (Table 4.3.1.1) and is attributed largely to a loss by leaching. This view is supported by results showing a rapid decrease in the amount of hot-water-soluble components in the litter of both species. It is probable that part of these hot-water-soluble constituents was also metabolised by micro-organisms since Melin (1930) has demonstrated that microbial decomposition is already proceeding in senescent litter prior to litter-fall. Bocock et al. (1960) have reported similar large decreases in water-soluble substances in leaf litter placed in the field.

After the initial rapid loss in weight there was generally no distinct periods of a very high rate of decomposition. The decrease was gradual except for the weight loss recorded in summer at Nelson where a sharp decline took place in beech and radiata (reg.) litter. However, litter of radiata did not show a similar trend. On the basis of these results, it is difficult to attribute such a sharp decline to greater decomposition associated with summer



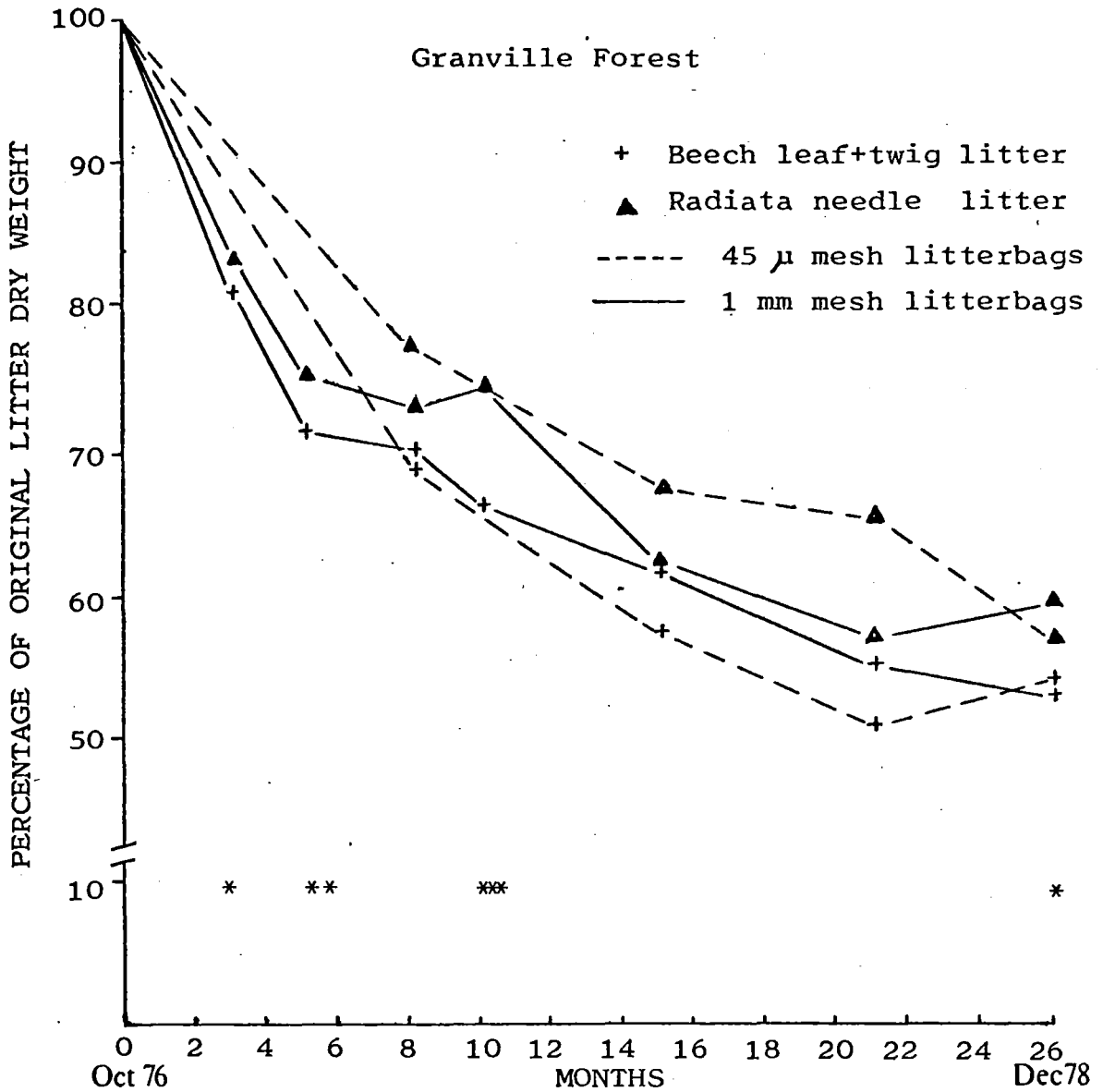


FIGURE 4.3.1.1.1 Percentage of the original litter dry weight remaining after various periods of decomposition. Value of each point is the mean of 10 replicate litterbags. Asterisks indicate significant difference, otherwise not, for 1 mm litterbags only.

\* significant,  $p = 0.05$   
 \*\* highly significant,  $p = 0.01$   
 \*\*\* very highly significant,  $p = 0.001$

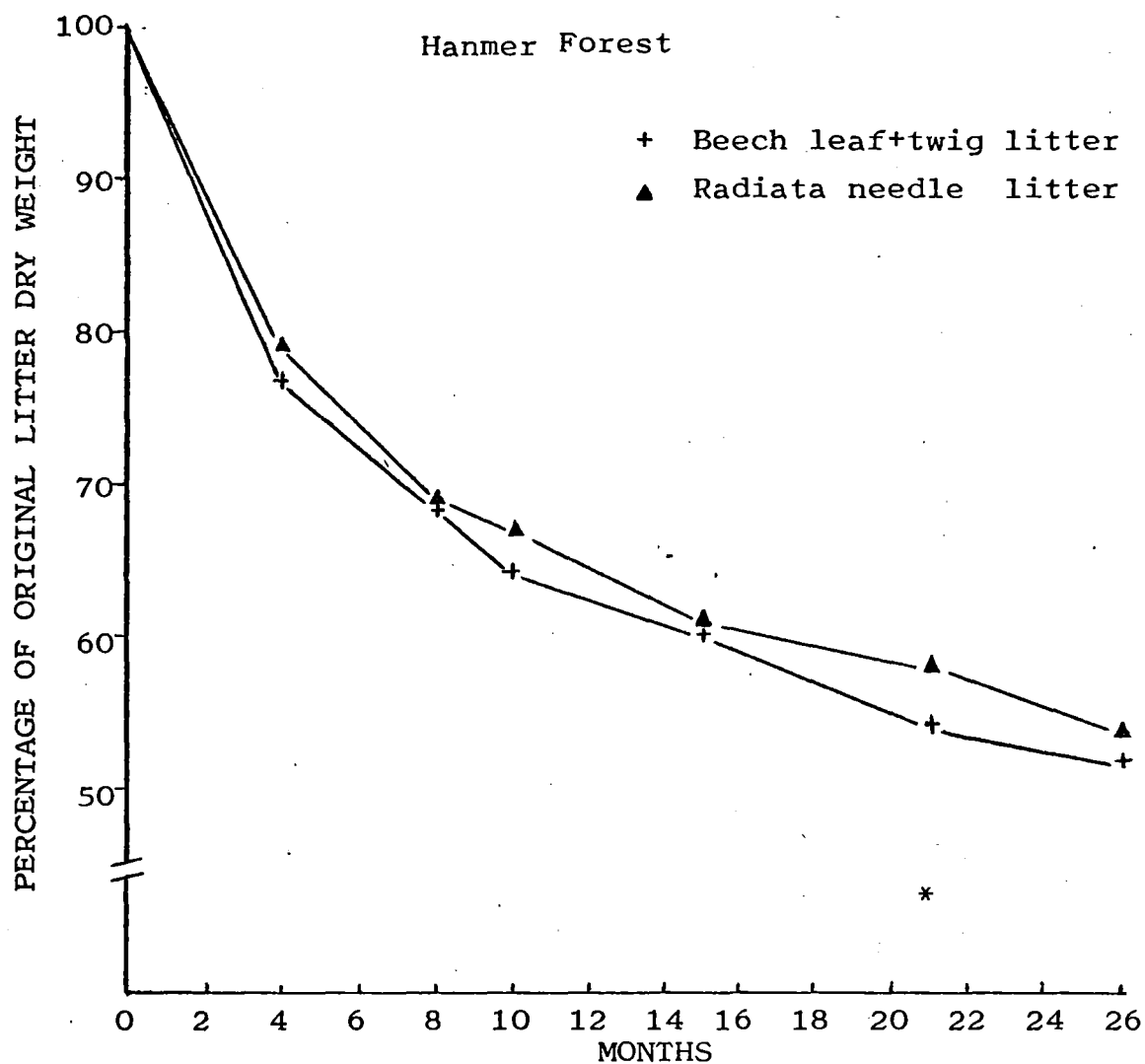


FIGURE 4.3.1.1.2 Percentage of the original litter dry weight remaining after various periods of decomposition. Value of each point is the mean of 10 replicate litterbags. Asterisk indicate significant difference, otherwise not.

\* significant,  $p = 0.05$

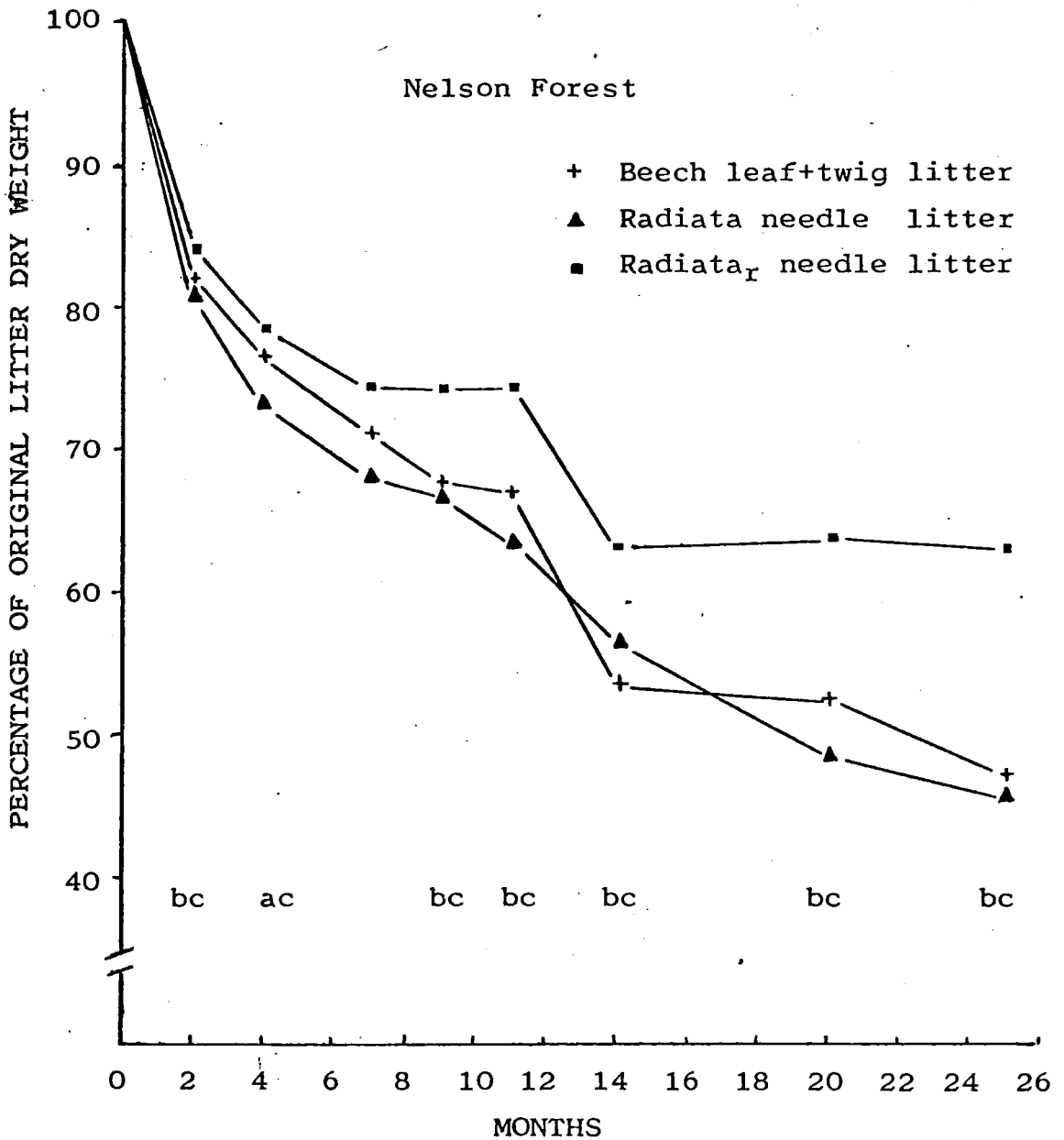


FIGURE 4.3.1.1.3 Percentage of the original litter dry weight remaining after various periods of decomposition. Value of each point is the mean of 10 replicate litterbags.

- a significant difference between Beech and Radiata
- b significant difference between Beech and Radiata<sub>r</sub>
- c significant difference between Radiata and Radiata<sub>r</sub>, all at  $p = 0.05$  level

TABLE 4.3.1.1 Percentage of initial weight of litter (%) lost over different time intervals at various stages of decomposition of litter

GRANVILLE	0 to 5th <sup>#</sup>	5th to 10th	5th to 26th
Beech	28.5	5.5	18.3
Radiata	24.4	0.5	15.8
HANMER	0 to 4th	4th to 8th	4th to 26th
Beech	23.3	8.2	24.9
Radiata	20.8	10.3	25.3
NELSON	0 to 4th	4th to 9th	4th to 25th
Beech	24.0	8.8	29.6
Radiata	26.9	6.5	27.4
Radiata <sub>reg.</sub>	21.7	4.3	15.1

# Decomposition stage in months

climatic conditions. One possible explanation underlying such a discrepancy is loss in weight from litter fragmentation during the processing of both the beech and radiata (reg.) litters.

It is often difficult to analyse weight loss patterns for seasonal variations. Several factors can interact to mask seasonal effects. For example, in summer, a period of normally greater decomposition, weight losses can be made up by the addition of contaminant litter such as insect frass, pollen and flowers. In certain cases, an absolute increase in total dry weight may be observed (Gosz et al., 1973). The use of 1.0mm mesh bags in the present study probably reduced the import of contaminant litter into the litter-bags as compared to that taking place in the 3.0mm mesh bags used by Gosz et al. (1973), although our bags had a comparatively larger collecting surface area.

Litter confined in 0.045mm mesh bags showed completely different patterns to corresponding litter in the 1.0mm mesh bags (Figure 4.3.1.1.1). In fine mesh bags, beech litter lost a greater weight while radiata litter showed a smaller weight loss when compared to those occurring in respective litter in the 1.0mm mesh bags. Greater weight loss in beech litter supports the view that contaminant litter may be masking the true weight loss. In addition, it may be significant in the later stages of the study that fine roots begin to immigrate into the 1.0mm mesh bags and integrate with the organic residues in the bags. Despite attempts to remove such roots whenever possible, considerable amounts had to be included in the weight determinations in order to

avoid removing true litter tissues. Although fine rootlets were also occasionally observed in radiata litterbags, such contamination was minimal compared to fungal development on the litter. The colonization of fungi was common to all three forests and occurred at a very early stage of decomposition. Styles (1967) also reported fungal development in radiata needles enclosed in 1.0mm mesh bags by the first year of decomposition. In the present study, as no quantitative estimation was carried out on the fungal mass, it was not possible to ascertain how much of the weight increase observed in Granville was directly attributable to this fungal growth. This clearly demonstrates the intricate situation concerning the ideal mesh size of litterbags. Studies with larger mesh sizes may show reduced losses or weight gains through possible importation of contaminant litter (Gosz et al., 1973) while smaller mesh sizes (0.5mm) has the effect of excluding larger organisms giving rise to a reduced decomposition rate (Edwards and Heath, 1963). However, due to the nature of the litter, that is small beech leaves, twigs and needles, the use of mesh sizes larger than 1.0mm would increase losses of litter through the netting, and also from fragmentation.

Differences between beech and radiata litter were not consistent enough to suggest that beech litter was decomposing faster than radiata litter. In Granville and Hanmer, beech litter decomposed faster than radiata litter (Figures 4.3.1.1.1 and 4.3.1.1.2). However, much of the differences were largely not statistically significant ( $p = 0.05$ ) except for the first few periods in Granville. In Nelson, radiata

litter lost weight both faster and slower than beech litter (Figure 4.3.1.1.3). Differences in litter weight loss between radiata (reg) and both beech and radiata were generally significant ( $p = 0.05$ ). Thus, there is no reason to suspect that radiata and beech litter were decomposing at rates very different from each other.

The inclusion of twig litter would certainly have influenced the overall rate of beech litter decomposition since this component of litter generally decomposes considerably slower than leaf litter (Cromack 1973). There is little doubt, too, that the chemical composition of the litter also influenced the decomposition rate. This aspect of decomposition will be examined later in this chapter.

Regression equations computed from the cumulative decomposition data are shown in Table 4.3.1.3. First-year decomposition rate constants ( $k$ ) derived from substituting 12 months in the respective regression equations ranged from 0.40 to 0.47 for beech and 0.33 to 0.48 for radiata. Within each forest, beech litter appeared to have a slightly larger decay rate constant than radiata litter. In Nelson forest, a comparatively large difference was found between the litter decomposition rates of the two radiata stands. The reason for this disparity is unknown although it is suspected that the result was due to a lower degree of sunlight penetration and greater fungal growth on the litter of the radiata (reg.) site. This unpruned stand had a much denser canopy than the other radiata stand.

First-year decomposition rates found for the beech and radiata sites used in the present study were within the

TABLE 4.3.1.2 Litter decomposition regression parameters obtained with and without the inclusion of initial weight of litter

	With Inclusion		Without Inclusion	
	Intercept(%)	Correlation Coefficient	Intercept(%)	Correlation Coefficient
GRANVILLE				
Beech	86.7	0.897***	80.6	0.893***
Radiata	89.1	0.833***	84.1	0.773***
HANMER				
Beech	87.2	0.905***	78.8	0.892***
Radiata	88.1	0.897***	80.3	0.871***
NELSON				
Beech	88.6	0.901***	84.1	0.894***
Radiata	87.6	0.924***	82.7	0.915***
Radiata <sub>reg.</sub>	87.3	0.796***	82.3	0.739***



TABLE 4.3.1.3 Semi-logarithmic regression analysis of beech and radiata pine litter decomposition

	Regression Equation	Standard Error of Slope	N	Correlation Coefficient	First-year Exponential Loss Rate	Half Time (yrs)	Wt. Remaining after 1 year (%)
GRANVILLE							
Beech	$\ln W = 4.4623 - 0.0214 T^{\#}$	0.0012	80	0.897***	0.399	1.74	67.1
Radiata	$\ln W = 4.4900 - 0.0194 T$	0.0015	80	0.833***	0.348	1.99	70.6
HANMER							
Beech	$\ln W = 4.4678 - 0.0228 T$	0.0013	70	0.905***	0.411	1.69	66.3
Radiata	$\ln W = 4.4785 - 0.0213 T$	0.0013	70	0.897***	0.382	1.81	68.2
NELSON							
Beech	$\ln W = 4.4840 - 0.0287 T$	0.0015	90	0.901***	0.466	1.49	62.8
Radiata	$\ln W = 4.4727 - 0.0293 T$	0.0013	90	0.924***	0.484	1.43	61.6
Radiata <sub>reg.</sub>	$\ln W = 4.4693 - 0.0162 T$	0.0013	90	0.796***	0.330	2.10	71.9

# W = percentage weight remaining of litter; T = time in months

TABLE 4.3.1.4 Comparison of annual decomposition rate (k) for beech and pine litter in New Zealand and other parts of the world

Tree Species	Site	k	Reference
<i>Pinus alba</i>	Tennessee, U.S.A.	0.51 <sup>#</sup>	Witkamp (1966b)
<i>Pinus radiata</i>	Kaingaroa, N.Z.	0.39 <sup>#</sup>	Will (1967)
<i>Pinus taeda</i>	Tennessee, U.S.A.	0.41 <sup>#</sup>	Thomas (1968)
<i>Pinus strobus</i>	North Carolina, U.S.A.	0.42 - 0.52	Cromack (1973)
<i>Pinus sylvestris</i>	Finland	0.43 <sup>#</sup>	Mälikönen (1974)
<i>Pinus radiata</i>	Granville, N.Z.	0.35	Present study
	Hanmer, N.Z.	0.38	"
	Nelson, N.Z.	0.33 - 0.48	"
<i>Fagus grandifolia</i>	U.S.A.	0.43 <sup>#</sup>	Shanks and Olson (1961)
	Hubbard Brook, U.S.A.	0.37	Gosz <u>et al.</u> (1973)
<i>Nothofagus truncata</i>	Granville, N.Z.	0.40	Present study
<i>Nothofagus solandri</i> <i>var. cliffortioides</i>	Hanmer, N.Z.	0.41	"
<i>Nothofagus</i> spp.	Nelson, N.Z.	0.47	"

# calculated from published litter weight loss data using the exponential decay model

range reported in the literature (Table 4.3.1.4). Direct comparison between studies is difficult due to the fact that a large number of factors could affect litter decomposition rates (see Section 2.3.4). However, it is notable that despite these differences, there appears to be no pronounced dissimilarity in the decomposition rates observed.

A semi-logarithmic linear regression analysis of the litter decomposition was carried out (Tables 4.3.1.2 and 4.3.1.3) using data recorded over the 26-month period to facilitate comparisons of annual decomposition rates of beech and radiata litter. Computation was done with and without inclusion of the initial weight of litter (i.e. 100 percent at time = 0). This consideration was pertinent since the initial rapid weight loss from the litter of water-soluble components may give rise to an over-estimation of the true loss rate (Anderson, 1973a; Gosz et al., 1973). However, results in Table 4.3.1.2 indicate that the inclusion of the initial value gave a predictive equation with a better accountability. This suggests that the initial rapid weight losses conformed to the logarithmic function .

#### 4.3.2 Nutrient Concentration and Total Content

Nutrient concentration in leaf, twig and needle and, total nutrient content in beech and radiata litter-bags after various periods of decomposition are shown in Figures 4.3.1.1.4 to 4.3.1.1.8. Detailed results are reported in Appendix III. First-year nutrient loss rates (k) are given in Table 4.3.2.1 . Regression equations from which these loss rates were derived are given in Tables 4.3.2.1.1 to 4.3.2.1.3 .

#### 4.3.2.1 Concentration

Results show that N is the only element studied which showed a continuous increase in concentration over time. The final N concentration recorded at the 26th month had attained a level more than double that found in the fresh litter initially used (e.g. Granville leaf litter, Figure 4.3.1.1.4). Increasing N concentrations in decaying leaf litter have also been reported by other workers (Bocock, 1963, 1964; Gosz et al., 1973).

In contrast, concentration patterns for P were somewhat less regular. In Granville, P levels in leaf litter increased continuously while in needle litter levels decreased gradually. Twig litter, on the other hand, showed a further increase in concentration after the decline following an initial peak. In Hanmer, P concentrations in leaf and twig litter remained higher than those found in the fresh litter used initially, while those in needle litter decreased continuously. In Nelson, P levels in leaf and twig litter fluctuated and showed relatively little increase or decrease over the 25-month period while those in needle litters decreased with time.

Nitrogen and P represent important elements which are primarily involved in the metabolism of an ecosystem. Their status in decomposing litter would therefore be expected to be closely related to the demands of the associated microbial population. Micro-organisms utilize and retain most of the N and P by incorporating these elements into microbial cells, thus effectively conserving N and P within the litter residue. This effect on N is demonstrated by the decreasing C:N ratios

# GRANVILLE FOREST

# HANMER FOREST

# NELSON FOREST

Mean chemical concentration in litter tissues after various periods of decomposition

Litter tissues are denoted by:

L	for beech leaves,
T	for beech twigs,
N	for radiata pine needles, and
N <sub>r</sub>	for radiata pine needles from the regenerated stand at Nelson.

Mean chemical content of litter remaining in litterbags after various periods of decomposition. Beech (leaf + twig) litterbags are represented by B , and radiata pine (needle) litterbags by R and R<sub>r</sub> , where R<sub>r</sub> refers to those from the regenerated radiata pine stand at Nelson.

For Granville and Hanmer forests, differences between beech and radiata pine litterbags are denoted by asterisks:

\* denotes  $p < 0.05$   
 \*\* denotes  $p < 0.01$   
 \*\*\* denotes  $p < 0.001$

For Nelson forest, differences between the litterbags are indicated by:

a between B and R,  
 b between B and R<sub>r</sub>, and  
 c between R and R<sub>r</sub>.

all at  $p = 0.05$  .

FIGURE 4.3.1.1 Definitions for Figures 4.3.1.1.4 to 4.3.1.1.16

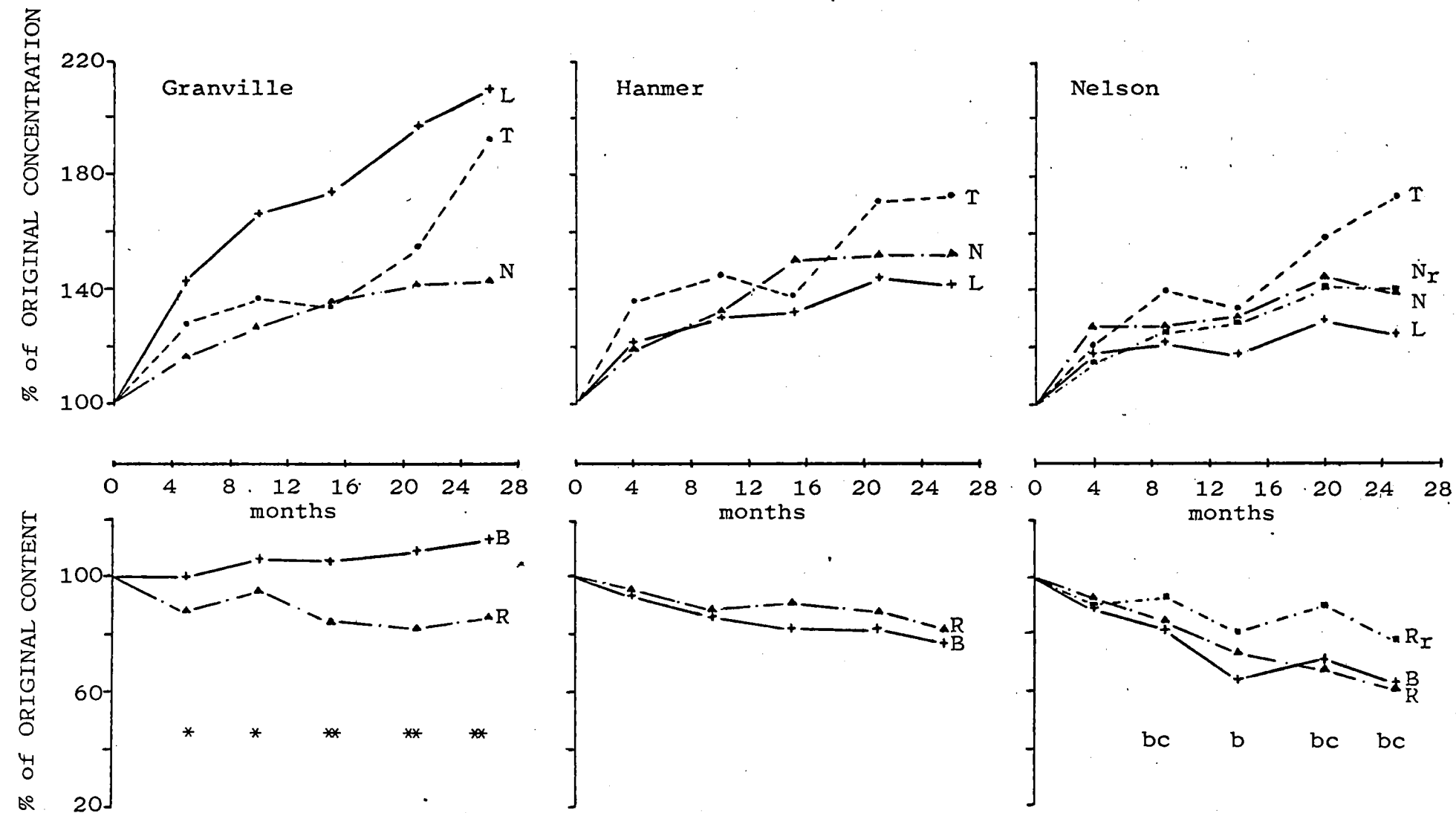


FIGURE 4.3.1.1.4 Nitrogen concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

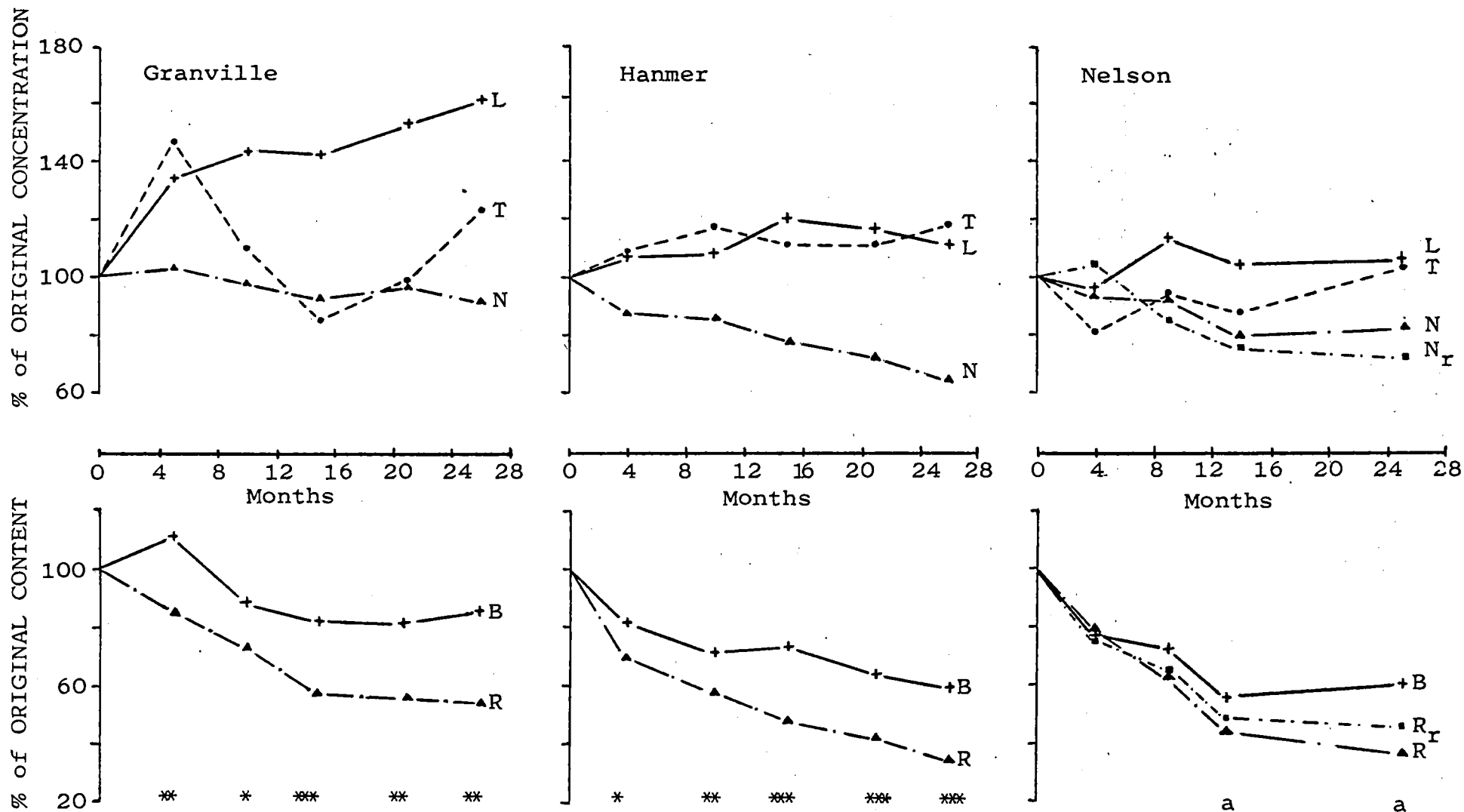


FIGURE 4.3.1.1.5 Phosphorus concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

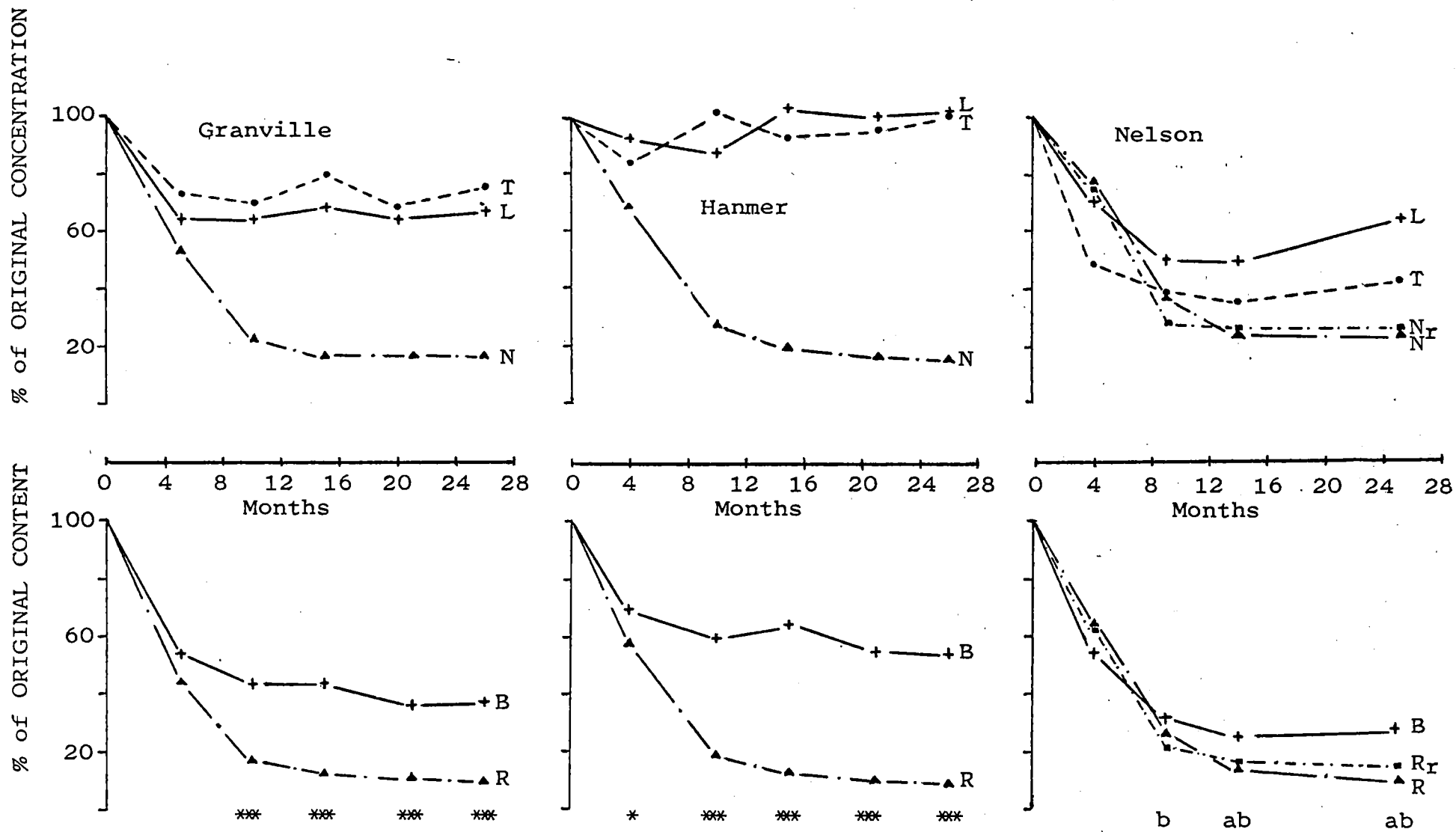


FIGURE 4.3.1.1.6 Potassium concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.



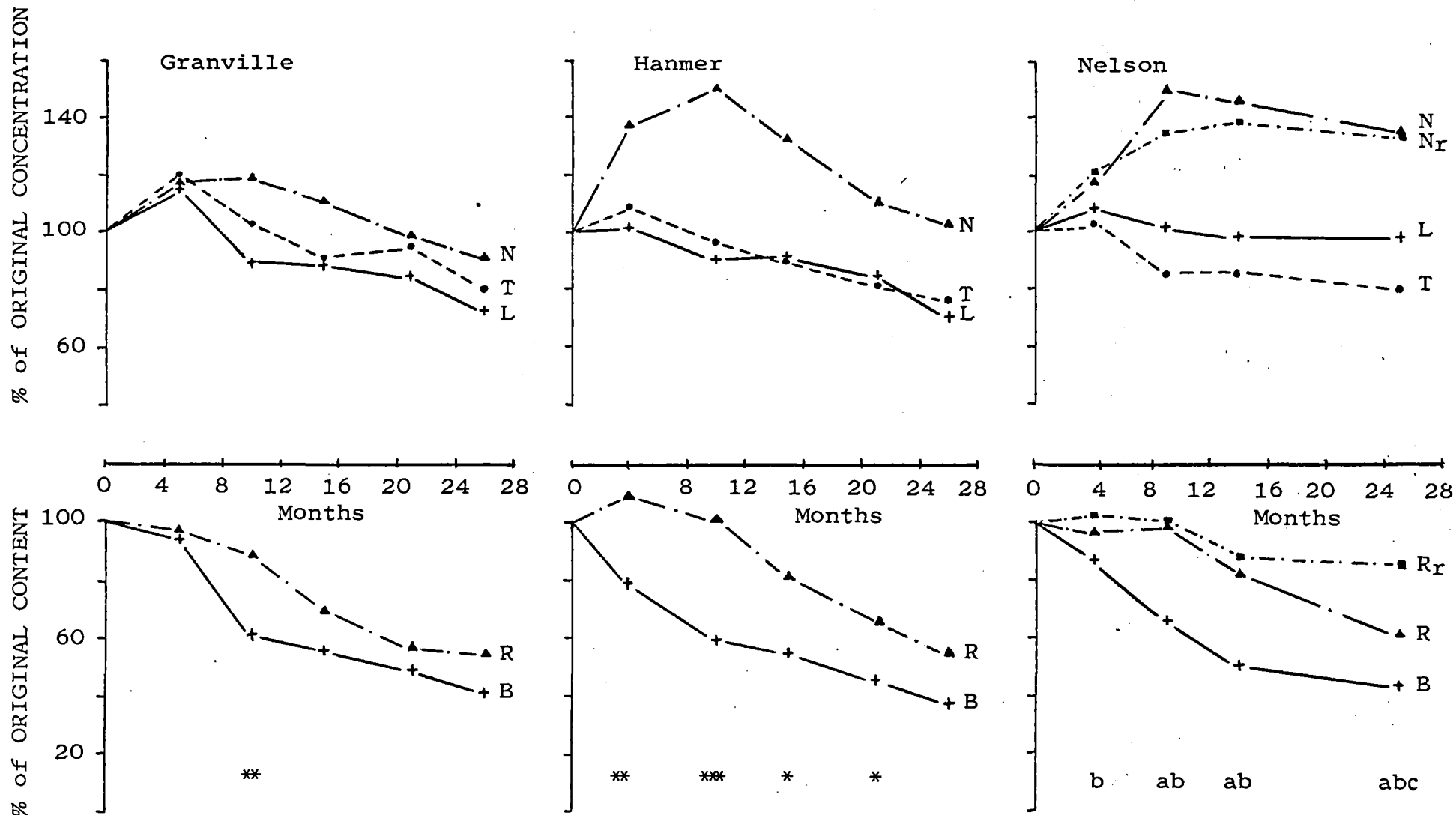


FIGURE 4.3.1.1.7 Magnesium concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

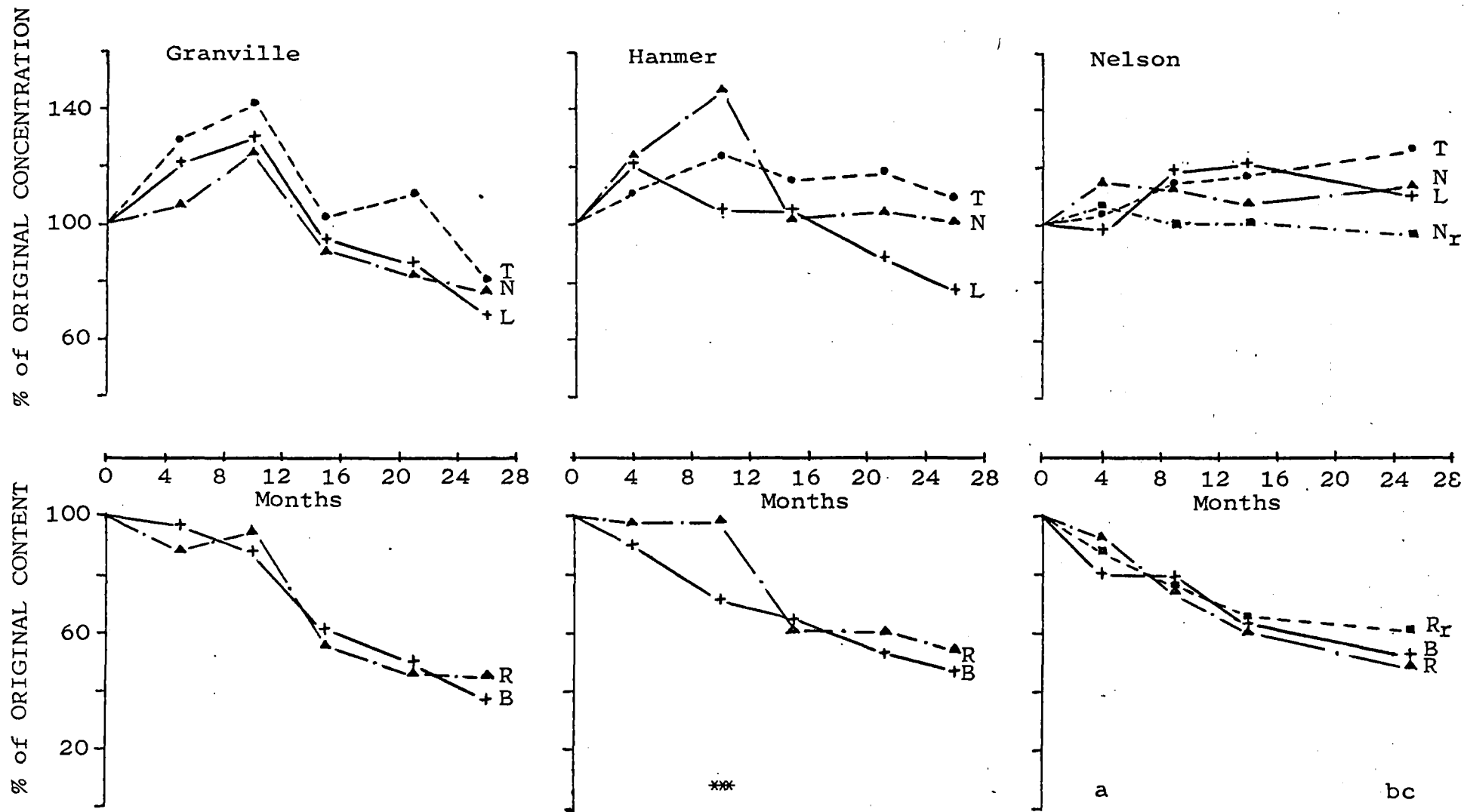


FIGURE 4.3.1.1.8 Calcium concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

TABLE 4.3.1.5 Mean C:N, N:P and C:P ratios of decomposing beech and radiata pine litter components

RATIO/ Decomposition Stage	GRANVILLE			HANMER			NELSON			
	Leaf	Twig	Needle	Leaf	Twig	Needle	Leaf	Twig	Needle	Needle <sub>reg.</sub>
C:N										
Initial	79.3	121.7	44.7	44.7	70.1	45.8	33.2	59.5	40.4	43.2
25th month	38.4	63.3	28.4	31.0	40.0	29.0	24.4	32.3	28.6	32.0
N:P										
Initial	13.0	11.6	12.9	10.7	8.9	7.3	13.2	9.2	8.6	8.3
25th month	16.6	18.6	20.9	13.6	13.0	14.1	15.3	15.7	14.4	15.8
C:P										
Initial	1031	1412	577	478	624	334	425	547	347	309
25th month	637	1177	594	422	520	409	373	507	412	506

with increasing decomposition (Table 4.3.1.5). In general, litter with high C:N ratios usually result in increasing immobilization of N in litter residues (Alexander, 1977). For P, decreasing C:P ratios with time were only observed in leaf and twig litter and not in needle litter. This discrepancy is attributed to the comparatively high initial P concentrations in needle litter than those in leaf or twig litter. Thus, P in needles was probably not as limiting as that in either leaves or twigs, and consequently resulted in more rapid release of the element from needle litter.

Besides biological immobilization, it is also possible that N may be immobilized during the formation of ligno-protein complexes (Waksman and Iyer, 1932, 1933) and during the oxidative polymerization of polyphenols and amino compounds (Parsons and Tinsley, 1975; see also Section 2.3.4.1.2). In the present study, N concentrations were significantly correlated with those of 'residual lignin' in both beech and radiata litter (beech,  $r = 0.827^{***}$ ; radiata,  $r = 0.719^{***}$ ) and also with polyphenol concentrations in beech litter (beech,  $r = -0.640^{***}$ ; radiata,  $r = -0.369^{n.s.}$ ) (see Table 4.4.1.2). Such immobilizing effects may account for part of the increase in N concentrations found during litter decomposition at the sites studied.

During the initial stages of decomposition (first 4 months or so), concentrations of Mg and Ca showed relative increases and then either remained constant or gradually declined (Figures 4.3.1.1.7 and 4.3.1.1.8). Only concentrations of K decreased markedly during these early stages except for those in leaf and twig litter at Hanmer which

showed little change during the 26 months (Figure 4.3.1.1.6). Thereafter, with the exception of the leaf and twig litter at Hanmer, K concentrations remained constant at about the eighth month.

Much of the increase in Mg and Ca concentrations found in the present study can be partly attributed to the rapid losses of substantially large amounts of water-soluble components. The loss of the water-soluble components resulted in an apparent increase in the concentrations of less mobile elements such as Mg and Ca. The absence of an initial increase in the concentration of K is consistent with the susceptibility of this element to leaching (Tukey, 1970). In comparison, Ca and to a lesser extent Mg, are involved in structural functions while K is not (Gilbert, 1957) and consequently Ca and Mg undergo a slower rate of loss when compared with K and the water-soluble components. In this connection, the differential degree of change in elemental concentrations between beech and radiata litter would be related to the disparity in the amount of water-soluble components present in the litter and the extent of loss.

These patterns in the concentrations of the elements studied may also be an artefact of the senescent condition of the litter used. Changes in concentrations were reported relative to that found in fresh litter used initially, thus loss of elements and part of water-soluble constituents during the time when the fresh litter was collected for litter-bags would have an effect on the subsequent pattern of changes in concentration between sites and forests. This effect certainly highlights the importance of the need

to use freshly fallen litter and emphasizes the necessity for estimating decomposition rates over longer periods in order to reduce errors and variability caused by this effect.

#### 4.3.2.2 Total Content

Changes in total content of the nutrient elements and carbon, shown in Figures 4.3.1.1.4 to 4.3.1.1.8, indicate that the total content of all these elements decreased with time, except for an increase in Mg content during the early stages of radiata pine needle decomposition at Hanmer and that of N in beech litter at Granville.

The observed increase in total content of N in beech litter enclosed in litter-bags at Granville and the slowly decreasing and fluctuating N contents in radiata and beech litters at Hanmer and Nelson (Figure 4.3.1.1.4) may be attributed to imported N. Major sources of imported N include atmospheric N fixation (Bormann and Likens, 1979), stem-flow and microbial uptake of N from atmospheric precipitation and through-fall, and from N-rich insect frass (Bocock, 1963). The physical incorporation of N-rich insect frass and plant tissues (e.g. flowers) through the 1.0mm mesh bags is also a real possibility and therefore cannot be discounted. However, as the pH of the litter and humus layers in all the beech and radiata stands were relatively low, between pH 3.1 to 3.5 and pH 4.3 to 4.8 respectively, N fixation would probably occur only to a very limited extent in these sites (Alexander, 1977).

A substantial proportion of the initial amount of the total P content in beech and radiata litter was lost during

the 26-month period (Figure 4.3.1.1.5). Presumably, the loss is through leaching. The presence of P in through-fall, at levels higher than in rainfall (Will, 1959; Levett, 1978), suggests that P is easily washed from tree foliage. The increase in the total weight of P at the early stages of decomposition at the Granville beech stand was probably caused by the unexplained high concentration of P in the twig tissues of that collection. The possibility of contaminant litter was not suspected since no similar pattern was observed at other collections or forests.

First-year nutrient loss rates (k) shown in Table 4.3.2.1 indicate that loss rates of P in beech litter were all less than the litter weight loss rates. The order was reversed for radiata. This suggests that immobilization of P is occurring to a greater degree in beech litter. Alexander (1977) gives evidence that the balance point between immobilization and mineralization in decomposing plant residues is 0.2 percent. All the litter tissues analysed in this study had P concentrations well below 0.2 percent at the time of litterfall. Although this view appears plausible, it is difficult to reconcile this with the observed rapid loss of P in the litterbags. Physical loss of P from fragmentation and leaching may account for the discrepancies between concentration and total P weight loss patterns. However, it is probable that a combination of all these processes was operating simultaneously.

Potassium weight loss patterns were distinctly different from those of Mg and Ca, and closely resembled the weight loss patterns of the water-soluble components

TABLE 4.3.2.1      Annual (first-year) nutrient and carbon loss rates (k) for beech and radiata pine litter in the forest stands at Granville, Hanmer and Nelson

Forest Stand	N	P	K	Mg	Ca	C
GRANVILLE						
Beech	-	0.09	0.69	0.43	0.16	0.39
Radiata	0.12	0.36	1.47	0.28	0.36	0.38
HANMER						
Beech	0.14	0.30	0.43	0.52	0.37	0.39
Radiata	0.10	0.57	1.47	0.18	0.25	0.37
NELSON						
Beech	0.27	0.44	0.99	0.48	0.35	0.50
Radiata	0.24	0.58	1.35	0.19	0.36	0.44
Radiata <sub>reg.</sub>	0.11	0.48	1.29	0.08	0.31	0.29



TABLE 4.3.2.1.1 Semi-logarithmic regressions of nutrient and carbon loss rates for beech and radiata pine litter in the forest stands at Granville

Forest/Element		Regression Model	Standard Error of Slope	Correlation Coefficient
Beech	N	$\ln Y = 4.5990 + 0.0040 T^{\#}$	0.0018	0.383*
	P	$\ln Y = 4.6359 - 0.1010 T$	0.0022	0.657***
	K	$\ln Y = 4.3093 - 0.0332 T$	0.0043	0.822***
	Mg	$\ln Y = 4.6068 - 0.0362 T$	0.0029	0.921***
	Ca	$\ln Y = 4.7280 - 0.0400 T$	0.0029	0.935***
	C	$\ln Y = 4.4811 - 0.0219 T$	0.0020	0.899***
Radiata	N	$\ln Y = 4.5649 - 0.0063 T$	0.0018	0.558**
	P	$\ln Y = 4.5564 - 0.0257 T$	0.0033	0.828***
	K	$\ln Y = 4.1624 - 0.0860 T$	0.0083	0.890***
	Mg	$\ln Y = 4.6658 - 0.0280 T$	0.0041	0.792***
	Ca	$\ln Y = 4.6710 - 0.0354 T$	0.0038	0.870***
	C	$\ln Y = 4.4990 - 0.0225 T$	0.0019	0.911***

#  $\ln Y$  refer to the natural logarithm of percentage weight remaining, T refer to the time in months; number of samples used = 30

TABLE 4.3.2.1.2 Semi-logarithmic regressions of nutrient and carbon loss rates for beech and radiata pine litter in the forest stands at Hanmer

Forest/Element		Regression Model	Standard Error of Slope	Correlation Coefficient
Beech	N	$\ln Y = 4.5809 - 0.0097 T^{\#}$	0.0018	0.709***
	P	$\ln Y = 4.5252 - 0.0183 T$	0.0019	0.876***
	K	$\ln Y = 4.4228 - 0.0202 T$	0.0032	0.761***
	Mg	$\ln Y = 4.5355 - 0.0375 T$	0.0042	0.861***
	Ca	$\ln Y = 4.5986 - 0.0301 T$	0.0025	0.915***
	C	$\ln Y = 4.5065 - 0.0240 T^@$	0.0021	0.940***
Radiata	N	$\ln Y = 4.5839 - 0.0064 T$	0.0017	0.574***
	P	$\ln Y = 4.4790 - 0.0371 T$	0.0023	0.950***
	K	$\ln Y = 4.3079 - 0.0977 T$	0.0069	0.937***
	Mg	$\ln Y = 4.7434 - 0.0263 T$	0.0030	0.853***
	Ca	$\ln Y = 4.6702 - 0.0265 T$	0.0025	0.894***
	C	$\ln Y = 4.5255 - 0.0239 T^@$	0.0018	0.952***

# as for TABLE 4.3.2.1.1 ,

@ number of samples used = 20

TABLE 4.3.2.1.3 Semi-logarithmic regressions of nutrient and carbon loss rates for beech and radiata pine litter in the forest stands at Nelson

Forest/Element		Regression Model	Standard Error of Slope	Correlation Coefficient
Beech	N	$\ln Y = 4.5581 - 0.0187 T^{\text{a}}$	0.0029	0.782***
	P	$\ln Y = 4.5124 - 0.0285 T$	0.0034	0.872***
	K	$\ln Y = 4.2279 - 0.0508 T$	0.0080	0.803***
	Mg	$\ln Y = 4.5554 - 0.0360 T$	0.0029	0.935***
	Ca	$\ln Y = 4.5580 - 0.0253 T$	0.0020	0.935***
	C	$\ln Y = 4.5072 - 0.0338 T$	0.0026	0.955***
Radiata	N	$\ln Y = 4.5982 - 0.0193 T$	0.0020	0.878***
	P	$\ln Y = 4.5142 - 0.0403 T$	0.0034	0.929***
	K	$\ln Y = 4.3497 - 0.0915 T$	0.0085	0.914***
	Mg	$\ln Y = 4.6657 - 0.0206 T$	0.0029	0.826***
	Ca	$\ln Y = 4.5974 - 0.0294 T$	0.0024	0.932***
	C	$\ln Y = 4.5396 - 0.0312 T$	0.0017	0.974***
Radiata <sub>reg.</sub>	N	$\ln Y = 4.5490 - 0.0042 T$	0.0018	0.397*
	P	$\ln Y = 4.5222 - 0.0331 T$	0.0033	0.901***
	K	$\ln Y = 4.2373 - 0.0772 T$	0.0111	0.824***
	Mg	$\ln Y = 4.6239 - 0.0084 T$	0.0034	0.455*
	Ca	$\ln Y = 4.5392 - 0.0203 T$	0.0021	0.897***
	C	$\ln Y = 4.5231 - 0.0172 T$	0.0022	0.875***

@ as for TABLE 4.3.2.1.1  
number of samples used :

N = 30  
P, K, Mg, Ca = 25  
C = 20

TABLE 4.3.2.6 Initial concentrations of macro-nutrient elements in litter used for decomposition study (Values given in mg/g)

Forest/Litter	N	P	K	Mg	Ca
GRANVILLE					
Beech leaf	6.46	0.50	1.73	1.67	11.01
twig	4.19	0.36	1.03	1.34	13.34
Radiata needle	12.10	0.94	4.34	1.63	6.32
HANMER					
Beech leaf	11.19	1.04	1.62	1.56	15.71
twig	7.30	0.82	1.30	1.41	18.01
Radiata needle	11.58	1.58	6.26	1.28	8.01
NELSON					
Beech leaf	15.68	1.19	2.62	1.68	16.25
twig	8.44	0.92	3.12	1.84	16.90
Radiata needle	12.62	1.47	5.18	1.23	8.59
Radiata needle (reg.)	11.68	1.41	4.95	1.60	9.22

(Figures 4.3.1.1.4 to 4.3.1.1.6 and 4.3.1.1.10 to 4.3.1.1.12). Initially, losses were rapid and then declined steadily after about the 8th month. This behaviour for K was also found in other studies (Will, 1967; Gosz et al., 1973) and is consistent with the high leachability of K (Tukey, 1970). Most of the residual K after the 8th month would probably constitute the proportion immobilized by microbial populations or held in exchange sites (e.g.  $\text{-COO}^-$  and  $\text{-O}^-$ ) of the decomposing litter.

Differences in K loss rates between beech and radiata litters could be attributed to the considerably higher K concentrations in the initial radiata pine needles (Table 4.3.2.6). First-year K loss rates were all substantially greater than the litter weight loss rates. This is consistent with the relative K and litter weight loss rates reported by Cromack (1973) for a number of hardwood species and white pine.

Both Mg and Ca exhibited similar slow weight loss over the first few months of decomposition. As Mg and Ca are commonly associated with structural functions, their loss rates would generally be expected to be governed by the litter decomposition rates. However, rates of loss of these elements observed appear to be lower than those of litter weight loss (Table 4.3.2.1) except for Mg in beech litter. This result suggests that a small proportion of Mg and Ca may be held in exchange sites on the decomposing residue.

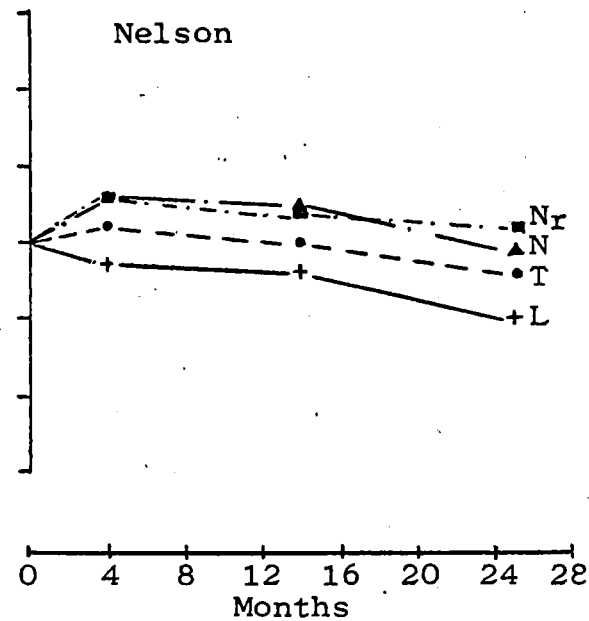
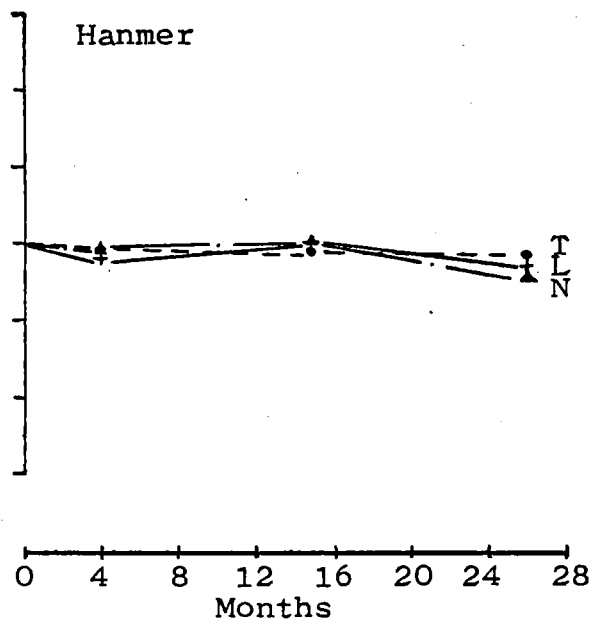
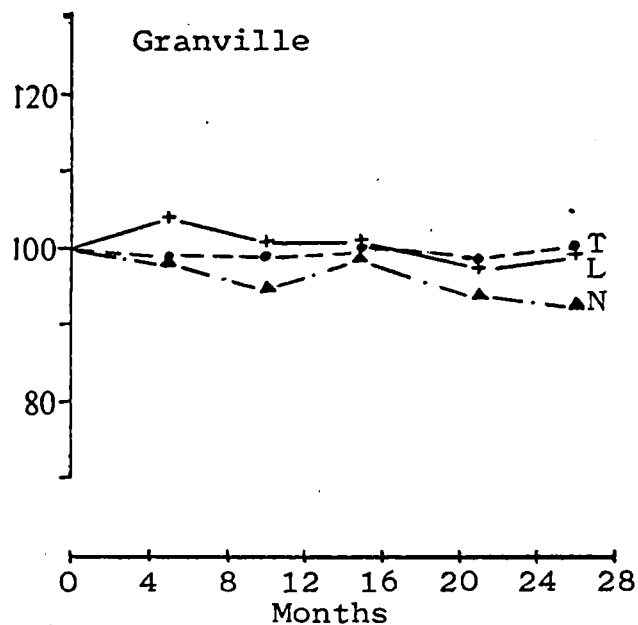
Similar slow rates of Ca weight loss were also reported by Gosz et al. (1973) for decomposing litters of a number of tree species, including beech. Will (1967) also

reported slow Ca loss, and even a nett Mg increase for decomposing radiata needles. In the present study, although there appears to be a small nett increase in Mg in radiata needle at Hanmer, the magnitude is by no means comparable. One possibility is that Mg was intercepted by the decomposing litter and consequently held in exchange sites. While this reasoning may account for the small increase recorded at Hanmer, it certainly would not account adequately for the relatively large increase reported by Will (1967).

Utilization of Ca by litter fungi is also a possibility by which substantial amounts of Ca are partially immobilised in litter. As initial fungi colonization would have begun long before leaf fall (Gray and Williams, 1975), it would be reasonable to expect the immobilization process could be sufficiently effective in the litter used in the present study. Fungal development was observed in radiata needles and this seems to reinforce the possibility.

For carbon, its percentage composition in litter remained relatively constant with time (Figure 4.3.1.1.9). Only small differences exist between leaf, twig and needle, and these differences were expressed slightly more clearly in Nelson than in the other forests. The cause of this discrepancy is unknown. First-year carbon loss rates were about similar to rates of weight loss of the respective litter (Table 4.3.2.1 ). At the end of the 26-month period, total carbon contents were reduced to between 42 to 65 percent of the original carbon content. Corresponding values for litter weight loss were between 46 to 63 percent. Differences in carbon losses between beech and radiata litter were not significant.

% of ORIGINAL CONCENTRATION



% of ORIGINAL CONTENT

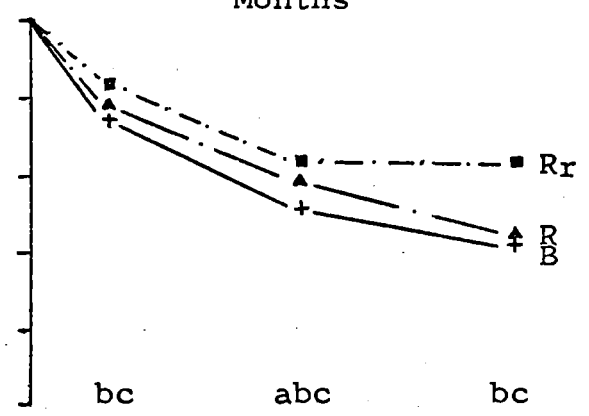
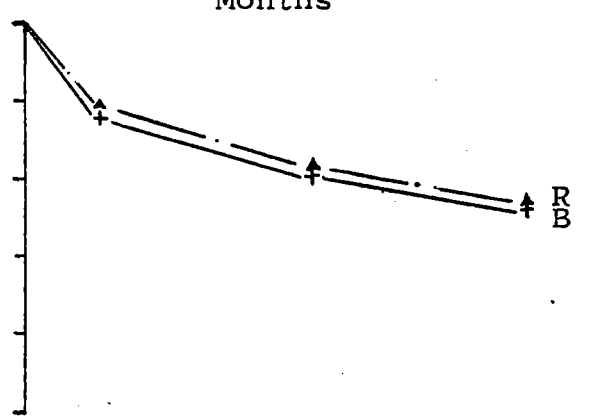
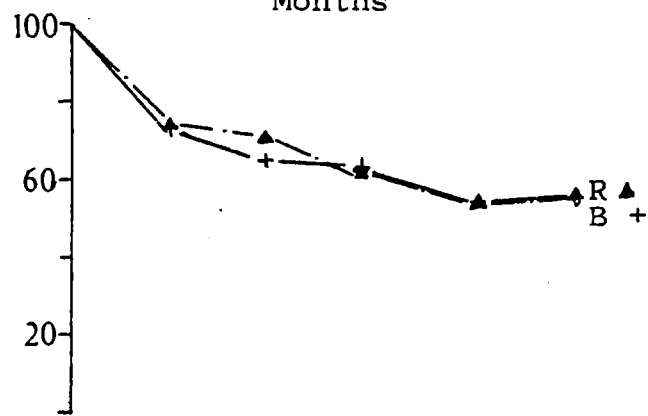


FIGURE 4.3.1.1.9  
of decomposition.

Carbon concentration and content of litter after various periods  
Legend as for Figure 4.3.1.1.

#### 4.3.3 Water-soluble Constituents

Changes in the concentration and content of the water-soluble carbohydrates (WSC), water-soluble polyphenols (WSP) and total water-soluble fraction (WSF) are shown in Figures 4.3.1.1.10 to 4.3.1.1.12. First-year loss rates of these constituents are shown in Table 4.3.3.1, and their respective regression equations in Table 4.3.3.1.1 and Table 4.3.3.1.2 .

Concentrations of WSC, WSP and WSF in leaves, twigs and needles all showed large decreases in concentration in the early stages of decomposition (first 4 or 5 months), except for twig litter at Hanmer which for some unknown reasons showed an overall increase in WSC and WSF. Thereafter decreases in these concentrations were generally small. Water-soluble polyphenols showed the largest decrease in concentration among the three components studied.

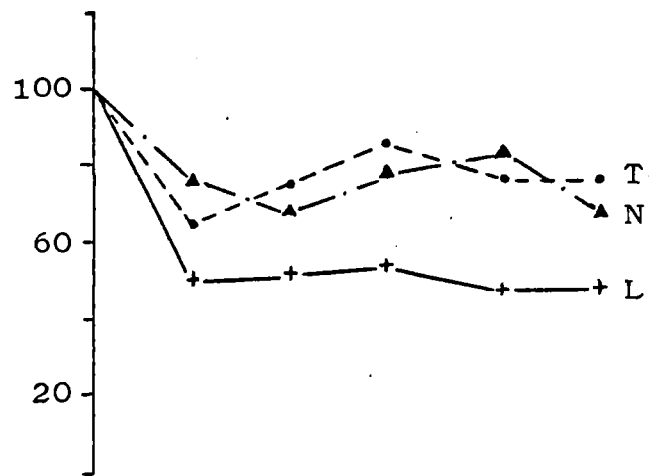
At Granville, WSF constituted 32.2 and 13.3 percent of the initial dry weight of beech leaves and radiata needles respectively. Five months after being placed in the field, these were reduced to 17.1 and 8.5 percent respectively. Such relatively rapid and large decreases in WSF concentration have been attributed to account for part of the observed increase in the concentrations of the immobile elements (Section 4.3.2.1). It is possible that a portion of the water-soluble components may have already been leached out during the 4 to 6 weeks before litter collection. Much larger losses of WSF from litter than those found in the present study have also been reported by other workers (Gilbert and Bocock, 1960).

Changes in total weights of WSC, WSP and WSF followed

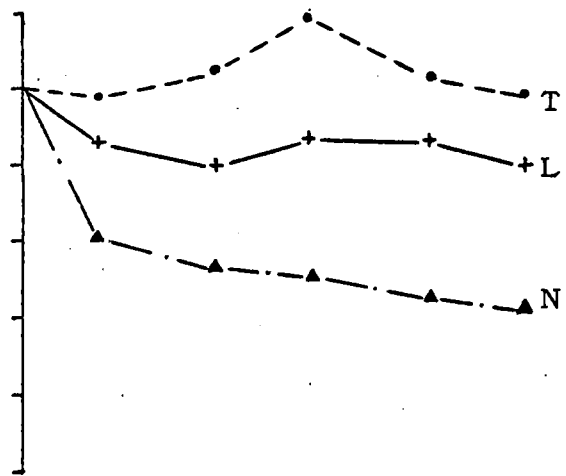


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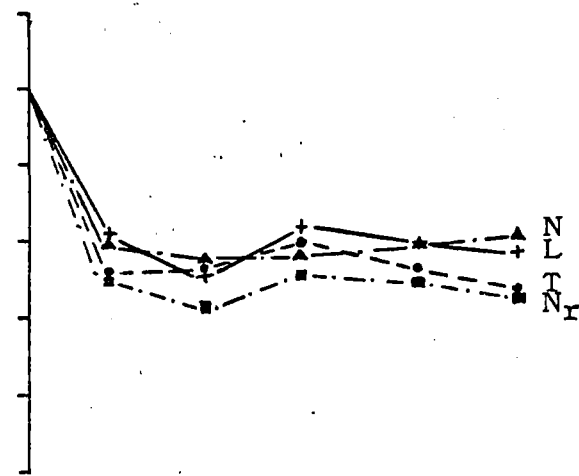
Granville



Hanmer



Nelson



% of ORIGINAL CONTENT

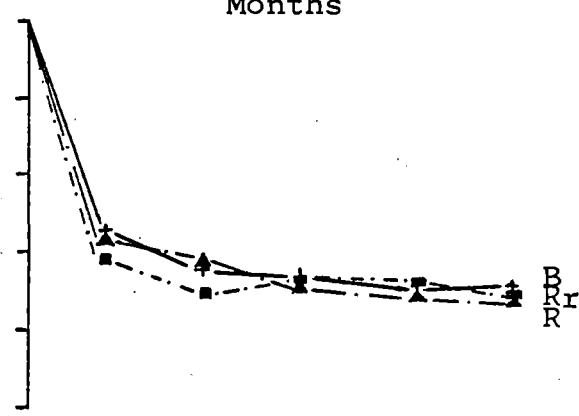
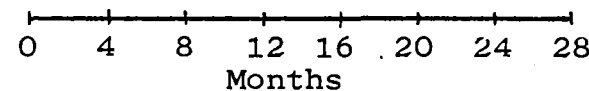
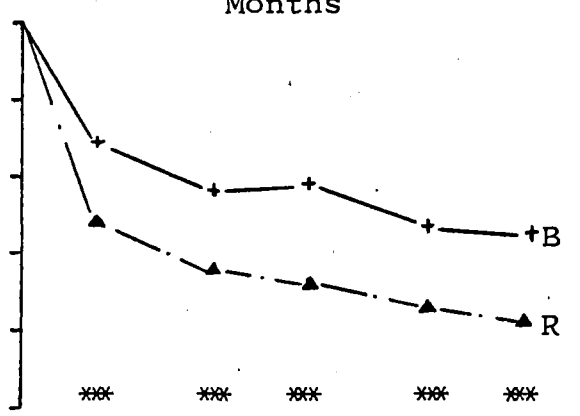
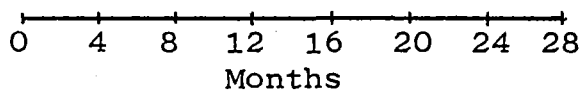
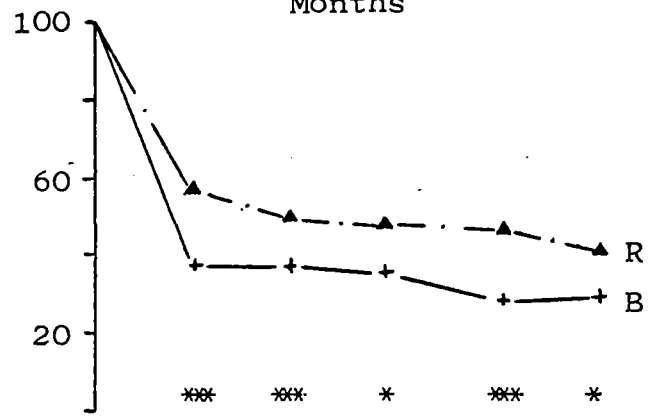
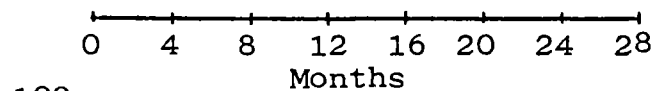


FIGURE 4.3.1.1.10 Water-soluble carbohydrate concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

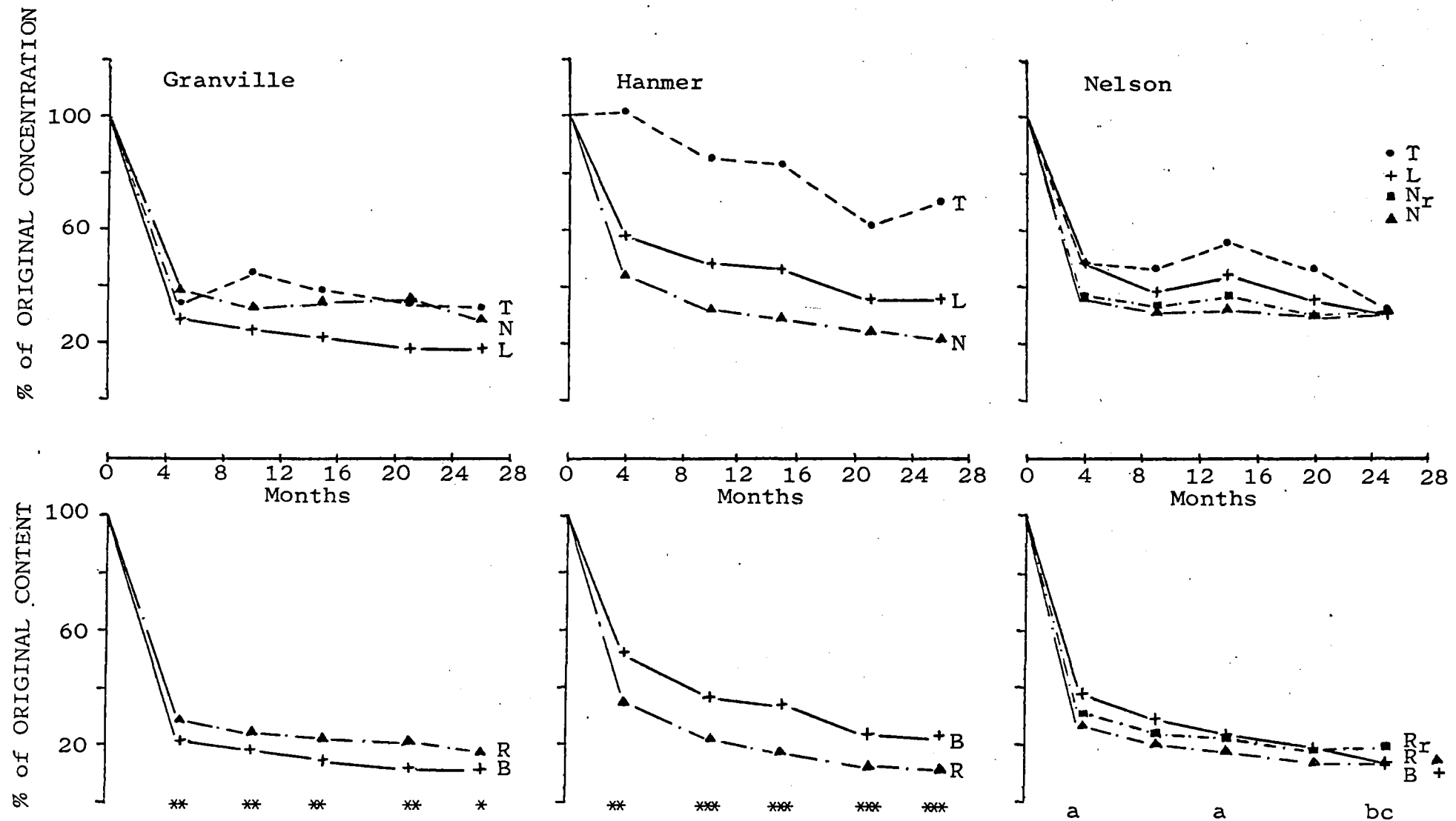


FIGURE 4.3.1.1.11 Water-soluble polyphenol concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

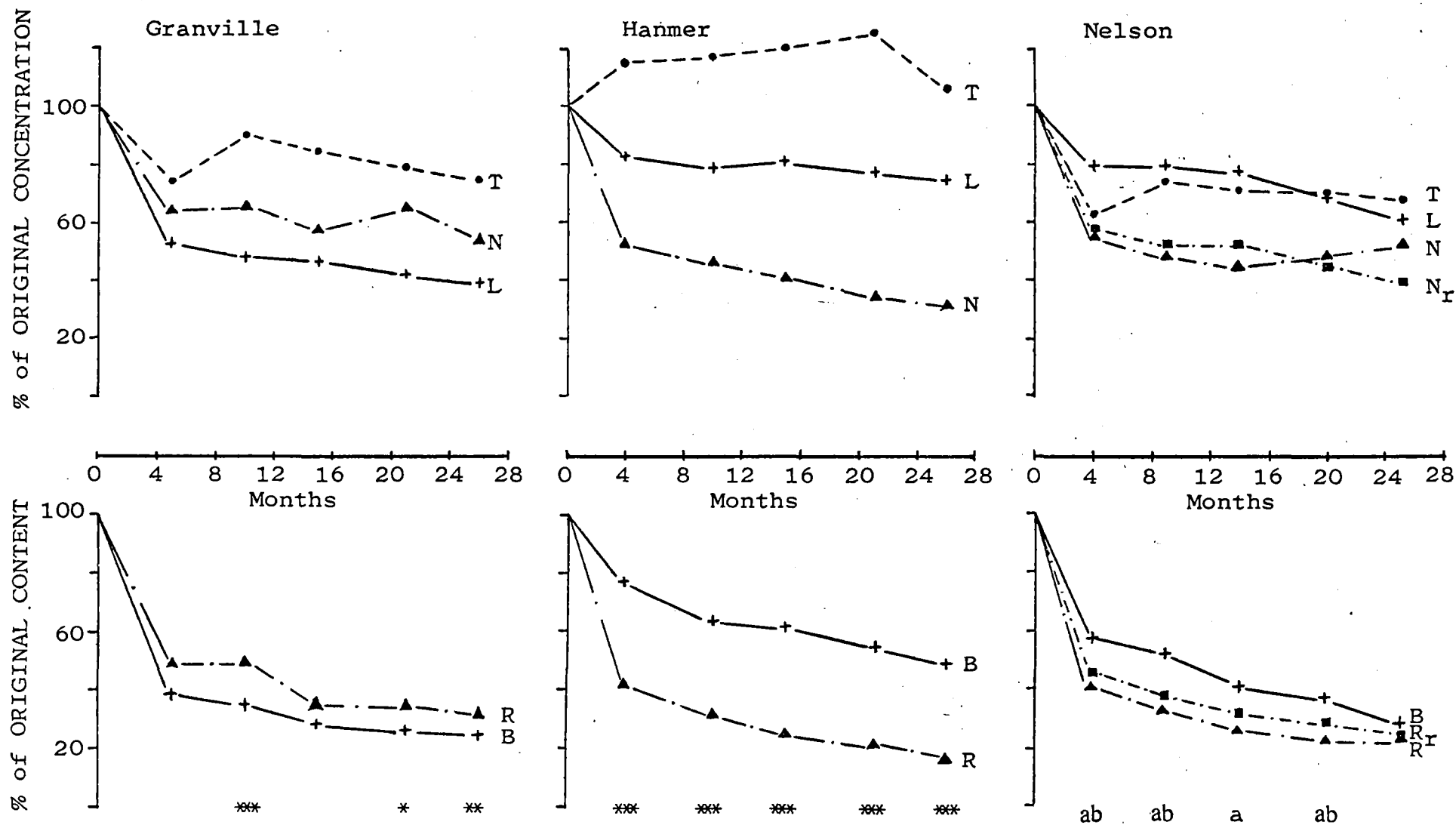


FIGURE 4.3.1.1.12 Total water-soluble fraction concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

TABLE 4.3.3.1 Annual (first-year) loss rates (k) for water-soluble components of beech and radiata pine litter in the forest stands at Granville, Hanmer and Nelson

Forest Stand	WSC @	WSP	WSF
GRANVILLE			
Beech	0.90	1.55	0.95
Radiata	0.58	1.22	0.74
HANMER			
Beech	0.50	0.91	0.42
Radiata	0.92	1.36	1.09
NELSON			
Beech	0.94	1.22	0.74
Radiata	0.95	1.41	1.06
Radiata (reg.)	0.95	1.23	0.93

@ WSC, WSP and WSF refer to water-soluble carbohydrates, polyphenols and total water-soluble fraction respectively

TABLE 4.3.3.1.1 Semi-logarithmic regressions of the different water-soluble components' loss rates for beech and radiata pine litter in the forest stands at Granville and Hanmer

Forest/Component		Regression Model	Standard Error of Slope	Correlation Coefficient
GRANVILLE				
Beech	WSC	$\ln Y = 4.1756 - 0.0388 T^a$	0.0058	0.786***
	WSP	$\ln Y = 3.9071 - 0.0712 T$	0.0091	0.828***
	WSF	$\ln Y = 4.2148 - 0.0465 T$	0.0054	0.854***
Radiata	WSC	$\ln Y = 4.3671 - 0.0282 T$	0.0039	0.807***
	WSP	$\ln Y = 4.0272 - 0.0536 T$	0.0079	0.786***
	WSF	$\ln Y = 4.3127 - 0.0376 T$	0.0050	0.820***
HANMER				
Beech	WSC	$\ln Y = 4.4406 - 0.0276 T$	0.0028	0.882***
	WSP	$\ln Y = 4.3142 - 0.0520 T$	0.0042	0.919***
	WSF	$\ln Y = 4.4938 - 0.0258 T$	0.0024	0.898***
Radiata	WSC	$\ln Y = 4.2799 - 0.0492 T$	0.0044	0.903***
	WSP	$\ln Y = 4.1013 - 0.0712 T$	0.0064	0.903***
	WSF	$\ln Y = 4.2221 - 0.0591 T$	0.0054	0.901***

@  $\ln Y$  refer to the natural logarithm of the percentage weight remaining, T refer to the time in months; number of samples used in the regression analysis = 30

TABLE 4.3.3.1.2 Semi-logarithmic regressions of the different water-soluble components' loss rates for beech and radiata pine litter in the forest stands at Nelson

Forest/Component		Regression Model	Standard Error of Slope	Correlation Coefficient
Beech	WSC	$\ln Y = 4.2142 - 0.0455 T^a$	0.0064	0.808***
	WSP	$\ln Y = 4.1839 - 0.0668 T$	0.0073	0.868***
	WSF	$\ln Y = 4.4028 - 0.0445 T$	0.0036	0.922***
Radiata	WSC	$\ln Y = 4.1950 - 0.0447 T$	0.0062	0.806***
	WSP	$\ln Y = 3.9561 - 0.0636 T$	0.0084	0.820***
	WSF	$\ln Y = 4.1524 - 0.0507 T$	0.0067	0.819***
Radiata <sub>reg.</sub>	WSC	$\ln Y = 4.1075 - 0.0373 T$	0.0070	0.709***
	WSP	$\ln Y = 3.9884 - 0.0512 T$	0.0086	0.748***
	WSF	$\ln Y = 4.2336 - 0.0463 T$	0.0056	0.843***

@ as for TABLE 4.3.3.1.1

a pattern similar to that of their concentrations (Figures 4.3.1.1.10 to 4.3.1.1.12). After 4 or 5 months in the field, initial contents of WSC, WSP and WSF in fresh litter were reduced by between 31 to 63 percent, 48 to 80 percent, and 24 to 60 percent respectively. Thereafter, in the next 21 to 22 months, the above losses amounted to only between 8 to 26 percent, 9 to 25 percent, and 16 to 30 percent, respectively.

In Granville and Hanmer forests, the amounts of WSC, WSP and WSF lost from litter between beech and radiata pine litter were significantly different throughout the 26-month period. At Granville, greater losses occurred in beech than radiata litter but the order was reversed at Hanmer. At Nelson, significant differences were more frequent in the amount of WSF lost between beech and radiata litter. Only small differences occurred in WSC and WSP. The above results were also evident from the annual loss rate constants (Table 4.3.3.1 ) calculated from respective regression equations (Table 4.3.3.1.1 and Table 4.3.3.1.2). First-year loss rates of WSP were greater than those of WSC and WSF.

#### 4.3.4 Organic Constituents

Changes in the distribution and total content of ether-extractable (EE), aqueous alcohol-extractable (AE), holocellulose (HOL) and residual lignin (RLIG) fractions in beech and radiata litter during various stages of decomposition are shown in Figures 4.3.1.1.13 to 4.3.1.1.16. First-year loss rate constants ( $k$ ) for these constituents are shown in Table 4.3.4.1 . These loss rate constants were calculated from regression equations given in Table 4.3.4.1.1 and Table 4.3.4.1.2 .

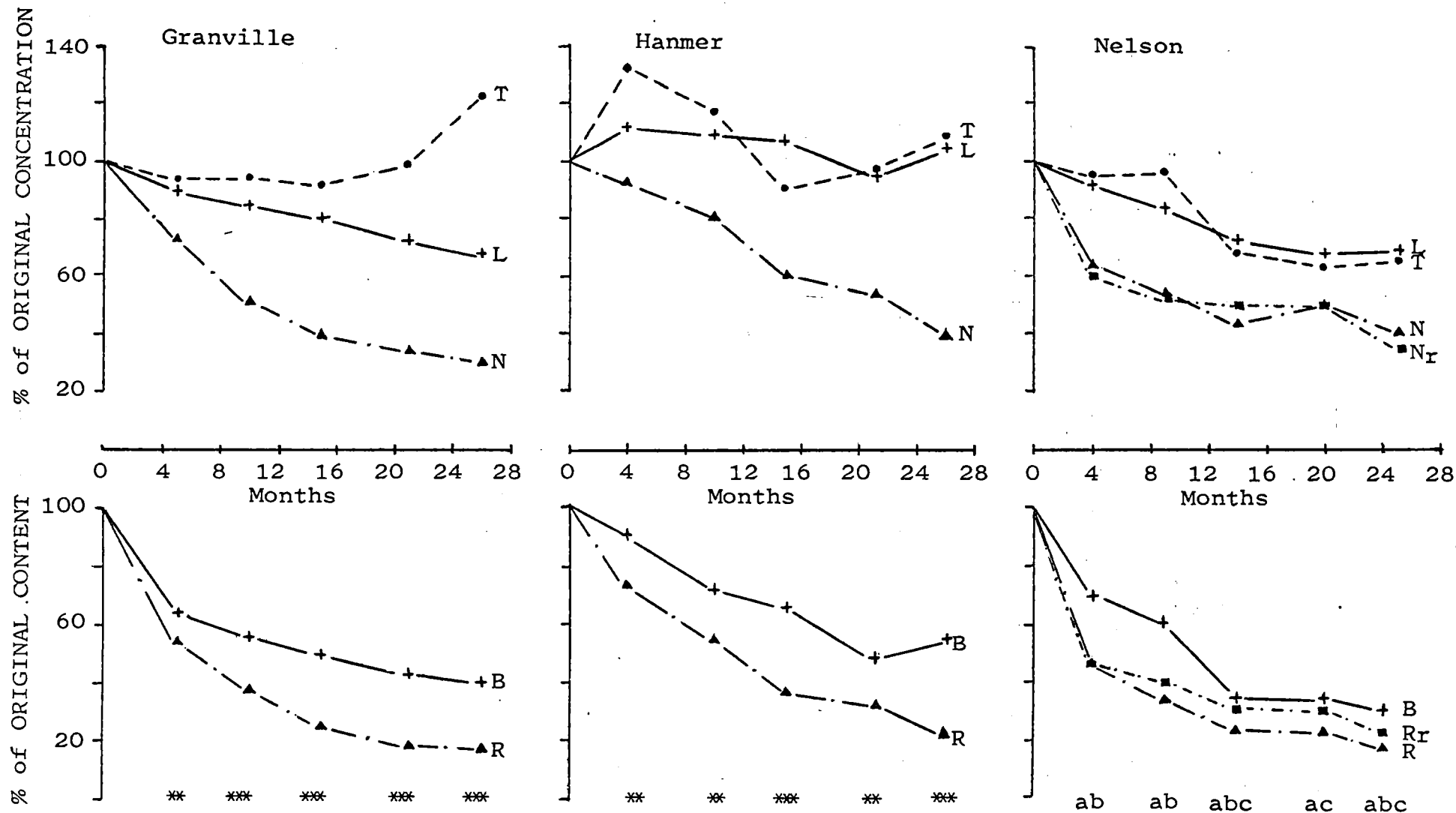


FIGURE 4.3.1.1.13 Ether extract concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.



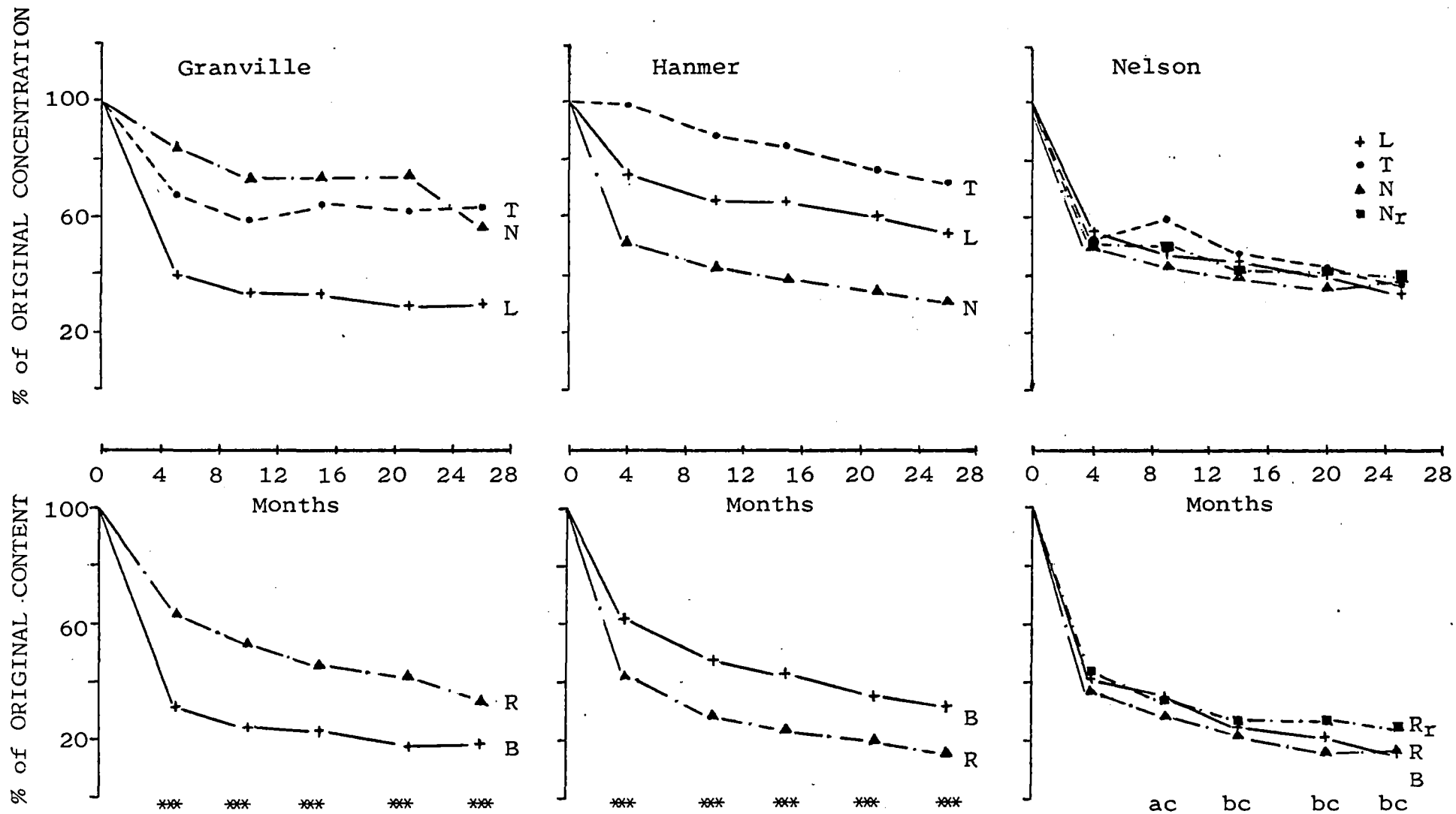


FIGURE 4.3.1.1.14 Aqueous ethanol extract concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

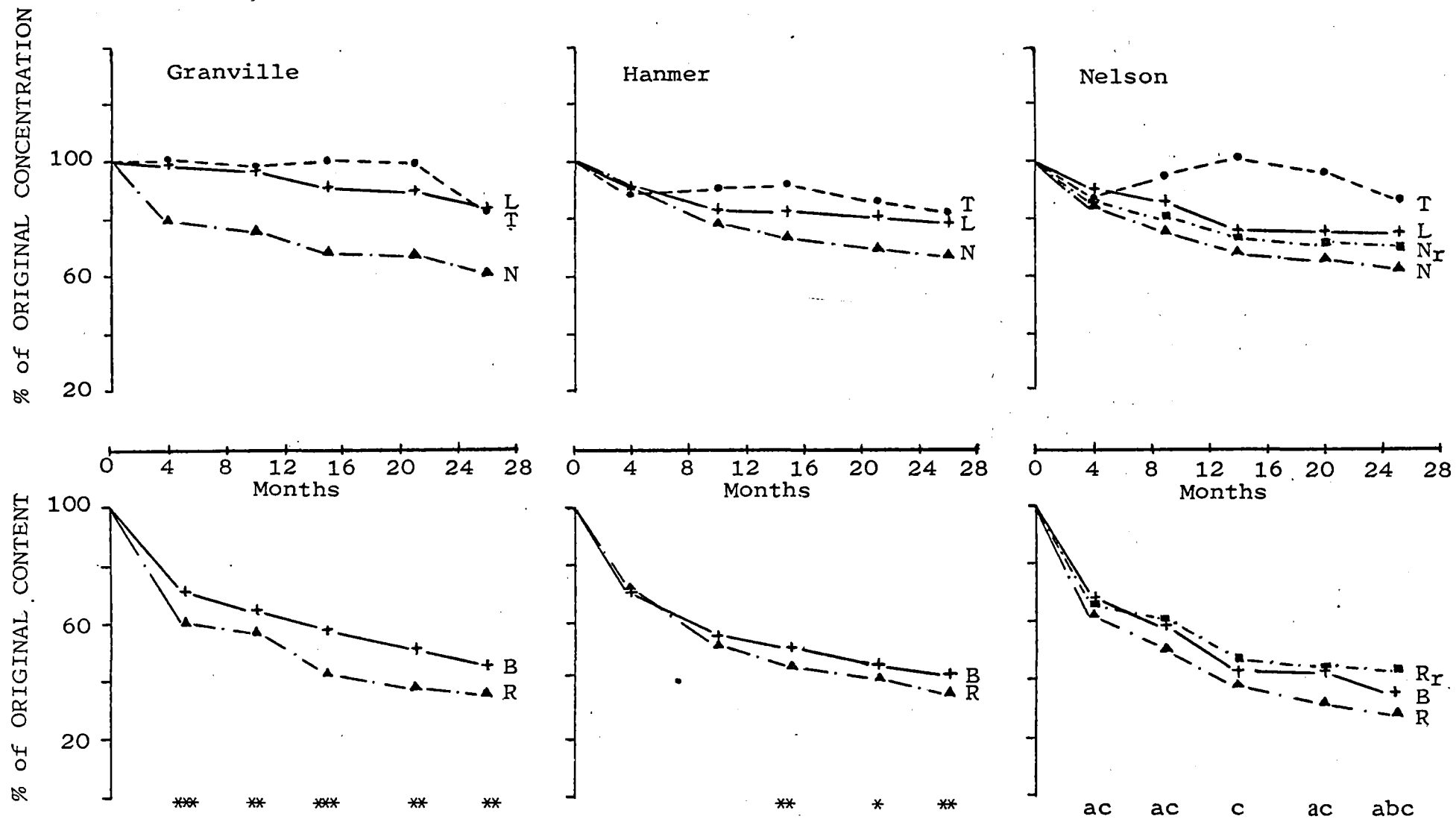


FIGURE 4.3.1.1.15 Holocellulose concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

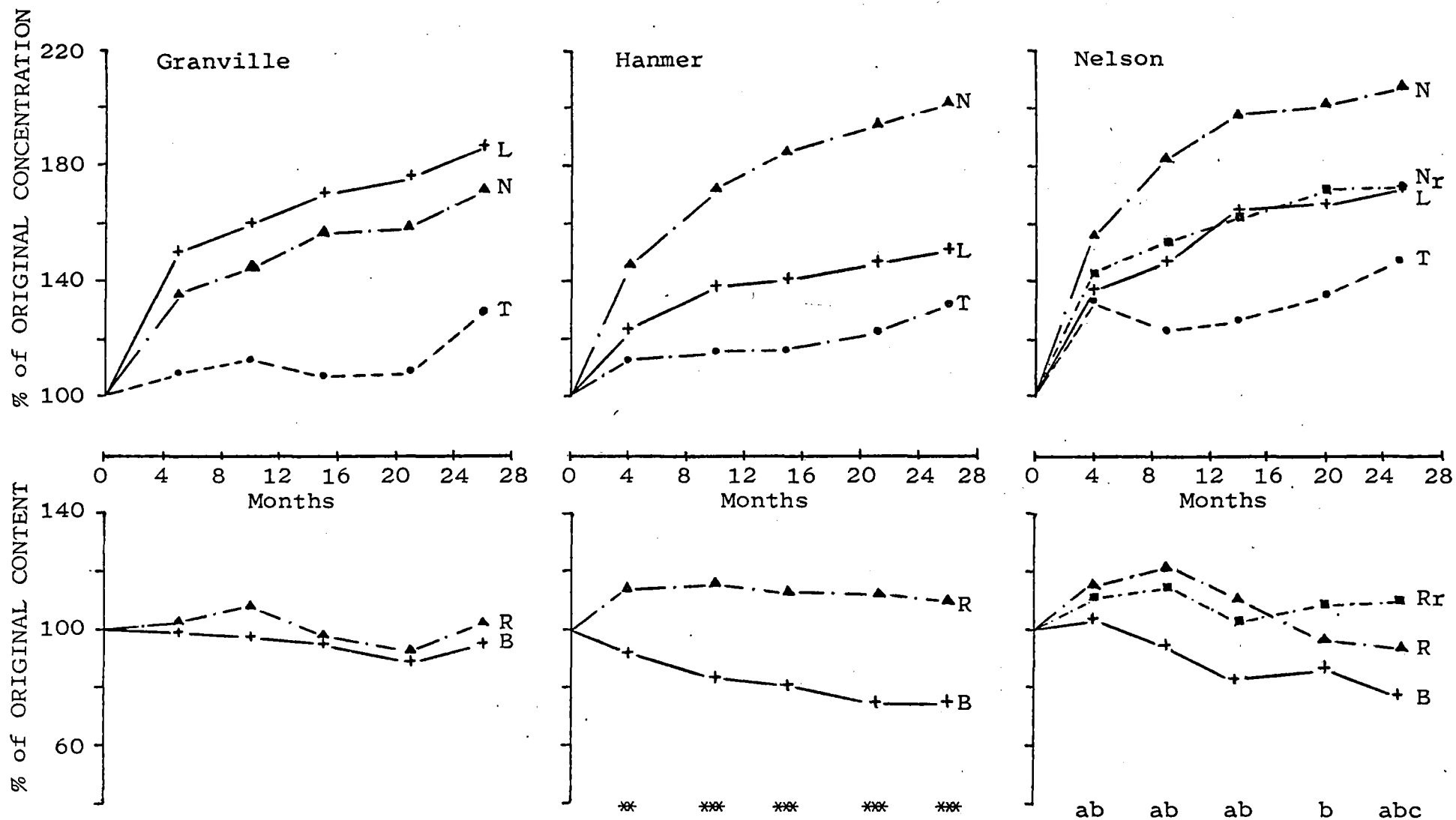


FIGURE 4.3.1.1.16 'Residual lignin' concentration and content of litter after various periods of decomposition. Legend as for Figure 4.3.1.1.

Additional data are given in Appendix III.

#### 4.3.4.1 Ether Extracts (EE)

Ether extracts constitute the smallest amount of the four organic components of litter studied. In the three forests studied, the greatest decrease in the amount of EE occurred in needle litter (Figure 4.3.1.1.13). The decrease in EE composition in leaf and twig litter was generally similar. However, twig litter showed greater fluctuations in the EE composition during litter decomposition. At Granville and Hanmer increases in the EE relative composition were observed. This result was probably due to a combination of factors including the varying proportions of bark material in twigs (which contains higher EE content than wood) and the rapid loss of more labile substrates. Nevertheless, results of other workers (Daubenmire and Prusso, 1963; Marten and Pohlman, 1942) show both increases and decreases in EE percentage composition also occurred in leaf litter during decomposition for a number of forest tree species. Although the results of these workers were obtained from laboratory decomposition studies, the comparison of relative changes in composition during decomposition between studies is considered not to be seriously in error.

In general, weight losses of EE from radiata litter were significantly more rapid than those from beech. This result was common in all the three forests studied (Figure 4.3.1.1.13). This effect was not reflective of the initial EE percentage compositions and therefore was probably due to the kind of EE and difference between the physical structure

of needle litter, and beech leaf and twig litter.

First-year loss rate (k) values (Table 4.3.4.1 ) show that the annual loss of EE from beech and radiata litter were greater than that of litter dry weight in the respective litter. It is probable that this disparity was due to the effects of weathering on the ether-soluble waxes on the surface of litter. Moreover, some surface EE substances such as cutin are generally considered as relatively slow decomposing components requiring specific micro-organisms for breakdown (Gray and Williams, 1975), therefore it is difficult to explain such rapid losses without attributing the effects of weathering. Furthermore, most needles at litter-fall were found to have lost much of the waxy appearance of green needles, thus attesting to the relative ease of removal of this ether-extractable component.

#### 4.3.4.2 Aqueous Ethanol Extracts

Decreases in the aqueous ethanol extract (AE) concentrations were most marked within the first 4 or 5 months of litter decomposition (Figure 4.3.1.1.14) after which only gradual decreases were observed. Differences in the magnitude of concentration changes with time in Granville and Hanmer were more pronounced than those in Nelson. There was also no consistent trend in the magnitude of concentration changes with time and in general between leaf, twig and needle. This result may be affected to a certain degree by the initial concentration found in fresh litter used. The magnitude of decreases in the AE concentration with time was related to their initial concentrations in the tissues,

TABLE 4.3.4 Initial distribution of the water-soluble components and organic constituents in litter used for decomposition study (Values given in percent)

Forest/Litter	WSC @	WSP	WSF	EE #	AE	HOL	RLIG
GRANVILLE							
Beech leaf	5.9	13.7	32.2	4.6	21.1	46.8	27.5
twig	3.2	7.3	15.5	1.6	8.6	52.5	37.4
Radiata needle	2.4	3.3	13.3	2.8	7.4	54.2	35.7
HANMER							
Beech leaf	3.3	4.6	16.3	3.1	10.7	54.4	31.8
twig	2.5	2.7	11.5	2.5	7.8	53.5	36.2
Radiata needle	4.6	5.2	24.5	3.0	17.4	50.3	29.4
NELSON							
Beech leaf	3.5	5.6	20.0	2.7	13.0	52.8	31.5
twig	4.0	9.3	22.0	4.4	15.5	44.0	36.2
Radiata needle	3.6	4.1	21.0	3.7	16.3	51.8	28.2
Radiata needle (reg.)	3.9	3.5	18.6	3.3	13.6	49.1	34.1

@, # as defined in TABLE 4.3.3.1 and TABLE 4.3.4.1 respectively

irrespective of the kind of tissue (Table 4.3.4).

First-year loss rates (Table 4.3.4.1 ) of AE from beech and radiata litter were greater than those of litter weight loss. This result was consistent with patterns observed in the loss of WSF from both litter, although the magnitude of loss rates of AE were constantly higher than those occurring in WSF. At the end of 25 to 26 months in the field, the AE content remaining in the litter enclosed in bags amounted to between 16 to 34 percent of the original content. Differences in rates of AE lost between beech and radiata were highly significant only in Granville and Hanmer. However, no evidence was obtained to indicate either beech or radiata lost larger amounts of AE over the other.

Although the aqueous ethanol extraction was carried out only to facilitate the isolation of holocellulose and not to serve a specific purpose, the results obtained show some significance. For example, at Granville the order in the magnitude of the decrease in AE concentration ( $L > T > N$ ) did not correspond to that occurring in WSF ( $L > N > T$ ). This deviation is attributed to the difference in the method used.

In the present study (Section 4.3.3), WSF was obtained by hot-water extraction ( $\sim 100^{\circ}\text{C}$ ) and thus inevitably includes some low melting point ether-extractable hydrophobic substances (see Braids and Miller, 1975) together with the water-soluble components. This effect was consistent with the observation that WSF on drying showed water-repellent properties. The result suggests that the use of hot-water extracts to quantify leaching losses may give rise to an over-estimation of the amount of leachable materials, and

conversely, to an under-estimation of the rate of weight loss by leaching. For example, the total amount of leachable materials as given by WSF would include some EE materials which are generally not leachable materials. On the other hand, the rate of loss of leachable materials will be apparently slowed down with the inclusion of EE materials in WSF.

#### 4.3.4.3 Holocellulose (HOL)

Percentage composition of holocellulose in leaf, twig and needle litter showed slow decreases with time (Figure 4.3.1.1.15). At the end of the 25-to 26-month period, the percentage composition in all litter tissues remained at more than 60 percent of the initial value. Among these tissues, needles showed the greatest decrease in all the three forests studied.

First-year loss rates (Table 4.3.4.1 ) of holocellulose were all greater than those occurring in the respective litter dry weight. Significantly greater loss of HOL content occurred in radiata litter than in beech. This disparity is probably due to the dissimilar rates at which EE was lost from litter. The more rapid loss of EE in radiata needles as compared to leaf and twig litter (Section 4.3.4.1) may have facilitated the decomposition of HOL. This view is supported by the results of Minyard and Driver (1972) which indicated that fungi are required to breakdown the waxes on the surface of needles before the cellular components can be acted upon. Waksman and Tenney (1928) also reported that the removal of ether-extractable materials from pine needles accelerated the subsequent decomposition of the residue.



TABLE 4.3.4.1      Annual (first-year) loss rates (k) for the organic constituents of beech and radiata pine litter in the forest stands at Granville, Hanmer and Nelson

Forest Stand	EE <sup>@</sup>	AE	HOL	RLIG
GRANVILLE				
Beech	0.56	1.16	0.44	0.05
Radiata	1.01	0.61	0.61	-
HANMER				
Beech	0.35	0.69	0.53	0.17
Radiata	0.74	1.12	0.59	-
NELSON				
Beech	0.69	1.14	0.62	0.10
Radiata	1.07	1.20	0.75	-
Radiata (reg.)	0.92	1.00	0.54	-

@ EE, AE, HOL and RLIG refer to petroleum ether-extractable materials, aqueous ethanol-extractable materials, holocellulose and residual lignin respectively

TABLE 4.3.4.1.1 Semi-logarithmic regressions of the different organic constituents' loss rates for beech and radiata pine litter in the forest stands at Granville and Hanmer

Forest/Constituent		Regression Model	Standard Error of Slope	Correlation Coefficient
GRANVILLE				
Beech	EE	$\ln Y = 4.4350 - 0.0325 T^@$	0.0027	0.914***
	AE	$\ln Y = 4.0500 - 0.0540 T$	0.0075	0.806***
	HOL	$\ln Y = 4.4922 - 0.0272 T$	0.0018	0.942***
	RLIG	$\ln Y = 4.6030 - 0.0038 T$	0.0016	0.397*
Radiata	EE	$\ln Y = 4.3992 - 0.0672 T$	0.0043	0.947***
	AE	$\ln Y = 4.4398 - 0.0370 T$	0.0030	0.919***
	HOL	$\ln Y = 4.4260 - 0.0360 T$	0.0028	0.925***
	RLIG	$\ln Y = 4.6340 - 0.0021 T$	0.0019	0.202
HANMER				
Beech	EE	$\ln Y = 4.5798 - 0.0271 T$	0.0027	0.885***
	AE	$\ln Y = 4.4068 - 0.0408 T$	0.0031	0.929***
	HOL	$\ln Y = 4.4423 - 0.0307 T$	0.0022	0.932***
	RLIG	$\ln Y = 4.5625 - 0.0110 T$	0.0011	0.877***
Radiata	EE	$\ln Y = 4.5559 - 0.0577 T$	0.0024	0.976***
	AE	$\ln Y = 4.2035 - 0.0598 T$	0.0052	0.910***
	HOL	$\ln Y = 4.4585 - 0.0370 T$	0.0022	0.953***
	RLIG	$\ln Y = 4.6848 + 0.0018 T$	0.0018	0.203

@  $\ln Y$  refer to the natural logarithm of percentage weight remaining, T refer to the time in months; number of samples used = 30

TABLE 4.3.4.1.2 Semi-logarithmic regressions of the different organic constituents' loss rates for beech and radiata pine litter in the forest stands at Nelson

Forest/Constituent		Regression Model	Standard Error of Slope	Correlation Coefficient
Beech	EE	$\ln Y = 4.4842 - 0.0475 T$	0.0033	0.940***
	AE	$\ln Y = 4.2459 - 0.0647 T$	0.0053	0.920***
	HOL	$\ln Y = 4.4516 - 0.0387 T$	0.0030	0.929***
	RLIG	$\ln Y = 4.6360 - 0.0112 T$	0.0016	0.795***
Radiata	EE	$\ln Y = 4.2740 - 0.0612 T$	0.0049	0.922***
	AE	$\ln Y = 4.1578 - 0.0627 T$	0.0061	0.888***
	HOL	$\ln Y = 4.4299 - 0.0476 T$	0.0028	0.956***
	RLIG	$\ln Y = 4.7321 - 0.0060 T$	0.0024	0.422*
Radiata reg,	EE	$\ln Y = 4.2680 - 0.0483 T$	0.0052	0.869***
	AE	$\ln Y = 4.1686 - 0.0468 T$	0.0060	0.827***
	HOL	$\ln Y = 4.4248 - 0.0298 T$	0.0032	0.871***
	RLIG	$\ln Y = 4.6603 + 0.0013 T$	0.0019	0.130

#  $\ln Y$  = natural logarithm of percentage weight remaining, T = time in months.  
Number of samples used in each regression analysis = 30

However, in general, a number of other litter constituents may also affect HOL decomposition, including polyphenolic content, nitrogen content and lignin content (see Review Section 2.3.4). For example, the higher polyphenol content observed in beech leaves (Section 3.3.7.1) may have also contributed to the differential loss rate, although such effects may be of a short-term significance due to the rapid loss of polyphenols from litter (Section 4.3.3). Benoit and Starkey (1968) have shown that tannins markedly reduced the decomposition of cellulose and hemicelluloses.

#### 4.3.4.4 Residual Lignin

Residual lignin (RLIG) percentage composition increased with decomposition in all litter tissues in all three forests studied (Figure 4.3.1.1.16). Such increases have also been reported by other workers (Marten and Pohlman, 1942; Daubenmire and Prusso, 1963; Katagiri and Tsutsumi, 1972). These increases observed in leaf, twig and needle litter appear to be inversely related to the RLIG percentage composition originally found in the respective fresh litter used (Table 4.3.4). Twig litter showed the least increase compared with leaf or needle. At Hanmer and Nelson, the RLIG percentage composition found in needle litter at the end of 25 to 26 months was more than double that found in the fresh litter used.

The total content of RLIG in litter showed differences in the amounts lost between beech and radiata litter. These differences were significant only in Hanmer and Nelson. Very little loss of RLIG occurred in radiata litter and

frequently RLIG contents were substantially higher than those present in the initial fresh litter used. Increases of up to 22 percent over the initial value were observed during the course of the present study. On the other hand, although small losses of RLIG from beech litter were found at Granville, corresponding losses at Hanmer and Nelson were more pronounced. For example, RLIG content of the beech litter remaining in litter-bags after 25 to 26 months of decomposition at Granville, Hanmer and Nelson respectively, amounted to 94, 75 and 78 percent of the original RLIG content of fresh litter.

It was difficult to determine the first-year loss rates of RLIG for radiata litter since regression equations of RLIG loss rates were not significant (Tables 4.3.4.1.1 and 4.3.4.1.2).

#### 4.3.5 Relationship between Annual Litter Weight Loss Rates and Initial Chemical Composition of Litter

Results of regression analysis on the relationships between decomposition rates and different initial chemical composition parameters in beech and radiata litter are given in Table 4.3.5.1. These initial chemical composition parameters were obtained from litter decomposition data summarised in Table 4.3.5.2 and given in Appendix III.

No significant correlations between annual loss rates of constituents including litter and different chemical composition parameters were obtained except for that between HOL and  $(C/N)(\% \text{ LIGNIN})/(\% \text{ CARBOHYDRATES})^{\frac{1}{2}}$ . The annual loss rates of litter weight showed the highest correlation coefficient with the initial RLIG percentage composition

TABLE 4.3.5.1 Correlation coefficients and levels of significance for relationships between first-year loss rates and initial chemical composition of litter #

	% RLIG	C/N	FACTOR	BASES	pH
Litter dry weight	- 0.61	- 0.14	- 0.32	0.49	0.10
Holocellulose	-	-	- 0.86*	-	0.70
Residual Lignin	-	-	0.29	-	- 0.39

\* denotes significant at  $p = 0.05$

# see Table 4.3.5.2

TABLE 4.3.5.2 First-year loss rates and values of litter constituents and initial chemical composition of litter

Forest/Litter	ANNUAL LOSS RATES			LITTER CHEMICAL COMPOSITION PARAMETERS					
	Litter Weight(k)	HOL (%)	RLIG (%)	C/N	Carbohy- drates(%)	RLIG (%)	FACTOR	pH	Σ Bases (%)
GRANVILLE									
Beech	0.40	- 35.6	- 4.9	84.9	52.3	29.5	346	3.3	1.47
Radiata	0.35	- 45.7	0.4	44.5	56.6	35.7	211	4.5	1.23
HANMER									
Beech	0.41	- 41.1	- 15.6	50.2	57.3	32.7	217	4.4	1.93
Radiata	0.38	- 44.6	10.7	45.7	54.9	29.4	181	4.9	1.56
NELSON									
Beech	0.47	- 46.2	- 9.2	36.9	54.6	32.4	162	5.1	2.08
Radiata	0.48	- 52.8	5.6	39.2	55.4	28.2	149	5.0	1.50
Radiata (reg.)	0.33	- 41.7	7.3	42.0	53.0	34.0	197	5.2	1.58

Carbohydrates(%) = holocellulose + water soluble carbohydrates

FACTOR = (C/N)(% LIGNIN)/(% CARBOHYDRATES)<sup>1/2</sup>

Σ Bases = sum of K, Mg, Ca concentrations

(0.61) and the lowest with pH (0.10). Almost all these results differ from those reported by other workers. For example, Cromack (1973) found that litter weight loss rates were significantly related to the initial lignin content of litter. Herman et al. (1977) reported that  $\text{CO}_2$  production and percent loss of carbohydrate was inversely related to  $(\text{C/N}) (\% \text{ LIGNIN}) / (\% \text{ CARBOHYDRATES})^{\frac{1}{2}}$  while percent loss of lignin was directly proportional to this factor. Marten and Pohlman (1942) observed that the extent of lignin and cellulose decomposition appeared to be associated with pH. The latter studies of Herman et al. (1977) and Marten and Pohlman (1942) however, were carried out in the laboratory.

Generally, these discrepancies between the results of the present study and those reported by the other workers are not entirely unexpected in view of the number of factors that may affect the relationship examined. For example, correlations computed in the present study used mainly litters of two forest species in three separate forests. As has been previously shown (Section 4.3.1), decomposition rates of these litters (beech and radiata) generally differed only marginally and showed no apparent relative order. Additionally, differences in the initial litter chemical composition between litter of similar species within a site and among forests were often large. Under such circumstances, the effects of other factors, both biotic and abiotic, may become relatively significant. Consequently, these factors could have masked the effects of initial chemical composition on decomposition rates.

Another factor that may help account for the



discrepancies between results of the present study and those reported by other workers relates to the introduction of twig litter in the present study. This increases the variability in decomposition rates between sites and forests.

The effects of climatic conditions on litter decomposition rates have been well established, and this aspect has been reviewed in Section 2.3.4.2. In the present study, seven sites in three forests were used, which differed in macro-climatic conditions (Table 3.2.1). Recently, Meentemeyer (1978) examined the effects of climate and lignin content on litter decomposition rates in 5 locations ranging from sub-polar to warm temperate sites, and found that actual evapotranspiration alone accounted for 51 percent of the variance in the litter decay rates. In the present study, although micro- and macro-climatic differences between forests and sites are likely to be smaller than those studied by Meentemeyer (1978) over a wider broader climatic zones, their effects are not to be ignored. This contention is supported by results obtained at Granville showing significant correlations between forest floor  $\text{CO}_2$  evolution rates and temperatures, thus indicating that temperature has a significant effect on litter decomposition rates.

On the basis of the results obtained in the present study, it would seem that it is not feasible to develop a general model for the prediction of litter decomposition rates for these forests using any single initial chemical composition of litter. These results, however, do not repudiate the claims that a relationship between decomposition rates and initial chemical composition exists. More

importantly, the present results indicate that there are certain limitations to the use of initial chemical composition parameters of litter to predict subsequent decomposition rates in the field. Furthermore, the degree of success of any model to predict decomposition rates in the field, including relative decomposition rates, would also depend on the micro-climatic and macro-climatic differences between the sites used and the duration of the period in which the decomposition rates of the litter was measured.

Generally, the pattern in the rate of litter decomposition is continuously being controlled by the amounts and rates of decomposition of the major constituents (e.g. cellulose, lignin) present in litter, and include the effects resulting from the microbial synthesis and chemical formation of stable compounds such as condensed phenolic compounds (Flaig *et al.*, 1975; Goh and Stevenson, 1971). Thus, within a period of one year after falling to the forest floor, it is probable that the overall annual weight loss rate of the litter would have been controlled, to varying degree, by the amounts and decomposition rates of the various major litter constituents. Such effects are considered and discussed in greater detail, in conjunction with pertinent results obtained, in the following Section 4.3.6.

The results of the present study, however, are consistent with those reported by Daubenmire and Prusso (1963). Data reported by these workers showed no relationship was evident between litter decomposition rates and initial lignin percentages, initial or final pH, and N concentrations in leaf litter of 13 tree species. No carbon values were reported by

these workers and the influence of C/N ratio cannot be compared.

#### 4.3.6 Relative Influence of the Organic Constituents on Overall Litter Decomposition Rate

A quantification of the relationship between total weights of beech and radiata litter remaining and those of their different organic constituents (EE, AE, HOL, RLIG) during decomposition in Granville, Hanmer and Nelson forests are given in Table 4.3.6.1. Such a relationship is illustrated in Figure 4.3.6.1 showing the total weights of beech and radiata litter and those of their organic constituents remaining after various periods of litter decomposition in Granville forest.

Linear regression analysis revealed that litter weight remaining after various periods of decomposition was most closely correlated with HOL weight remaining (Table 4.3.6.1). More than 96 to 99 percent of the variability in litter weight remaining with time was accounted for by this constituent. The relationship appears to extend over the entire 26-month period (Figure 4.3.6.1).

Significant correlations between weights of litter remaining and those of EE ( $r^2$  of greater than 0.86 to 0.96) and AE ( $r^2$  of greater than 0.89 to 0.96) were also obtained. The relationship between litter weight and that of AE was especially evident during the early stages of decomposition ( $< 5$  months).

Relationship between weight of litter and that of RLIG was more variable and insignificant in some cases (Significant  $r^2$  between 0.13 to 0.91). Little change in

TABLE 4.3.6.1    Linear regression equations and coefficients of determination ( $r^2$ ) for litter weight and its organic constituents' weights remaining after various periods of litter decomposition

Forest/ Litter	Ether Extracts	Aq.Ethanol Extracts	Holocellulose	Residual Lignin
Regression Equations				
GRANVILLE				
Beech	W = 3.515 + 19.187(EE)	W = 7.290 + 2.752(AE)	W = 1.607 + 1.822(HOL)	W = - 2.954 + 3.128(RLIG)
Radiata	W = 10.379 + 17.848(EE)	W = 7.195 + 8.741(AE)	W = 6.906 + 1.248(HOL)	W = 1.188 + 1.838(RLIG)
HANMER				
Beech	W = 1.626 + 28.362(EE)	W = 5.850 + 7.236(AE)	W = 3.417 + 1.531(HOL)	W = -13.103 + 4.883(RLIG)
Radiata	W = 7.676 + 19.104(EE)	W = 9.470 + 3.052(AE)	W = 5.523 + 1.414(HOL)	W = 33.734 - 3.257(RLIG)
NELSON				
Beech	W = 4.214 + 24.750(EE)	W = 7.034 + 4.629(AE)	W = 2.968 + 1.637(HOL)	W = - 9.447 + 4.138(RLIG)
Radiata	W = 6.310 + 17.285(EE)	W = 6.928 + 3.750(AE)	W = 4.123 + 1.473(HOL)	W = 3.623 + 1.429(RLIG)
Coefficients of Determination				
GRANVILLE				
Beech	0.962***	0.898***	0.986***	0.209*
Radiata	0.921***	0.896***	0.963***	0.138*
HANMER				
Beech	0.866***	0.979***	0.994***	0.914***
Radiata	0.960***	0.926***	0.991***	0.178*
NELSON				
Beech	0.965***	0.910***	0.989***	0.669***
Radiata	0.926***	0.891***	0.985***	0.067 <sup>ns</sup>

\* Denotes  $p < 0.05$ ;    \*\* Denotes  $p < 0.10$ ;    \*\*\* Denotes  $p < 0.001$ ;    ns Denotes not statistically significant  
W = Weight of litter

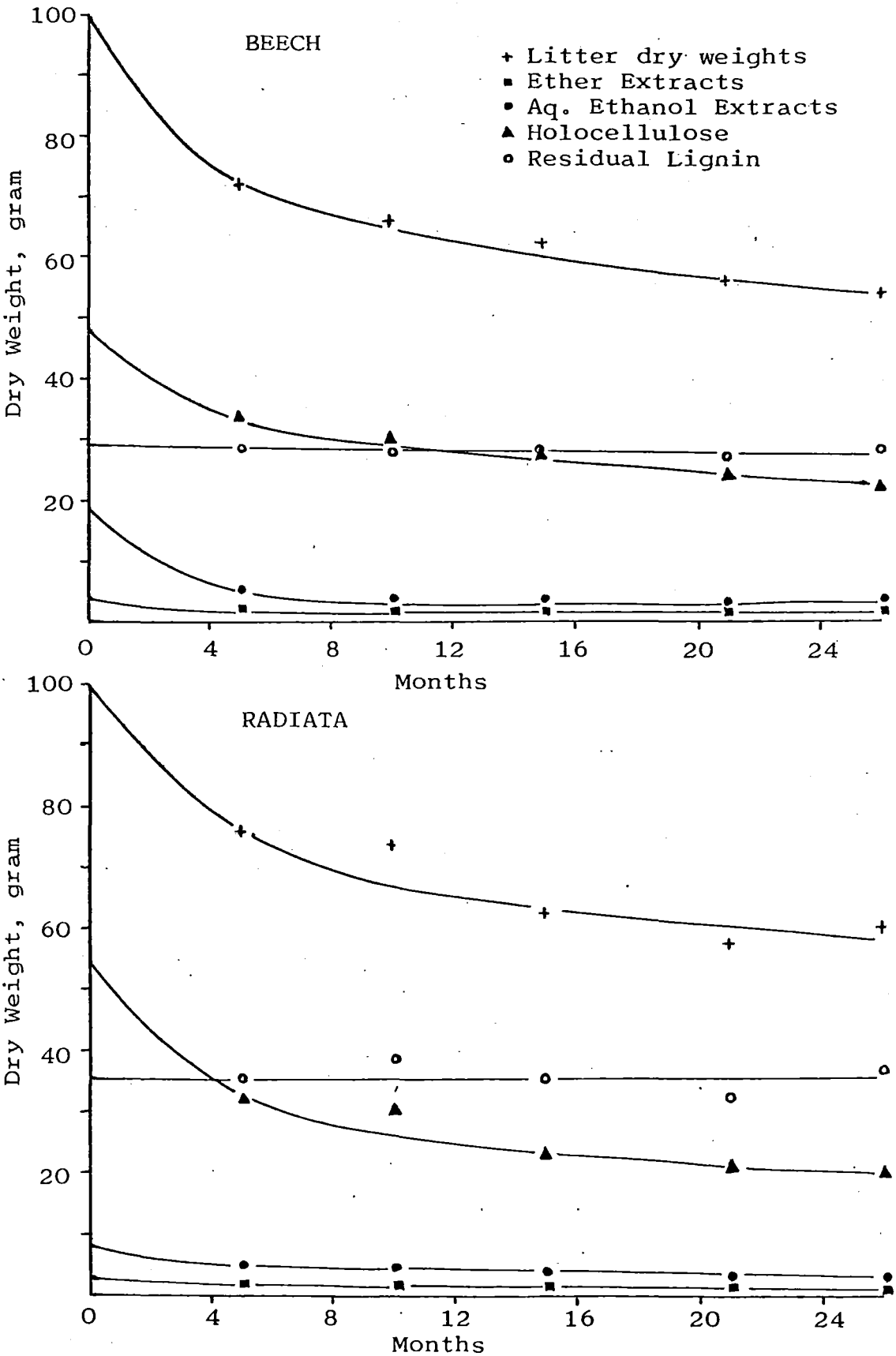


FIGURE 4.3.6.1 Dry weight remaining after various periods of decomposition at Granville forest. Weight of constituents are based on an initial 100g of litter.

the weight of RLIG remaining with time was found in Granville (Figure 4.3.6.1) although at Hanmer and Nelson, somewhat larger changes occurred. These results have been discussed earlier (see Section 4.3.4.4). The possibility that the variability in the relationship between RLIG and litter weights remaining resulted from the procedure used to estimate RLIG by difference (Section 3.2.4.8) cannot be ignored.

A useful theoretical application of the above results relates to the estimation of EE, AE and HOL contents from litter weight remaining at various periods of decomposition using these regression equations. This applies particularly to HOL since the gradient of regression lines are relatively similar between species and forests. The ranges of gradients were HOL (1.25 to 1.82), EE (17.29 to 28.36) and AE (2.75 to 8.74).

#### 4.3.7 Relative Contributions of Weight Changes of the Individual Organic Constituents to the Weight Changes of Litter

The relative contributions of the weight changes of EE, AE, HOL and RLIG to the weight changes of litter occurring (expressed as percentages) during the different periods of litter decomposition in beech forests and radiata plantations in general are given in Table 4.3.6.2. The procedure by which these values were calculated using decomposition results (Appendix III) discussed previously (see Section 4.3.4) is described below.

For example, litter weight loss recorded in the first 5 months of litter decomposition for radiata litter in

Granville was 24.4 g, based on an initial litter weight of 100 g (for simplification). Weight losses in EE, AE and HOL in this corresponding period were 1.3, 2.7 and 21.5 g respectively, while a gain in weight of 1.1 g was recorded in RLIG. The relative percentage contribution to the weight change of litter by each of these organic constituents is then given by:

$$\frac{|\Delta \text{ weight of constituent}|}{\sum |\Delta \text{ weights of constituents}|} \times 100$$

For example, the relative contribution from EE amounted to

$$\frac{1.3}{1.3 + 2.7 + 21.5 + 1.1} \times 100 = 4.9\%$$

Calculated over various periods of decomposition, this procedure provides a satisfactory estimate of the influence of each organic constituent on the change in litter weight as a function of time. However, it is important to emphasize that this procedure gives only approximations since variability and errors tend to increase with decomposition as the weights of some constituents become small (e.g. EE, AE), and the isolation of constituents become complicated by the synthesis of by-products (see Review Section 2.3.4.1.4).

Results obtained (Table 4.3.6.2) showed that in the first 5 months of decomposition, losses in weights of both beech and radiata litters were mainly attributed to the losses in weights of AE (30 and 25 percent respectively) and HOL (60 and 59 percent respectively). In the entire 26-month period, these relative contributions from HOL remained

TABLE 4.3.6.2 Relative contributions (%) of the changes in weight of the different organic constituents to the total weight loss of litter which occurred at various periods of decomposition for beech and radiata litter

	Decomposition period in months				
	0 to 5th	5th to 10th	10th to 15th	15th to 20th	21st to 26th
Ether Extracts					
Beech	3	4	7	6	4
Radiata	5	5	5	3	8
Aq. Ethanol Extracts					
Beech	30	16	9	13	8
Radiata	25	17	10	9	9
Holocellulose					
Beech	60	60	60	50	56
Radiata	59	58	61	43	48
Residual Lignin					
Beech	7	20	24	31	32
Radiata	11	20	24	45	35



relatively constant and substantial ( > 43 percent) while those from AE declined from about 28 percent to 9 percent. In the same 26-month period, the relative contributions from RLIG increased from 9 percent to 34 percent. Relative contributions from EE varied from 3 to 8 percent throughout this period and showed no definite pattern of increase or decrease with time.

These above results clearly indicate that even within a period of one year, weight losses (and therefore weight loss rates) of beech and radiata litters were governed to different extents by the organic constituents according to the various stages of decomposition. Thus, it is probable that the weight loss rates of litter during the early stages of decomposition (e.g. first few weeks) could be accurately predicted by the initial amounts of the AE (and water-soluble materials) in the litter. Thereafter when most of these AE and water-soluble materials have been removed, the weight loss rates are then determined predominantly by the contents of the more resistant constituents such as holocellulose, and eventually by the content of lignin. Unfortunately, the short length of time in which the decomposition of litter was measured would not allow a good test of the above hypothesis to be undertaken in the present study.

Changes in the degrees of relative contributions of the different organic constituents to weight loss rates of litter over time may very well explain the difficulty in obtaining significant correlations between annual weight loss rates and the initial chemical composition of litter in the present study. In general, it is possible that such a

situation also applies to decomposition of litter of any species and under different climatic conditions. However, as far as the author is aware, no similar experimental approach leading to this conclusion has been reported in the literature to allow such a possibility to be inferred.

Minderman (1968), however, has also elaborately discussed the influence of the separate chemical constituents of litter on the overall decomposition rate of litter, and on organic matter accumulation.

#### 4.4 GENERAL DISCUSSION

In the present decomposition study, values of litter weight loss for beech represent combined weight losses of leaf and twig tissues. Several reasons contributed to this choice. Bray and Gorham (1964) estimated that non-leaf litter may form between 21 and 42 percent of the litter-fall in most types of temperate forests, yet this component has been largely ignored in most decomposition studies when only leaves were used. Twig litter was estimated to constitute about 20 percent of the total litter-fall in the three beech forests examined in the present study. Therefore, such a decomposition study of twig litter in combination with leaf litter is ecologically more meaningful. Furthermore, combined litter may create a more natural environment for decomposition. For example, the introduction of twig litter may reduce the matting of leaves in later stages of decomposition, thus maintaining aeration.

Basically the forest floor is a natural accumulation of both leaf, twig and miscellaneous litter. According to Cromack (1973), twig litter may influence forest floor decomposition rates since twigs act as colonization bases from which a vegetative network of litter fungi grow into the surrounding leaf litter, thereby linking together the separate processes of leaf and twig litter decay. The overall decomposition rates should therefore provide a more useful estimate of litter turnover, which is one of the major objectives of this study. Litter used in this study had been collected by large nettings and was representative of the forest floor tissue relative composition.

In general, rates of release of nutrient elements from beech litter and radiata litter (Table 4.3.2.1a) were found to follow the sequence:

Beech: (K, Mg) > (Ca, P) > N

Radiata: K > P > Ca > (Mg, N)

Elements grouped in parentheses were found to change relative positions with one another according to the forests.

Several additional notable points were evident from the results. Despite lack of significant difference in the rate of litter weight loss, radiata litter exhibited a more rapid release of essential nutrients (P, K and possibly N). However, it is possible that the rapid rate of K loss may be only an artefact of the higher initial concentrations. Magnesium loss rate was greater in beech litter while calcium showed similar loss rates in both litters. Such a differential rate in nutrient release would therefore suggest that

TABLE 4.4.1.1 Amounts of macro-nutrients ( kg/ha ) released from and immobilized in decomposing beech and radiata pine litter in a period of two years #

MACRO-NUTRIENTS	GRANVILLE		HANMER		NELSON		
	Beech	Radiata1955	Beech	Radiata1960	Beech	Radiata1956	Radiata <sub>req.</sub> 1956
NITROGEN							
Input	73.4	62.3	41.4	18.1	85.4	74.7	62.2
Release	- 3.7	7.5(12.0)	6.5(15.7)	1.9(10.5)	20.8(24.4)	17.8(23.8)	6.7(10.8)
Immobilization	77.1	54.8	34.9	16.2	64.6	56.9	55.5
PHOSPHORUS							
Input	5.0	4.5	7.6	3.7	10.0	10.6	9.0
Release	0.5(10.0)	1.5(33.3)	2.4(31.6)	1.8(48.6)	3.6(36.0)	4.8(45.3)	3.6(40.0)
Immobilization	4.5	3.0	5.2	1.9	6.4	5.8	5.4
POTASSIUM							
Input	20.1	17.5	21.9	14.9	37.3	37.7	27.3
Release	10.3(51.2)	13.4(76.6)	8.6(39.3)	11.6(77.8)	17.5(46.9)	28.3(75.1)	19.9(72.9)
Immobilization	9.8	4.1	13.3	3.3	19.8	9.4	7.4
MAGNESIUM							
Input	17.7	9.7	11.5	3.5	15.0	14.0	11.8
Release	6.8(38.4)	2.4(24.7)	5.2(45.2)	0.7(20.0)	5.8(38.7)	2.8(20.0)	1.1( 9.3)
Immobilization	10.9	7.3	6.3	2.8	9.2	11.2	10.7
CALCIUM							
Input	100.5	36.1	82.7	18.4	147.2	69.5	66.5
Release	34.4(34.2)	11.7(32.4)	29.9(36.2)	4.6(25.0)	45.5(30.9)	22.8(32.8)	18.9(28.4)
Immobilization	66.1	24.4	52.8	13.8	101.7	46.7	47.6

# excluding branch and pine cone litter  
data in parenthesis refer to % of total input

radiata pine was more efficiently recycling and possibly re-utilizing the essential nutrient elements than beech.

Macro-nutrient releases from decomposing litter were quantitatively estimated using data of nutrient returns in quarterly litter-fall (Section 3.3.11) and nutrient loss rates derived from regression equations (Section 4.3.2.2). Calculations were based on the assumption that "other" (miscellaneous) litter, which contained considerable amounts of fragmented leaf and twig tissues, decomposed at the same rate as combined leaf and twig tissues. For example, litter collected in the first quarter were viewed to have undergone two years of decomposition, that collected in the second quarter at 21 months of decomposition and so on. The amounts of nutrients released from litter-fall at the end of the two-year period were obtained by summing these quarterly contributions. Physical leaching and biological decomposition would constitute the predominant mechanisms by which such nutrients were released (Gosz et al., 1973).

Results presented in Table 4.4.1.1 indicated that nutrient inputs by litter-fall were generally greater in beech than radiata stands. However, total weights of P and K released from decomposing litter in the two-year period were greater for radiata than beech, although the order was reversed with Mg and Ca. No definite order was observed with N but there appears to be a nett immobilization in the beech stand at Granville. It is possible that this was the consequence of the import of contaminant litter into the litter-bags as discussed previously (Section 4.3.2.2). Generally, beech stands were immobilizing, and therefore

accumulating greater amounts of all macro-nutrients studied.

Generally speaking, a large accumulation of organic residue in the forest floor may not necessarily imply a large supply of plant available nutrients since much of these nutrients could be immobilized within the organic residue. The accumulation simply represents the amounts of nutrients and carbon transferred from the root zone and atmosphere to the forest floor, and consequently may be beyond the reach of the tree root systems. This effect is illustrated by the results of the present decomposition study. Despite a smaller amount of litter-fall and an apparently slower rate of litter decomposition in the radiata site compared to those in the beech site, release rates of P and K in the radiata site were relatively more rapid. On a short term basis, such rapid releases of nutrients, especially P, is beneficial since there may be an excess of element uptake over element release during the growing season. This effect becomes more important as the peak litter-fall occurred early in each growing season. Furthermore, rapid nutrient release is most advantageous where soils are relatively infertile, similar to those in the beech and radiata sites studied (Section 5.3.3).

The above contention is nevertheless based on the assumption that leaching losses from the ecosystems are small. However, data reported by Levett (1978) for a number of sites under *Pinus* spp. and hardwood stands showed small losses of P and a general reduction of nutrient fluxes in soil drainage during its passage from below the organic horizon to below the rooting zone. Thus the assumption used in the present study for P may not be seriously in error.

In beech and radiata stands, rates of loss of various organic constituents from the litter decreased in the following order:

Beech : AE > (EE, HOL) > RLIG

Radiata : AE > EE > HOL > RLIG

Constituents in parentheses change relative positions according to forest.

Results of loss rates of organic constituents (Table 4.3.4.1 ) indicate that both EE and HOL were lost more rapidly from radiata needles than from beech litter. In contrast, RLIG content in radiata litter increased with decomposition while that in beech litter decreased. No definite order was observed between beech and radiata litter in the loss rates of AE. These results therefore suggest that litter decomposition processes occurring in radiata plantations would eventually lead to a forest floor accumulation which may comprise largely of lignin-like organic residues, both of plant and microbial origin.

As these organic constituents are major components of litter, the order in the rates of loss of the organic constituents would therefore suggest that the rate of litter weight loss will eventually be governed by that of the much more slower decomposing constituent of RLIG, once the more labile and easily decomposable components have been removed. A similar conclusion has also been expressed by Minderman (1968).

Results obtained in the present study also indicate that it is probable that the apparent disparity in the rate

of loss of litter weight between beech and radiata litters was reflective of the difference found in the content of RLIG between the two litters. For example, the RLIG content of radiata litter increased with decomposition, which was not the case with beech litter (Section 4.3.4.4). This view is supported by the fact that despite greater loss rates of EE and HOL from radiata litter, the magnitude of litter weight lost from radiata litter was generally found to be smaller than that from beech litter. It is unlikely the slower loss rates of EE and HOL of beech litter, when compared to those of radiata litter, were due to the inclusion of twig litter tissues since no marked differences were observed in the loss rates of EE and HOL between leaf and twig litter.

In the present study, although there was a considerable difference in the pH of the litter between beech and radiata (pH 3.3 and pH 4.5 respectively), no significant relationship was found between pH values and loss rates of HOL and RLIG (Table 4.3.5.1). Many factors can contribute to this result. They include the synthesis of lignin-like materials by fungi involved in the decomposition process. This possibility is supported by observed increased decomposition of EE and HOL in radiata litter which is mainly accomplished by fungi. The proliferation of fungal development in radiata litter was also observed.

In comparison, these results differed from those reported by Marten and Pohlman (1942). These workers found that the extent of lignin and cellulose decomposition of a number of leaf litter, including those of beech and pine, appeared to show a direct relationship with pH, with higher



rates of decomposition occurring at high pH. However, these workers studied decomposition under controlled laboratory conditions and consequently this may make pH effect more significant than would be under field conditions where other different factors are also involved.

According to Falck (1931) various species of fungi may act on leaf litter either by decomposing the cellulose and leaving a lignin-rich residue, or by decomposing cellulose and lignin simultaneously. In the present study, although no analysis was carried out to identify the fungi population associated with the litters of beech and radiata pine, it is possible that differences observed in loss rates of HOL and RLIG in beech and radiata litter could have resulted from differences in fungi species.

The significance of studying decomposition dynamics of the organic residues in conjunction with the nutrient elements is illustrated by results shown in Table 4.4.1.2. Significant correlations were obtained between RLIG, WSP and N percentage compositions in beech litter, and between RLIG and N percentage compositions in radiata litter (at Granville). It is possible that these significant correlations obtained were caused by the polymerization reactions between polyphenols and amino compounds (Parsons and Tinsley, 1975) and the formation of ligno-protein complexes (Waksman and Iyer, 1932, 1933).

No significant correlation was obtained between WSP and N for radiata litter. This may be due to the smaller WSP concentrations in radiata litter than those found in beech litter. A number of other workers have also reported

TABLE 4.4.1.2 Correlation coefficient (r) for residual lignin, water-soluble polyphenols and nitrogen content in beech and radiata pine litter at Granville forest

CONSTITUENT	Beech	Radiata
Residual lignin and nitrogen	0.827***	0.719***
Residual lignin and water-soluble polyphenols	-0.691***	-0.233 <sup>ns</sup>
Water-soluble polyphenols and nitrogen	-0.640***	-0.369 <sup>ns</sup>

\*\*\* Denotes  $p < 0.001$ ; ns Denotes not statistically significant

increases in N and lignin percentage compositions after a period of decomposition (Flaig et al., 1975), and increases in crude protein and lignin percentage compositions in litter with increasing decomposition (Katagiri and Tsutsumi, 1972).

#### 4.5 CONCLUSIONS

Only small differences were found in the rates of decomposition between beech and radiata litters. In Granville and Hanmer forests, beech litter appears to decompose slightly more rapidly than radiata pine litter. In Nelson, beech litter decomposed slower than the first rotation radiata pine litter but more rapidly than that of the second rotation radiata pine. Annual (first-year) decomposition rate constants ( $k$ ) for beech litter (leaf + twig) and radiata pine needle litter ranged from 0.40 to 0.47 and from 0.33 to 0.48 respectively in the forests at Granville, Hanmer and Nelson.

Relatively large decreases in weight in beech and radiata litters in these sites occurred during the early stages of decomposition, when between 21 to 29 percent of the original weight used was lost in a period of about 4 to 5 months. These losses were due mainly to the loss of water-soluble materials.

Pattern of change in elemental concentrations (N, P, K, Ca, Mg, C) varied according to the element and type of litter tissue (leaf, twig or needle). Nitrogen, and to a

lesser degree P, were the only elements which showed increases in concentration with increasing decomposition. The most rapid decrease in concentration was found in K, which occurred during the early stages of decomposition.

Relatively, K content in litter was reduced most rapidly during decomposition and N content was least. The annual loss rates of nutrient content occurring in the forest sites used were generally in the order:

Beech :  $K > (Mg, Ca, P) > N$

Radiata :  $K > P > Ca > (Mg, N)$

Elements in parenthesis interchanged positions according forests. Annual loss rates of P and K contents from radiata pine litter and, K and Mg contents from beech litter were greater than those of respective litter weight. Changes in carbon content were similar to those of litter weight.

The losses in the amounts of P and K from radiata litter at various stages of decomposition (in the 26-month period) were greater than those from beech. A reverse order in the amount lost was found for Mg.

Concentrations and total contents in litter of the water-soluble carbohydrates, water-soluble polyphenols and total water-soluble fraction decreased rapidly. However, the greatest change in concentration and total content occurred in the WSP fraction.

Except for residual lignin, the percentage composition and total content of ether extracts, aqueous ethanol extracts and holocellulose generally decreased with increasing decomposition. Residual lignin percentages in all litter

tissues increased with decomposition. Residual lignin contents in radiata litter remained constant or increased slightly while those of beech decreased with time.

The annual loss rates of EE, AE, HOL in beech and radiata litters were all greater than those of litter weight. In comparison, the annual loss rates of organic constituents in beech and radiata were:

$$AE > EE > HOL > RLIG$$

The proportions of EE and HOL lost from radiata litter were greater than those from beech (in a corresponding period) at various stages of decomposition, while a reverse order was found for RLIG. No definite order was evident in the loss of AE contents.

Prediction of annual loss rates of beech and radiata litter in the forest studied, using litter chemical composition parameters, was not feasible. Two factors were attributed as the underlying cause of the unsuccessful exercise. The first relates to the differing climatic conditions which exists between forests. The second relates to the varying degree of influence on the overall litter decomposition rate by the various groups of organic constituents. Within a period of a year, the rate of litter decomposition was influenced to a different extent by AE, HOL and RLIG.

Weight of holocellulose accounted from about 43 to 61 percent of weight changes in beech and radiata litters at various stages of decomposition during the 25 to 26-month period. Contributions from aqueous ethanol-extractable fraction (including water-soluble fraction) were significant

only during the early stages of decomposition ( < 5 months). Although the contributions from residual lignin increased with time, this constituent remained the second most important factor after holocellulose, even after 26 months of decomposition.

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## CHAPTER 5

### ORGANIC MATTER ACCUMULATION

#### 5.1 INTRODUCTION

In general, a large accumulation of organic matter on the forest floor does not necessarily represent a large supply of available nutrients to the trees associated with the site. It only constitutes a sink and an indication of the size of nutrient pool and energy storage within a stand. As almost the entire root system of trees is generally found in the mineral soil horizon, the nutrient status in this compartment is, therefore, a better index of the potential of a site for utilization or re-utilization.

The objective of this investigation was to estimate and compare the nutrient and organic matter content of the forest floor of stands of native species and that in adjacent stands of radiata pine, of similar soil type and possibly of similar macro-climatic conditions. From these results, the possibility for deriving some conclusions on the nutrient and energy status associated with radiata plantations on a longer term basis is examined.

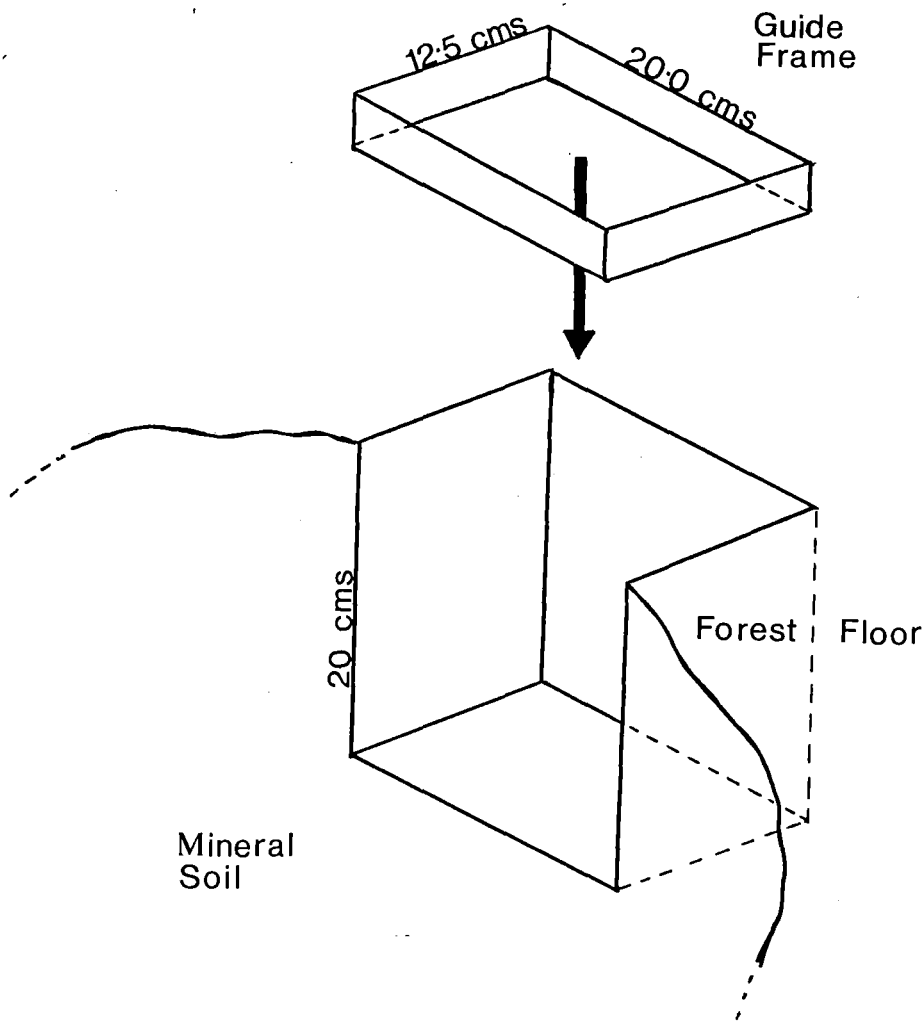


FIGURE 5.2.2.1 Apparatus and procedure used in the sampling of forest floor and top-soil of native and radiata forest stands

## 5.2 MATERIALS AND METHODS

### 5.2.1 Study Areas

The study was conducted on five forests located in the South Island. Representative stands of indigenous forests and adjacent radiata plantations were selected and these were:

- (a) Granville Forest: beech and *P. radiata* (1955)
- (b) Hochstetter Forest: podocarp and *P. radiata* (1964)
- (c) Hanmer Forest: (i) beech and *P. radiata* (1960)  
(ii) beech and *P. radiata* (1926)
- (d) Golden Downs Forest: beech, *P. radiata* (1967, 1956, 1947) and *P. radiata* (Nelson) (reg. 1956)
- (e) Peel Forest: podocarp and *P. radiata* (approx. 1937)

The criteria for selection of stands were:

- (i) similarity in soil type
- (ii) within close distance from each other, and
- (iii) similar site conditions (e.g. aspect and slope)

Some of these site properties are given in Table 3.2.1 .

Sites at Granville, Hanmer and Nelson forests included the experimental areas used for the present litter production and litter decomposition studies (Chapters 3 and 4, respectively).

### 5.2.2 Sampling Procedure

With each forest stands, five samples of the forest floor were obtained using a 0.025 m<sup>2</sup> aluminium frame (Figure 5.2.2.1). Samples, at least 1 metre apart were

collected along the line of predominant slope in each site. At each sampling point, the frame was initially driven through the organic layer and the organic matter was separated into L and F+H layers in the field. The thickness of each L and F+H layer was estimated by averaging the thickness found at the four corners of the frame. Samples were stored in polythene bags.

A soil block (20cm in depth) was then obtained by cutting through the top-soil around the guide frame. It was necessary to remove the soil around this block on the down-slope in order to facilitate the collection of this soil block. Such approach also allows easy access to roots and rocks encountered during sampling. These materials were proportionally collected. Additionally, samples were obtained from areas as far removed as possible from trees. This procedure avoids sampling of disturbed areas caused by tree roots and stem flow, and allows standardization of sampling technique for comparisons between stands and forests.

### 5.2.3 Sample Preparation

Samples of L, F+H and top-soil were processed separately.

#### 5.2.3.1 L and F+H Samples

These samples were air-dried and individually weighed and the bulk density determined. All data were corrected to an oven-dried basis using subsamples for moisture determinations. No separation of the various litter components was undertaken. L and F+H were then proportionally bulked and ground to pass through a 40 mesh (0.4mm) sieve before chemical analyses.

#### 5.2.3.2 Soil Samples

Soil samples were air-dried and separated into the different particle sizes of stones (2 to 20cm), gravels (0.2 to 2cm) and fine soil ( $< 0.2$  cm). Total bulk density, fine soil bulk density (i.e.  $< 0.2$ cm) and root content were also determined.

#### 5.2.4 Chemical Analysis

Chemical analysis was done on each replicate L+F+H and top-soil samples (5 per site) unless otherwise reported.

##### 5.2.4.1 Total Carbon and Total Nitrogen

Total carbon and total nitrogen concentrations of both L+F+H and top-soil samples were determined according to the procedures described in Sections 3.2.4.2 and 3.2.4.3 respectively.

##### 5.2.4.2 Total K, Mg, Ca and P

Different methods were used for L+F+H and top-soil samples.

###### 5.2.4.2.1 L+F+H Samples

Sample solutions were prepared using the nitric-perchloric acid digestion procedure (Metson, 1972). Determinations of the different elements were carried out according to the procedure given in Section 3.2.4.4 .

###### 5.2.4.2.2 Soil Samples

Soil sample solutions were prepared by the sodium carbonate fusion method (Allen, 1974). Each soil sample

(about 0.2 g) was fused with excess  $\text{Na}_2\text{CO}_3$  (about 1.2 g) at  $950^\circ\text{C}$  in a platinum crucible for 15 minutes. The fusion mixture was then cooled, dissolved in 6ml of  $6\text{M}$   $\text{HCl}$  and digested over a steam bath for 1 hour. The solution was appropriately diluted for elemental determinations as described in Section 3.2.4.4.. Only 3 replicates per site were analysed.

#### 5.2.4.3 Simple Carbohydrates, Polyphenols and Ether-extractable Fraction

Water-soluble and polyphenolic compounds were determined following the procedure described in Section 3.2.4.5. Ether-extractable fraction was determined according to the method given in Section 8.2.

#### 5.2.4.4 Cation Exchange Properties

Only soil samples were analysed. Cation exchange capacity (CEC) and exchangeable cations (K, Mg, Ca, Na) were determined by leaching soil samples with  $1\text{M}$   $\text{NH}_4\text{OAc}$ , pH 7.0, according to the procedure described by Blakemore *et al.* (1977). Additionally, CEC of the soils was determined using  $1\text{M}$   $\text{KCl}$  (at field pH). Only 3 replicates per site were analysed.

#### 5.2.4.5 pH

For soil samples (air-dried), the soil:water ratio (w/w) used was 1:2.5, and for L+F+H samples, it was 1:10 (Blakemore *et al.*, 1977). The pH was determined with glass electrodes.

#### 5.2.4.6 Bray-Phosphorus

"Available" phosphate (referred to as Bray-P in the present study ) levels were determined by the Bray No. 2 method (Bray and Kurtz, 1945).

### 5.3 RESULTS AND DISCUSSION

#### 5.3.1 Forest Floor Accumulation

Total mass of the forest floor (L+F+H) in native forest and radiata plantation sites studied ranged from 25 to 464 tonnes/ha and 9 to 79 tonnes/ha respectively (Table 5.3.1.1). High values (380 and 464 tonnes/ha) were obtained for the two native sites in the West Coast. With the exception of these two sites and their adjacent radiata sites, no significant difference was observed in the mass of forest floor between adjacent stands of native and radiata pine.

The F+H horizon was responsible for the bulk of the total forest floor (L+F+H) mass, and accounted, on the average, 89 percent in native forest stands and 78 percent in radiata pine stands. As the sampling of the forest floors was undertaken in late spring (mid-October to end of November), these values represent estimates which are relatively lower than at other times of the year. Previous results (Section 3.3.2) obtained in the present study have shown that early spring represents the period of peak litter-fall for both beech and radiata pines. Thus, present estimates for the mass of the L horizon are likely to be close to the maximum

TABLE 5.3.1.1 Mass and pH value of forest floor in native and radiata pine forest stands

Forest/Site		Mass (tonnes/ha)		F+H
		Litter layer	L+F+H layer	pH
GRANVILLE	BEECH	5.8 ± 1.5 <sup>@</sup>	380 ± 108	3.2 - 3.5(3.3) <sup>#</sup>
	RAD1955	3.9 ± 1.1	15 ± 4	4.3 - 4.8(4.5)
HOCHSTETTER	PODOCARP	6.9 ± 4.7	464 ± 100	3.3 - 3.7(3.5)
	RAD1967	-	9 ± 5	5.1 - 5.8(5.4)
HANMER	BEECH	7.7 ± 4.9	64 ± 7	4.1 - 4.7(4.4)
	RAD1960	5.8 ± 2.9	25 ± 10	4.8 - 5.2(4.9)
	BEECH	11.0 ± 3.6	76 ± 45	4.1 - 4.6(4.4)
	RAD1926	9.0 ± 3.3	22 ± 11	4.7 - 4.8(4.8)
NELSON	BEECH	9.0 ± 2.7	27 ± 19	4.8 - 5.4(5.1)
	RAD1967	6.1 ± 2.6	79 ± 8	4.9 - 5.1(5.0)
	RAD1947	4.9 ± 3.6	19 ± 6	4.9 - 5.2(5.0)
	RAD1956reg.	5.4 ± 1.3	40 ± 27	4.9 - 5.6(5.2)
PEEL	PODOCARP	-	25 ± 13	5.2 - 5.4(5.3)
	RAD1937	7.5 ± 2.3	44 ± 27	3.7 - 4.0(3.8)

@ mean values ± 95 percent confidence intervals

# range of values, mean value given in parenthesis



of the year. However, it is not known whether this is the same with podocarp forests which appear to have peak litter-fall in summer (Levett, 1978).

Depths of L and F+H horizons of forest floor (Table 5.3.1.2) show large variation within stands. Values given in Table 5.3.1.2 are depths of accumulation on the predominant slope and therefore do not take into account areas where there was little or no forest accumulation, such as on mounds and steep slopes. The variation in the depths of L and F+H layers, in particular the latter, was also governed by the micro-topography of each sampled area of the forest floor. Deeper layers were measured in depressions of the mineral soil. In view of the large variability in measured forest floor depths, no comparison is made between depths of forest floors of beech and radiata sites. The results of the present study, however, help to illustrate the difficulty, and frequently, the inaccuracy associated with this approach in quantifying forest floor accumulation.

In general, depth is not a good index of relative organic matter accumulation. This is demonstrated by bulk density measurements. The mean bulk densities of L and F+H in the forest floor of beech stands were generally greater than those of radiata stands (Table 5.3.1.2). Thus, for an equal depth, there would be a larger mass of organic matter in the beech stand than in the radiata. On this basis, it is necessary to use mass estimates instead of depths in any comparative studies on organic matter accumulation.

This effect is primarily due to the difference in the shape of the litter. Beech leaves are flat and allow a

TABLE 5.3.1.2 Depth (cm) and bulk density (g/cm<sup>3</sup>) of L, F+H and top-soil (0-20cm) of native and radiata pine forest stands

Forest/Site		L layer		F+H layer		Fine Soil ( < 2mm )	Total Soil
		Depth	Bulk Density	Depth	Bulk Density	Bulk Density	Bulk Density
GRANVILLE	BEECH	1.0-2.0 <sup>@</sup>	0.03-0.05(0.04) <sup>#</sup>	25.0-35.0	0.07-0.10(0.09)	0.33-0.75(0.61)	0.64-0.86(0.78)
	RAD1955	1.0-2.5	0.02-0.03(0.02)	0.5- 2.5	0.05-0.08(0.07)	0.50-0.86(0.67)	0.67-1.15(0.93)
HOCHSTETTER	PODOCARP	0.5-2.5	0.05-0.07(0.06)	20.0-25.0	0.12-0.15(0.14)	0.41-0.72(0.53)	0.44-0.75(0.57)
	RAD1967	included in F+H		0.5- 2.0	0.05-0.10(0.08)	0.59-0.82(0.68)	0.87-1.41(1.16)
HANMER	BEECH	0.5-3.0	0.05-0.08(0.06)	3.0- 5.0	0.13-0.19(0.15)	0.89-1.09(1.01)	1.04-1.32(1.16)
	RAD1960	1.0-3.0	0.03-0.04(0.03)	1.0- 4.0	0.05-0.18(0.08)	0.55-0.83(0.72)	1.04-1.31(1.17)
	BEECH	0.5-2.0	0.07-0.09(0.08)	3.0- 5.0	0.08-0.19(0.12)	0.79-0.89(0.80)	0.84-1.15(0.96)
	RAD1926	0.5-2.5	0.03-0.08(0.06)	0.5- 3.0	0.09-0.12(0.09)	0.99-1.55(1.32)	1.34-1.69(1.53)
NELSON	BEECH	1.0-2.5	0.04-0.10(0.06)	1.0- 4.0	0.04-0.13(0.08)	0.45-0.77(0.64)	1.09-1.94(1.38)
	RAD1967	0.5-3.5	0.02-0.07(0.04)	1.0-10.0	0.07-0.17(0.12)	0.39-0.75(0.55)	1.07-1.84(1.48)
	RAD1956	0.5-3.5	0.03-0.09(0.04)	0.5- 2.5	0.06-0.16(0.11)	0.72-0.97(0.84)	1.03-1.29(1.12)
	RAD1947	1.0-2.0	0.03-0.06(0.04)	2.0- 8.0	0.05-0.08(0.06)	0.35-1.37(0.76)	1.39-1.69(1.49)
	RAD1956reg.	1.0-3.0	0.03-0.07(0.05)	1.5- 4.0	0.08-0.11(0.09)	0.69-0.98(0.85)	0.93-1.16(1.06)
PEEL	PODOCARP	included in F+H		1.0- 4.0	0.06-0.11(0.09)	0.70-1.01(0.84)	0.77-1.05(0.89)
	RAD1937	1.0-2.5	0.04-0.05(0.04)	1.0- 3.5	0.11-0.25(0.17)	0.87-0.94(0.91)	0.90-0.96(0.93)

@ range of depths

# range of bulk densities, data in parenthesis refer to mean value

greater degree of compaction than would be the situation with the longer cylindrical radiata needles. In addition, there is a larger proportion of twig litter in beech stands (Section 3.3.3.4) which must contribute in some way to the overall bulk density.

Large accumulation of organic matter and its extreme variability in depths, as found in both the beech and podocarp sites in the West Coast, are not uncommon. Substantially larger accumulations have been reported in a predominantly beech forest at the Maimai Experimental Catchment areas in the West Coast (Webster, 1977). It is not known whether such large accumulations are typical of the West Coast native forests, although results obtained in the present study indicate that this feature was not common in the beech forests of other regions.

Several factors influence the formation of the forest floor within the forests studied. These include litter production, litter decomposition rates of the species and components, site properties and previous and current managerial activities (see Review Section 2.4.2).

In the present study, the results obtained (Table 5.3.1.1) suggest that management practices is the most important factor affecting forest floor accumulation. At Hanmer, there was a larger accumulation in the 16-year-old radiata stand than in the 50-year-old stand (at sampling) despite the considerably younger trees in the former stand. The 16-year-old radiata stand had previously been thinned to waste from 500 to 250 st/ha (about 3 years prior to sampling) and consequently a substantial amount of organic

matter was deposited on the site. This also helps to account for the greater accumulation in this stand than in other comparatively older radiata stands. Prior to replanting with radiata pines, the forest floor of these two sites at Hanmer was destroyed by burning (P. Hay, pers. comm.).

At Nelson, accumulations in some of the radiata stands used were generally larger than those found in the beech stand. However, except for the 9-year-old radiata stand (at sampling), these differences were not statistically significant. This is primarily attributed to the inclusion of the forest floor from the previous vegetation. After clear-cutting of the former vegetation (beech), waste cuttings were not burned off before replanting of radiata pines (D. Cooper, pers. comm.). This effect resulted in a considerable amount of organic matter remaining on the sites.

The precise reason underlying the comparatively large accumulation in the 9-year-old radiata stand at Nelson is unknown, although the dense stand stocking is suspect (1850 st/ha compared to 600 st/ha in the 1947-planted radiata and 870 st/ha in the 1956-planted radiata stands). No regression analysis was carried out between accumulation and tree density or age, because it is uncertain whether the amounts of organic matter left on each site from the previous vegetation were initially similar before replanting. Thus, any correlation may not reflect the effect of tree density.

Large differences observed in the amounts of accumulated organic matter between the native stands and

corresponding radiata stands in the West Coast is likely to be due to the effect of burning, as burning is commonly carried out in the West Coast forests. As a result of this, fire had destroyed the forest floor of the previous vegetation.

Results of litter production (Section 3.3.1) and litter decomposition rates (Section 4.3.1) obtained in the present study also support the view that management practices is the predominant factor affecting the amount of accumulated organic matter. Litter production at Granville, Hanmer and Nelson were found to be greater in beech than adjacent radiata stands (Section 3.3.1). However, there were generally only small and inconsistent differences in rates of litter decomposition between beech (leaf + twig) and radiata (needle) litters. Therefore, based on these results, a larger accumulation of organic matter would be expected in the beech stands studied. This was not found to be the case at Hanmer and Nelson where management effects greatly affected the accumulation results.

Forest floor accumulation in organic matter is also influenced by the slopes of stands and wind currents which may cause a downslope movement of litter. The steepness of the slopes vary between the stands (Appendix I) and although the sites have similar aspect, the prevailing wind current is governed by the canopy of the trees. Thus, the extent of litter movement would differ between sites. However, exactly how these factors interact to influence the forest floor accumulation over the long term at each stand, is uncertain. This aspect needs to be included in any future forest floor characterization studies.

### 5.3.2 Chemical Concentration and Content of Forest Floor

Carbon and nutrient concentrations and contents in the forest floor of the forest stands studied are given in Table 5.3.1.3 and 5.3.1.4 respectively. Corresponding results for the top-soils in these stands are shown in Table 5.3.1.6 and 5.3.1.7 respectively.

For each forest, consistently higher carbon and nutrient concentrations were not encountered in the forest floor of one species compared with the other. However, some notable points are worth mentioning in the data given in Table 5.3.1.3. Potassium and Ca concentrations in the forest floor of the native stands in the West Coast were markedly lower than those in the forest floor of their adjacent radiata stands and also stands of other regions. This result may be explained by the distribution of nutrient elements at different depths of the forest floor in the native stands of the West Coast.

The above effect is illustrated by the results obtained from the beech stand at Granville (Table 5.3.1.5). Potassium and Ca, and apparently P, were found in decreasing concentrations with increasing depths of the forest floor. For P, its concentration in humus at depths greater than 25cm was closely similar to that in fresh litter. Among the cations studied, Ca showed the greatest decline in concentration with depth of forest floor and in the transformation from fresh litter to humus (from 0.87 percent decreasing to 0.01 percent). This loss was reflected in the low pH of the humus (pH 3.3) compared to that of fresh litter (pH 4.1).

TABLE 5.3.1.3 Percentages of carbon and nutrient concentrations in forest floor (LFH) of native and radiata pine forest stands

Forest/Site		C	N	P	K	Mg	Ca
GRANVILLE	BEECH	41.2 ± 2.0 <sup>#</sup>	1.11 ± 0.12	0.043 ± 0.005	0.04 ± 0.02	0.15 ± 0.04	0.11 ± 0.06
	RAD1955 <sup>@</sup>	34.4 ± 8.9	1.06 ± 0.17	0.057 ± 0.010	0.19 ± 0.07	0.14 ± 0.03	0.32 ± 0.05
HOCHSTETTER	PODOCARP	38.7 ± 5.5	1.35 ± 0.17	0.048 ± 0.004	0.08 ± 0.02	0.22 ± 0.02	0.15 ± 0.04
	RAD1967	27.3 ± 12.9	0.74 ± 0.32	0.069 ± 0.014	0.43 ± 0.20	0.30 ± 0.06	0.46 ± 0.16
HANMER	BEECH	32.8 ± 6.9	0.86 ± 0.24	0.083 ± 0.008	0.20 ± 0.07	0.20 ± 0.09	0.65 ± 0.31
	RAD1960	43.9 ± 2.2	1.56 ± 0.14	0.102 ± 0.014	0.16 ± 0.08	0.21 ± 0.04	0.77 ± 0.04
	BEECH	36.6 ± 8.6	0.92 ± 0.16	0.088 ± 0.007	0.15 ± 0.04	0.17 ± 0.06	0.79 ± 0.14
	RAD1926	39.7 ± 3.0	0.99 ± 0.06	0.075 ± 0.012	0.17 ± 0.05	0.17 ± 0.02	0.67 ± 0.24
NELSON	BEECH	35.7 ± 7.9	0.84 ± 0.12	0.076 ± 0.008	0.15 ± 0.04	0.15 ± 0.03	1.43 ± 0.18
	RAD1967	14.8 ± 6.6	0.66 ± 0.41	0.067 ± 0.017	0.30 ± 0.05	0.25 ± 0.03	0.60 ± 0.20
	RAD1956	32.8 ± 0.8	0.99 ± 0.06	0.076 ± 0.011	0.19 ± 0.01	0.20 ± 0.02	0.86 ± 0.07
	RAD1947	43.8 ± 2.7	1.26 ± 0.20	0.093 ± 0.022	0.12 ± 0.03	0.18 ± 0.04	1.23 ± 0.26
	RAD1956reg.	33.7 ± 5.4	0.87 ± 0.12	0.069 ± 0.004	0.15 ± 0.02	0.17 ± 0.01	0.80 ± 0.10
PEEL	PODOCARP	40.9 ± 4.1	0.90 ± 0.03	n.d.	n.d.	n.d.	n.d.
	RAD1937	34.3 ± 4.2	0.99 ± 0.12	n.d.	n.d.	n.d.	n.d.

<sup>#</sup> Values given are mean ± 95 percent confidence intervals

<sup>@</sup> denotes *Pinus radiata* and year planted

TABLE 5.3.1.4 Carbon and nutrient contents (kg/ha) of native and radiata pine forest floors (LFH)

Forest/Site		C	N	P	K	Mg	Ca
GRANVILLE	BEECH	160,000 ± 42,000 <sup>#</sup>	4,348 ± 1,319	158 ± 36	127 ± 40	569 ± 206	322 ± 131
	RAD1955 <sup>@</sup>	5,100 ± 1,500	160 ± 60	9 ± 4	28 ± 12	21 ± 8	47 ± 11
HOCHATETTER	PODOCARP	182,000 ± 64,000	6,256 ± 1,882	209 ± 46	384 ± 124	1,065 ± 303	549 ± 110
	RAD1967	2,200 ± 700	65 ± 30	6 ± 4	44 ± 39	30 ± 22	42 ± 21
HANMER	BEECH	21,000 ± 3,600	553 ± 138	53 ± 7	128 ± 50	134 ± 64	423 ± 212
	RAD1960	10,800 ± 4,400	387 ± 168	25 ± 11	41 ± 28	52 ± 27	191 ± 73
	BEECH	29,700 ± 20,400	734 ± 470	68 ± 40	100 ± 48	116 ± 63	592 ± 366
	RAD1926	8,600 ± 4,200	215 ± 110	16 ± 7	35 ± 14	38 ± 21	133 ± 51
NELSON	BEECH	8,800 ± 4,200	215 ± 126	20 ± 12	45 ± 46	44 ± 43	367 ± 223
	RAD1967	11,700 ± 4,800	523 ± 302	53 ± 11	232 ± 27	197 ± 12	476 ± 153
	RAD1956	6,100 ± 1,700	184 ± 51	14 ± 43	35 ± 10	38 ± 12	164 ± 60
	RAD1947	17,400 ± 11,800	512 ± 384	40 ± 36	51 ± 49	67 ± 38	507 ± 410
	RAD1956reg.	11,700 ± 4,700	299 ± 111	24 ± 10	52 ± 25	58 ± 25	284 ± 140
PEEL	PODOCARP	9,600 ± 5,700	224 ± 124	n.d.	n.d.	n.d.	n.d.
	RAD1937	15,300 ± 9,800	446 ± 291	n.d.	n.d.	n.d.	n.d.

<sup>#</sup>, <sup>@</sup> As for Table 5.3.1.3.



TABLE 5.3.1.5 Mean concentrations (%) of carbon and nutrient elements in decomposing litter and in the forest floor at different depths of the beech stand at Granville

ELEMENT	Litter <sup>#</sup>		L+F+H layer	Humus layer	
	Fresh	22-months old	5 cm	5 to 25 cm	>25 cm
C	50.8	51.0	39.7	43.6	35.2
N	0.59	1.14	1.14	1.18	1.01
P	0.033	0.067	0.051	0.042	0.035
K	0.166	0.112	0.068	0.029	0.024
Mg	0.165	0.117	0.137	0.147	0.167
Ca	0.873	0.800	0.242	0.078	0.013

# weighted mean concentrations of leaf + twig litter

In contrast, Mg concentrations increased with forest floor depths, although there was no difference in its concentration between fresh litter and humus at depths greater than 25cm.

These depth trends in element concentrations observed in the present study are generally consistent with those of Gosz et al. (1976) for the forest floor in a hardwood stand at New Hampshire. Their results showed a decline in the concentrations of K and Ca with depth, while that of Mg was more variable and showed little change down the profile. Although these workers reported results for the L, F and H horizons of the forest floor, comparison between studies of the trend in element concentrations is considered not erroneous.

The concentration of nitrogen was not observed to increase with increasing depths, as might be expected with increasing stages of decomposition. In the present study, it was shown that N concentrations in litter increased continuously with decomposition over a 26-month period (Section 4.3.2.1). These results therefore suggest that a continuously increasing gradient in N concentrations would probably be found in the L+F+H (5cm) fraction. At about 1.1 percent N, the concentration remained fairly constant and did not appear to change markedly with depths. Nitrogen, together with carbon and phosphorus are particularly important elements in terms of heterotroph nutrition. Thus, these elements were rapidly immobilized within the decomposing litter and humus, resulting in little or slow decrease with depth.

In general, concentrations of elements in the forest floor were found to decrease in the following order:

Native:  $C \gg N > (Ca, Mg) > K > P$

Radiata:  $C \gg N > Ca > (Mg, K) > P$

An exception to this order was found at the beech site in Nelson where Ca concentration was greater than that of nitrogen. This deviation could be attributed to the effect of the inclusion of large amounts of fresh litter in the L+F+H fraction. Litter-fall in the beech site at Nelson was shown to contain comparatively higher Ca than N and this would be reflected in the overall concentration in the L+F+H fraction.

The order of abundance of the elements studied in the forest floor of native and radiata stands follows the order:

$$C \gg N \gg Ca \gtrsim Mg \gtrsim K > P$$

except for the beech stands at Granville and Nelson where  $P > K$  and  $Ca > N$  respectively. This sequence differed from that observed in the nutrient returns by litter-fall (Section 3.3.8) where the abundance was:

Beech:  $C \gg Ca > N > K > Mg > P$

Radiata:  $C \gg N > Ca > K > Mg > P$

The discrepancy may be explained by the relative mobility of the nutrient elements, particularly K (Gosz *et al.*, 1976). This effect was discussed previously (Section 4.3.2).

With the exception of the Nelson forest, forest floors in the native stands studied had larger contents of carbon and nutrient elements when compared to those in their adjacent radiata sites. This effect is probably due to the large biomass of the forest floor in the native stands since only small apparent differences were found in the concentrations of these elements in the forest floor between species (Table 5.3.1.3).

### 5.3.3 Chemical Concentration and Content of Top-soil

The carbon and nutrient concentrations of the top-soil (0-20cm) showed no consistent differences in carbon or nutrient concentrations of one species compared with those of the other (Table 5.3.1.6). Of the nutrients, K showed the highest relative concentration and P the lowest. This pattern was found to be common in all stands of the forests studied.

The comparatively low carbon and nitrogen concentrations in the top-soil of the young radiata stand (9 years old at sampling) at Hochstetter forest is believed to be partly caused by the removal of the forest floor by burning prior to replanting with radiata pines. Furthermore, the absence of litter-fall during the early stages of stand development subsequently resulted in little transfer of organic matter and nitrogen into the top-soil horizon. This effect is evident from the negligible accumulation of litter on the mineral soil in this stand. Annual litter-fall in this radiata stand was not determined in the present study. However, data reported by Levett (1978) for a 10-year-old radiata pine stand in the West Coast region showed only very little deposition of litter in the young stand used.

Results of carbon and nutrient contents of the top-soil (Table 5.3.1.7) indicate that, except for carbon, the nutrient contents of the top-soil under radiata pines were apparently higher than those under native species. There were, however, some deviations from this observation, and these were found in the two young radiata stands at Hochstetter and Nelson. As discussed previously, this effect was due

TABLE 5.3.1.6 Percentages of carbon and nutrient concentrations in top-soil (0-20cm) of native and radiata pine forest stands

Forest/Site		C	N	P	K	Mg	Ca
GRANVILLE	BEECH	5.9 ± 2.1 <sup>#</sup>	0.18 ± 0.06	0.017 ± 0.008	0.81 ± 0.54	0.27 ± 0.40	0.30 ± 0.22
	RAD1955 <sup>@</sup>	3.3 ± 0.5	0.17 ± 0.06	0.032 ± 0.007	1.04 ± 0.30	0.22 ± 0.16	0.30 ± 0.22
HOCHSTETTER	PODOCARP	7.8 ± 2.8	0.34 ± 0.03	0.036 ± 0.004	1.81 ± 0.44	0.18 ± 0.06	0.15 ± 0.02
	RAD1967	1.6 ± 0.5	0.05 ± 0.02	0.048 ± 0.003	1.89 ± 0.10	0.44 ± 0.02	0.29 ± 0.30
HANMER	BEECH	2.7 ± 0.9	0.12 ± 0.04	0.044 ± 0.008	1.18 ± 0.18	0.65 ± 0.16	0.31 ± 0.06
	RAD1960	3.3 ± 0.1	0.24 ± 0.01	0.085 ± 0.006	1.73 ± 0.08	0.69 ± 0.02	0.51 ± 0.08
	BEECH	3.1 ± 0.7	0.15 ± 0.03	0.073 ± 0.005	1.37 ± 0.62	0.49 ± 0.24	0.35 ± 0.02
	RAD1926	2.4 ± 0.5	0.15 ± 0.01	0.061 ± 0.003	1.88 ± 0.32	0.50 ± 0.06	0.57 ± 0.02
NELSON	BEECH	3.0 ± 0.2	0.13 ± 0.02	0.039 ± 0.005	1.31 ± 0.32	0.45 ± 0.10	0.57 ± 0.12
	RAD1967	3.2 ± 2.5	0.14 ± 0.10	0.054 ± 0.009	1.55 ± 0.26	0.38 ± 0.08	0.60 ± 0.08
	RAD1956	2.5 ± 0.5	0.11 ± 0.02	0.038 ± 0.009	1.56 ± 0.62	0.57 ± 0.32	0.56 ± 0.12
	RAD1947	2.9 ± 0.9	0.12 ± 0.03	0.047 ± 0.003	1.54 ± 0.10	0.40 ± 0.04	0.64 ± 0.08
	RAD1956reg.	2.6 ± 0.5	0.11 ± 0.03	0.029 ± 0.006	1.28 ± 0.16	0.29 ± 0.04	0.54 ± 0.04
PEEL	PODOCARP	6.2 ± 1.5	0.38 ± 0.10	0.063 ± 0.010	1.44 ± 0.14	0.43 ± 0.06	0.92 ± 0.02
	RAD1937	6.2 ± 0.9	0.39 ± 0.04	0.090 ± 0.003	1.29 ± 0.04	0.55 ± 0.04	0.71 ± 0.02

# Values given are mean ± 95 percent confidence intervals

@ denotes *Pinus radiata* and year planted

TABLE 5.3.1.7 Carbon and nutrient contents (kg/ha) of top-soil (0-20cm) in native and radiata pine forest stands

Forest/Site		C	N	P	K	Mg	Ca
GRANVILLE	BEECH	67,700 ± 21,500 <sup>#</sup>	2,122 ± 706	202 ± 92	8,287 ± 3,769	2,551 ± 1,007	2,981 ± 943
	RAD1955 <sup>@</sup>	43,700 ± 11,600	2,168 ± 344	429 ± 151	13,806 ± 4,760	2,991 ± 2,051	3,939 ± 2,473
HOCHSTETTER	PODOCARP	78,900 ± 15,300	3,385 ± 455	373 ± 79	20,849 ± 13,888	2,020 ± 666	1,694 ± 947
	RAD1967	21,700 ± 7,500	721 ± 351	648 ± 95	25,170 ± 1,249	5,873 ± 405	3,806 ± 3,048
HANMER	BEECH	54,000 ± 16,900	2,410 ± 815	879 ± 147	22,847 ± 3,311	12,580 ± 134	6,184 ± 1,758
	RAD1960	47,200 ± 9,200	3,387 ± 601	1,220 ± 183	27,081 ± 4,650	10,730 ± 2,167	8,012 ± 692
	BEECH	49,500 ± 9,200	2,353 ± 415	1,164 ± 150	31,882 ± 9,758	7,844 ± 3,801	5,755 ± 647
	RAD1926	62,300 ± 3,400	3,946 ± 652	1,605 ± 311	52,457 ± 17,109	13,849 ± 2,549	15,704 ± 3,404
NELSON	BEECH	38,600 ± 6,800	1,694 ± 240	501 ± 158	18,973 ± 6,258	6,477 ± 1,718	8,157 ± 2,362
	RAD1967	20,500 ± 8,600	962 ± 424	584 ± 142	17,171 ± 9,273	4,326 ± 3,082	6,671 ± 3,449
	RAD1956	42,200 ± 9,300	1,812 ± 264	638 ± 167	28,169 ± 9,920	10,293 ± 4,724	10,060 ± 1,225
	RAD1947	42,300 ± 15,300	1,902 ± 1008	724 ± 305	23,074 ± 20,136	6,056 ± 5,552	9,552 ± 8,303
	RAD1956reg.	45,200 ± 15,300	1,916 ± 450	495 ± 112	20,544 ± 8,397	4,622 ± 1,897	8,574 ± 3,051
PEEL	PODOCARP	102,000 ± 13,700	6,285 ± 1095	1,091 ± 543	24,349 ± 6,066	7,395 ± 2,350	15,788 ± 4,841
	RAD1937	113,200 ± 13,300	7,034 ± 624	1,617 ± 203	23,135 ± 2,433	12,844 ± 1,098	9,099 ± 749

<sup>#</sup>, <sup>@</sup> As for Table 5.3.1.6

mainly to the absence of litter input in the early years of stand development.

Of the available nutrients (Bray-P, K, Mg, Ca), the greatest difference in relative amounts between top-soil of native species and radiata pines appears to occur in the Bray-P. Higher levels of Bray-P were encountered in top-soils of radiata stands (range: 3.0 to 25.9  $\mu\text{g/g}$ ; mean: 11.8  $\mu\text{g/g}$ ) than those in native stands (range: 0.4 to 5.2  $\mu\text{g/g}$ ; mean: 2.5  $\mu\text{g/g}$ ). In terms of potential chemical limitations of soils for radiata pine growth (Adams and Mew, 1976), the top-soils in the stands used in the present study may be rated accordingly:

<u>Rating</u>	<u>Forest and Stand</u>
Severe limitation	Granville beech, Hochstetter podocarp, Hanmer beech(i), Nelson beech
Intermediate	Hanmer beech(ii), Nelson radiata <sup>reg.</sup> , Granville radiata, Hanmer radiata(ii), Nelson radiata(1956)
Negligible limitation	Hochstetter radiata, Hanmer radiata(i), Nelson radiata(1967), Nelson radiata(1947)

The results obtained in the present study therefore suggest that a rating of severe limitation was common among the top-soils of the native forests in many regions of the South Island. Severe limitation ratings of the soils from the two native forest stands in the West Coast is supported by the data of Adams and Mew (1976) which indicate a similar status for Bray-P levels in similar and other soil types of the Grey Valley on the west coast of the South Island.

Levels of exchangeable cations (K, Mg, Ca) in the top-soil (0-20cm) of radiata stands were generally higher than those of the native forest (Tables 5.3.8.1.1 and 5.3.8.1.2). However, an exception to this was found in the Peel Forest stands, where the levels of these exchangeable cations in the top-soil of the radiata stand were considerably lower than those in the top-soil of the nearby podocarp forest stand. The cause of this deviation is unknown although the pH effect is suspect. Lower pH conditions were found in the L+F+H horizon and top-soil of the radiata stand compared with that in the corresponding horizon of the podocarp stand. This relativity in pH was in a reversed order compared with that found in both L+F+H and top-soil horizons of the forests in other regions used in the present study. This effect probably reflects the previous human activities that have taken place in the radiata stand which formed part of a sheep grazing land.

Among the cations, levels of exchangeable sodium was most constant between stands and between forests. In terms of relative levels, Ca was highest and Na lowest. Potassium and Mg were intermediate. In general, the levels of exchangeable cations studied (K, Mg, Ca) may be considered to be in the low to very low status according to the cation exchange ratings used for New Zealand soils (Miller, 1968).

#### 5.3.4 Concentrations of Some Organic Litter

##### Constituents in Forest Floor and Top-soil

Concentrations of the ether-extractable fraction (EE), and water-soluble carbohydrates (WSC) and polyphenols (WSP)



TABLE 5.3.1.8.1 Cation exchange capacity, exchangeable cations, pH and Bray-P of top-soil (0-20cm) in native and radiata pine forest stands at Granville, Hochstetter and Hanmer

Forest/Site	CEC (m.e.%)		Exchangeable Cations (m.e.%)				pH(H <sub>2</sub> O)	Bray - P (µg/g)
	(NH <sub>4</sub> Ac)	(KCl)	K	Mg	Ca	Na		
GRANVILLE								
BEECH	17.7-38.7 <sup>#</sup> (28.3)	12.0-22.5 (17.2)	0.06-0.14 (0.10)	0.18-0.45 (0.33)	0.11-0.12 (0.12)	0.10-0.15 (0.13)	4.0-4.6 (4.2)	0.2-0.7 (0.4)
RAD1955	10.5-18.5 (14.9)	7.2-13.8 (11.1)	0.08-0.41 (0.22)	0.12-0.20 (0.16)	0.17-0.43 (0.38)	0.06-0.08 (0.07)	4.2-4.9 (4.5)	0.3-10.2 (3.1)
HOCHSTETTER								
PODOCARP	24.8-39.8 (32.2)	15.2-18.2 (17.1)	0.17-0.26 (0.22)	0.26-0.45 (0.33)	0.03-0.06 (0.04)	0.18-0.23 (0.21)	4.1-4.7 (4.3)	0.3-0.4 (0.4)
RAD1967	6.3-9.5 ( 7.3)	6.5-7.5 ( 6.9)	0.23-0.33 (0.27)	0.20-0.44 (0.32)	0.57-1.74 (1.07)	0.02-0.03 (0.03)	5.5-5.7 (5.6)	12.2-27.5 (19.0)
HANMER								
BEECH	21.7-24.0 (23.3)	20.7-26.8 (23.4)	0.29-0.39 (0.33)	0.17-0.25 (0.21)	0.27-0.39 (0.35)	0.05-0.08 (0.07)	4.8-5.2 (5.0)	0.3-4.1 (1.5)
RAD1960	21.7-22.0 (21.9)	14.8-17.2 (16.3)	0.75-0.77 (0.76)	0.90-1.04 (0.96)	2.73-3.35 (2.99)	0.07-0.09 (0.08)	5.3-5.5 (5.4)	19.2-29.9 (25.9)

# range of values; data in parenthesis refer to the mean value

TABLE 5.3.1.8.2 Cation exchange capacity, exchangeable cations, pH and Bray-P of top-soil (0-20cm) in native and radiata pine stands at Hanmer, Nelson and Peel Forest

Forest/Site	CEC (m.e.%)		Exchangeable Cations (m.e.%)				pH(H <sub>2</sub> O)	Bray-P (µg/g)
	(NH <sub>4</sub> Ac)	(KCl)	K	Mg	Ca	Na		
BEECH	18.3-23.5 <sup>#</sup> (21.1)	14.3-19.0 (16.3)	0.16-0.27 (0.22)	0.14-0.22 (0.17)	0.09-0.26 (0.16)	0.04-0.11 (0.07)	4.8-5.5 (5.1)	4.2-6.4 (5.2)
RAD1926	15.6-17.5 (16.5)	12.5-14.7 (13.8)	0.26-0.32 (0.29)	0.65-1.10 (0.81)	2.27-2.94 (2.50)	0.04-0.09 (0.07)	5.3-5.8 (5.5)	3.4-7.1 (5.1)
NELSON								
BEECH	19.0-20.8 (19.9)	17.2-18.2 (17.6)	0.13-0.45 (0.25)	0.35-0.58 (0.49)	0.62-2.61 (1.31)	0.05-0.10 (0.08)	4.6-5.2 (4.8)	0.4-2.8 (1.3)
RAD1967	13.5-15.0 (14.3)	10.3-11.8 (11.0)	0.20-0.62 (0.34)	0.33-0.76 (0.52)	0.86-2.03 (1.44)	0.05-0.06 (0.05)	5.2-5.3 (5.2)	5.6-39.7 (20.0)
RAD1956	16.5-17.5 (16.8)	12.8-14.5 (13.9)	0.27-0.54 (0.42)	0.72-0.92 (0.81)	1.60-2.22 (1.88)	0.10-0.14 (0.12)	5.1-5.3 (5.2)	2.6-6.3 (4.8)
RAD1947	12.0-15.8 (14.0)	10.2-12.9 (11.4)	0.30-0.44 (0.36)	0.88-1.12 (1.02)	1.63-2.60 (2.03)	0.04-0.07 (0.05)	5.1-5.4 (5.2)	4.6-20.7 (13.1)
RAD1956reg.	13.0-15.8 (14.4)	9.6-11.2 (10.2)	0.14-0.25 (0.19)	0.58-0.86 (0.68)	1.01-1.48 (1.20)	0.05-0.07 (0.06)	4.9-5.0 (4.9)	0.6-4.4 (3.0)
PEEL								
PODOCARP	20.3-24.8 (23.0)	14.5-20.5 (17.2)	0.39-0.44 (0.41)	0.78-1.10 (0.99)	1.46-2.68 (2.26)	0.10-0.14 (0.12)	4.1-4.8 (4.5)	n.d. -
RAD1937	26.5-30.0 (28.3)	16.1-19.1 (17.1)	0.19-0.24 (0.22)	0.13-0.18 (0.16)	0.12-0.23 (0.16)	0.07-0.11 (0.08)	4.0-4.6 (4.3)	n.d. -

# range of values; data in parenthesis refer to the mean value

TABLE 5.3.1.9 Concentrations (mg/g) of ether-extractable fraction, water-soluble carbohydrates and polyphenols in forest floor and top-soil (0-20cm) of beech and radiata pine stands at Granville, Hanmer and Nelson

Forest/Site		L+F+H Layer			Top-soil	
		Ether Extract	Carbohydrates	Polyphenols	Ether Extract	Polyphenols
GRANVILLE	BEECH	15.2 ± 1.4 <sup>#</sup>	25.5 ± 2.4	10.2 ± 1.9	0.61 ± 0.45	0.23 ± 0.11
	RAD1955	6.8 ± 1.6	15.0 ± 1.3	6.8 ± 1.5	0.34 ± 0.17	0.14 ± 0.05
HANMER	BEECH	15.9 ± 4.5	16.9 ± 5.1	6.5 ± 2.1	0.10 ± 0.08	0.06 ± 0.02
	RAD1960	8.5 ± 1.8	14.1 ± 3.7	7.1 ± 1.3	0.11 ± 0.03	0.08 ± 0.01
NELSON	BEECH	13.6 ± 2.2	20.2 ± 4.7	13.6 ± 4.2	0.39 ± 0.27	0.12 ± 0.04
	RAD1956	12.8 ± 1.8	16.4 ± 1.9	8.1 ± 1.2	0.15 ± 0.10	0.11 ± 0.02
	RAD1956reg.	9.8 ± 3.6	16.7 ± 2.5	7.6 ± 1.1	0.06 ± 0.09	0.11 ± 0.01

# mean concentration ± 95 percent confidence intervals

in forest floor and top-soil (0-20cm) in adjacent beech and radiata stands at Granville, Hanmer and Nelson are given in Table 5.3.1.9.

Except for the polyphenol concentration at Hanmer forest, the concentrations of EE, WSC and WSP in the L+F+H layer were generally higher in beech stands when compared with those in the adjacent radiata stands. The apparently higher polyphenol concentration in radiata forest floor compared with that in beech at Hanmer is attributed to a larger amount of litter materials in the forest floor of the radiata stand as a result of the recent stand thinning.

Only apparent differences were found in the EE and WSP concentrations of top-soils between adjacent beech and radiata stands. Thus, the large differences in the amounts of WSP released between beech and radiata litter (Section 4.3.3) were not reflected in the WSP concentrations of the top-soils. The results suggest that a large proportion of polyphenolic compounds released from litter must be leached through the top-soil. These data also suggest that phenolic hydroxyl groups (  $\text{>O}^-$  ) probably made about similar contributions to the cation exchange capacities of the top-soils in the beech and radiata pine stands.

#### 5.4 GENERAL DISCUSSION

Gross differences between native forests and adjacent radiata plantations in the total amounts of carbon and nutrients in forest floor and top-soil(0-20cm) were obtained in the present study. Of greater significance was the finding that larger amounts of nutrients were held in the top-soils under radiata pine than in those under native species. This differentiation between stands is clearly illustrated by data given in Table 5.3.1.10. The range and mean of ratios (ratio given by the amount of nutrient element in native stand/amount of same element in adjacent radiata stand) for forest floor and top-soil indicate that, in general, larger amounts of nutrients were accumulated in the forest floor of native stands than in those of adjacent radiata stands. However, these differences were smaller in the top-soil and for some nutrient elements (e.g. P, K, Ca), radiata stands accumulated apparently larger amounts than adjacent native stands.

It is notable that in the west coast forests, this situation also occurred despite markedly larger accumulations of biomass and nutrients in the forest floor in the native stands, compared to those in radiata stands. Therefore, it seems that the radiata pine ecosystem possesses a better ability to transport a larger proportion of organic substrates and nutrients from the forest floor to the top-soil. For some elements (e.g. P, K), this situation is related to the more rapid release rates occurring in radiata litter (Section 4.3.4.6). This apparent ability to rapidly recycle nutrients is certainly an important asset in terms of ecosystem productivity.

TABLE 5.3.1.10 Ratio (native/radiata) of carbon and nutrient contents of forest floor and top-soil (0-20cm) in native and radiata pine forest stands

Layer	C	N	P	K	Mg	Ca
L+F+H	0.5 - 82.7 <sup>#</sup> (15.4) <sup>@</sup>	0.4 - 96.2 (16.4)	0.4 - 34.8 (7.7)	0.2 - 8.7 (2.8)	0.2 - 35.5 (8.9)	0.8 - 13.1 (4.0)
Top-soil	0.8 - 3.6 (1.4)	0.6 - 4.7 (1.4)	0.5 - 1.0 (0.7)	0.6 - 1.1 (0.8)	0.3 - 1.5 (1.0)	0.4 - 1.2 (0.8)

# range of ratio

@ mean of ratio

Generally speaking, these results suggest that the nutrient status of the top-soil under radiata pines would be relatively more favourable for sustaining tree growth than would be the case with those under beech. Such a view is additionally supported by more favourable levels of exchangeable nutrient supply in top-soils under radiata compared to those under beech. However, in ecosystems where organic matter accumulation is large (as with the West Coast stands), the ability of trees to draw part of their nutrient requirement from this compartment may be also important.

The dissimilarities in levels of exchangeable cations in soils between native forest and radiata pine stands probably reflected the differences in acidity. This may have resulted from differences in quantities of  $\text{CO}_2$  and organic acid (e.g. phenolic acids) produced during decomposition. In the present study evidence was obtained indicating higher  $\text{CO}_2$  production (Section 6.3.2.1.2) and greater quantities of polyphenolic compounds released from decomposing litter (Section 4.3.3) in beech stands compared to those in radiata stands. Apparent relationships between  $\text{CO}_2$  production and pH and levels of exchangeable cations are discussed in Section 6.4.

Another result of some significance is the higher levels of Bray-P in soils of radiata than in those of native forests. This increased P availability associated with radiata pines is believed to be due to the more rapid release of P from decomposing needle litter (Section 4.3.4.6) and possibly increased P mineralization (Fisher and Stone, 1969) in the rhizosphere of radiata pines. It is not possible to ascertain

whether such increased P availability was the result of previous burning of the forest floor, since this increased P availability was also evident in the Nelson forest where such a practice was not carried out. On this basis, the relatively more favourable Bray-P availability may be a long-term effect, until perhaps when litter-fall declined to a level where the amount of phosphorus released from litter-fall drops below that of plant uptake. However, as peak production of organic matter and maximum nutrient demand by radiata pine occur early after planting (Forrest and Ovington, 1970; Madgwick, 1979), and since litter production appears to remain relatively constant at about 23 years of tree age (Section 3.3.1), it is probable that this depletion may not occur before clearfelling of the radiata pine stand at about ages 30 to 35 years (see Will, 1964).

There is insufficient evidence in the present study to suggest that higher levels of Bray-P were associated directly with age of stand, since there seems to be no obvious relationship between age and levels of Bray-P in the results obtained (Tables 5.3.1.8.1 and 5.3.1.8.2). However, stands which had been thinned (Hanmer, radiata 1960), densely stocked (Nelson, radiata 1967) and where previous burning had taken place (Hochstetter, radiata 1967) were among the stands found showing relatively high levels of Bray-P.

The possibility of plant uptake as a factor causing the differences in Bray-P levels between stands is considered to be unimportant. The sampling procedure used in the present study ensured that samples from stands of both species were obtained away from trees and likely areas of extensive root disturbances.



## 5.5 CONCLUSIONS

Total mass of the forest floors in native forest and radiata plantation stands were between 25 to 464 tonnes/ha and 9 to 79 tonnes/ha respectively. The weights of fresh litter (at maximum) accounted for about 11 and 22 percent of the total weights of respective forest floors.

Comparatively large accumulations of forest floor seem to be a frequent feature in the West Coast native stands than in stands of the other regions studied. The extent of forest floor accumulation in the stands studied appeared to be governed by management practices, which include forest floor burning and stand thinning.

In general, no significant differences were found in the carbon and nutrient (N, P, K, Mg, Ca) concentrations in the forest floors between adjacent native and radiata stands. No definite trend in the magnitude of the concentrations of these elements was observed. Concentrations of some elements such as K and Ca decreased with depths of forest floor.

The order of abundance of the elements studied in the forest floor was:

$$C \gg N \gg Ca \gtrsim Mg \gtrsim K > P$$

With the exceptions of the stands at Nelson, native stands generally had larger contents of these elements than their adjacent radiata stands.

No significant difference was found in the concentration of nutrients and carbon in top mineral soil between adjacent beech and radiata stands. Comparatively low concentrations of carbon and N in the top-soil of a 9-year-old radiata stand

was attributed to the effects of previous burning of the forest floor and the small contributions from litter-fall.

Nutrient and carbon contents of top-soil between adjacent beech and radiata stands did not differ significantly. However, higher levels of exchangeable cations and Bray-P were clearly evident in top-soils of radiata stands as compared to those in beech stands. In general, top-soil in radiata stands appeared to be more favourable, in terms of nutrient availability and sustaining tree growth, than those under native forests.

## CHAPTER 6

## CARBON AND NITROGEN MINERALIZATION

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## CHAPTER 6

## CARBON AND NITROGEN MINERALIZATION

## 6.1 INTRODUCTION

Patterns of carbon and N mineralization of forest floors determine the rate of nutrient release to forest trees and thus the production of a site. This aspect has not been studied previously in the West Coast forests. In Granville, carbon and N mineralization were measured over a period of 27 months from July 1976 to October 1978. At Larry's Creek, the effects of clearcutting and burning on carbon mineralization were also examined.

Main specific objectives of the present study were:

- (1) to measure and compare the rates of  $\text{CO}_2$  evolution and N mineralization occurring in the forest floors of beech and radiata pine stands at Granville,
- (2) to measure and compare the rates of  $\text{CO}_2$  evolution in forested, clearcut and burned plots in the beech forest at Larry's Creek,
- (3) to determine the forest floor temperatures in these two study areas, and
- (4) to examine the relationships between carbon and N mineralization, and the abiotic factors including temperature and moisture.

## 6.2 MATERIALS AND METHODS

### 6.2.1 Sites

The two main sites studied are the Granville forest and the Larry's Creek Experimental Area. Detailed descriptions of the Granville forest stands have been given in Section 3.2.1 and additional forest stand characteristics are shown in Table 6.2.1. The Larry's Creek Experimental Area is located approximately 40km N-E of Granville forest. A large scale research programme was conducted in this area, examining the effects of clearcutting and burning on nutrient cycling (Phillips, 1981). The beech forest had been clear-cut in May 1976 and selected plots were burned in February 1977.

### 6.2.2 Experimental Procedure

The apparatuses and their arrangements in the field used in the measurements of  $\text{CO}_2$  evolution, N mineralization and forest floor temperature are illustrated in Figure 6.2.2.

#### 6.2.2.1 Measurement of $\text{CO}_2$ Evolution

Rates of  $\text{CO}_2$  evolution from the forest floor were measured using 4-litre capacity plastic boxes (Figure 6.2.2), a method similar to that described by Witkamp (1966a, 1969). These boxes, with bottoms removed, were inserted into the forest floor to a depth of about 4cm. Evolution rates were measured only after allowing a 24-hour equilibrating period to reduce forest floor disturbance effect. During measurements,  $\text{CO}_2$  evolved was absorbed in 5ml 2.0M NaOH and

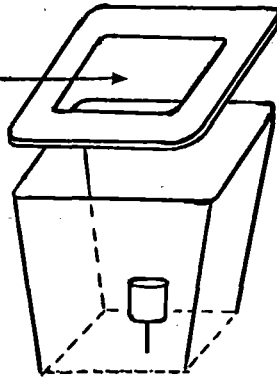
TABLE 6.2.1 Physical and chemical description of beech and radiata pine forest stands at Granville used for the study of carbon and nitrogen mineralization

Forest stand	Soil Horizon	Forest Floor Depth (cm)	Topography		Chemical Properties				pH
			Slope	Aspect	%C	%N	C/N	Ex.Cat.#	
BEECH	L+F+H	26 to 37	20-25 <sup>o</sup>	S - W	41.1	1.11	37.1	-	3.1 - 3.5 <sup>@</sup> (3.3)
	Top-soil (0-20 cm)	-			5.9	0.18	32.2	0.66	4.0 - 4.8 (4.2)
RADIATA	L+F+H	1.5 to 5	20-25 <sup>o</sup>	S	34.4	1.06	32.5	-	4.3 - 4.8 (4.5)
	Top-soil (0-20 cm)	-			3.3	0.17	19.4	0.83	4.2 - 4.9 (4.5)

# total exchangeable cations (K, Mg, Ca, Na) in m.e. %  
 @ range of values; data in parenthesis refer to the mean

clear window to  
maintain  
natural light  
intensity

FOREST FLOOR



- (A) Apparatus used to measure  $\text{CO}_2$  evolution rates in the field

5 ml 2.0M NaOH

FOREST FLOOR

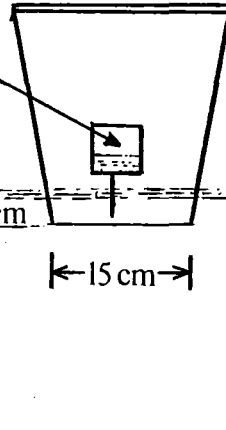
Incubation  
of humus  
and soil

4cm

15cm

8cm

Sucrose  
solution



- (B) Arrangement used to measure  $\text{CO}_2$  evolution rates, nitrogen mineralization and forest floor temperature

FIGURE 6.2.2 APPARATUS AND ARRANGEMENT USED IN THE MEASUREMENT OF  $\text{CO}_2$  EVOLUTION RATES, NITROGEN MINERALIZATION AND MEAN FOREST FLOOR TEMPERATURE



the amount absorbed was determined titrimetrically using 0.1M HCl. Excess (about 5ml) 0.5M BaCl<sub>2</sub> was used to precipitate the carbonate formed before each titration was carried out. Measurement of CO<sub>2</sub> evolution rates was made over a 24-hour period to minimize diurnal effects (Witkamp, 1969).

Two 'respirometers' and one control (consisting of a complete plastic box) were used for each experimental plot at Granville, while 10 'respirometers' and 5 controls were used for each forested, clearcut and burned plot at Larry's Creek. These 'respirometers' were randomly installed and remained on the forest floor throughout the entire length of the study period.

Internal temperature and light intensity associated with this 'respirometer' were examined prior to installation. The results are discussed in Section 6.3.2.3 .

#### 6.2.2.2 Measurement of N Mineralization

The method used in the present study is shown diagrammatically in Figure 6.2.2.2.1 . Humus (F+H) and top-soil (0-20cm) samples were obtained with a tubular probe (diameter 4.0cm) and placed separately in plastic bags. This process was repeated until 2 or 3 cores had been taken. The bags were then shaken to provide a thorough mixing of the different core samples. Visible fine roots and large stones were removed from the bags. When this was done, soil sample was then placed in a nylon tube (0.045 mm aperture) and firmly packed to a length of 20cm. A constriction was made on the tube above the soil surface

before filling the remaining length of the tube (6 to 8cm) with humus. This prepared core sample was finally placed into one of the holes made during sample collection and covered with fresh litter. The plastic bags containing the remaining humus and soil samples were sealed and kept for analysis.

The whole procedure was repeated in the preparation of other core samples. Two core samples were used for each experimental plot in the beech and radiata pine forest stands at Granville. All collected samples, fresh or field-incubated, were transported in cool bins to the laboratory. Samples were not frozen since Soulides and Allison (1961) have indicated that freezing and thawing cycles can influence mineralization.

The use of nylon tubes is a modification of the method described by Ellis (1974) where plastic vials were used to incubate soil samples in the field. This modification is required to allow drainage of soil water in order to avoid water-logging and anaerobic conditions which could result when samples are incubated over long periods (1 to 3 months). Consequently, this method will not account for loss of mineralized N due to leaching, but would allow a better contact between core samples and the forest floor.

Humus and soil ( $\leq 2\text{mm}$ ) samples were extracted for ammonium-N and nitrate-N using 2M KCl, extracting time of 1 hour and extractant:sample ratio of 10:1 (wet weight basis). Ammonium-N was determined according to the procedure described by Weatherburn (1967). Nitrate-N was initially reduced to nitrite-N using a cadmium column

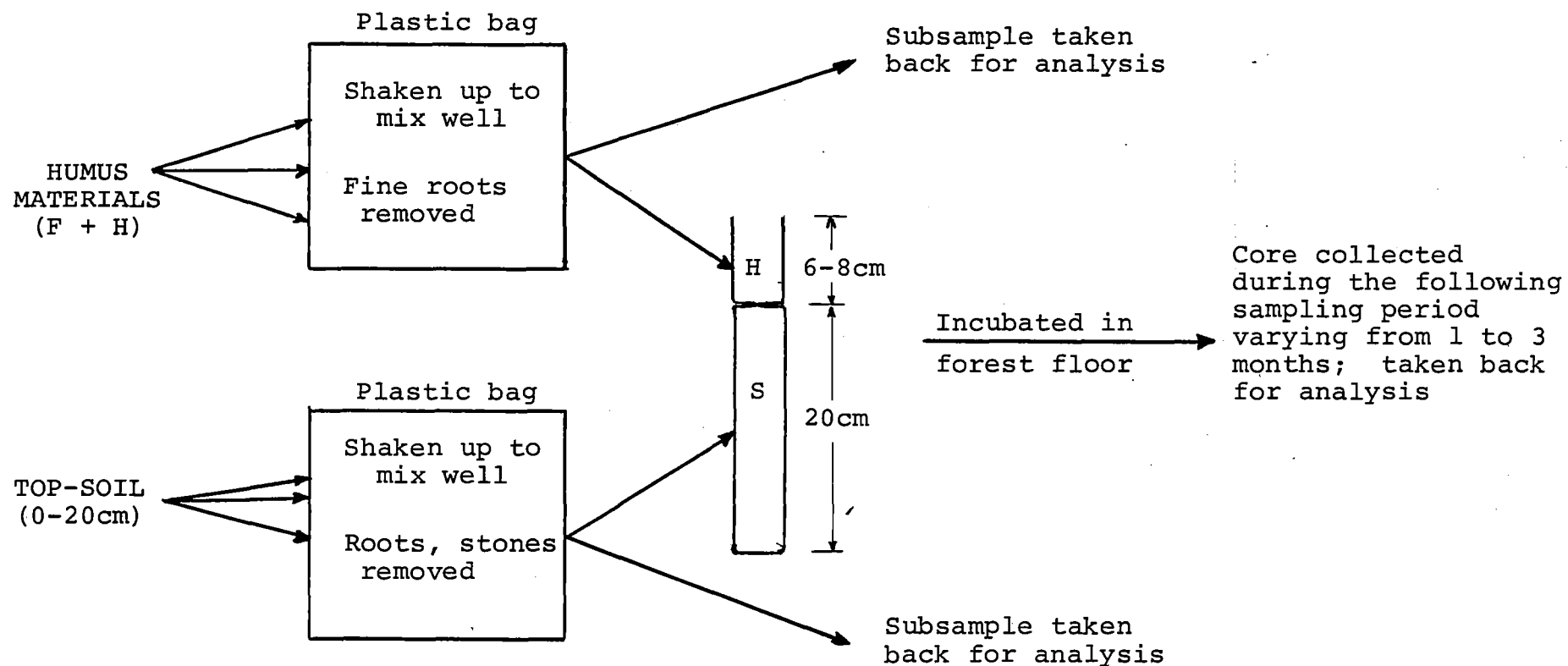
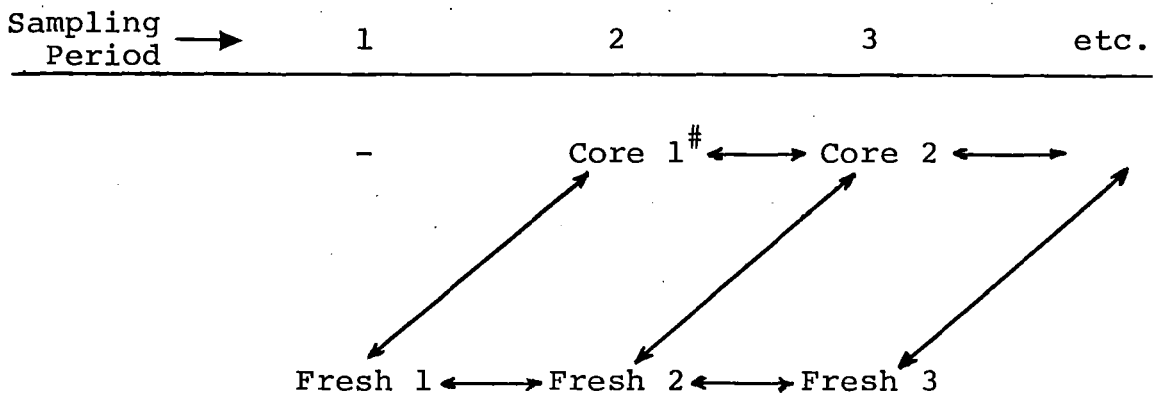


FIGURE 6.2.2.2.1 Diagrammatic representation of method used to measure nitrogen mineralization

reductor and the nitrite-N determined by the method described by Grasshoff (1969). A Technicon Auto-Analyser system was used for both determinations.

Total-N was only determined in fresh humus and soil samples, using the procedure described in Section 3.2.4.3 . All concentration values found were corrected to an oven-dried basis

Comparison of N mineralization between sampling periods is diagrammatically shown below:



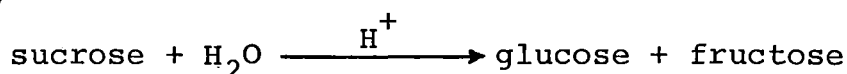
# prepared in sampling period 1 and field-incubated in the period of time between sampling 1 and sampling 2 .

The comparison between fresh samples and between core samples was used to show seasonal pattern in N mineralization in forest floor for undisturbed and disturbed samples respectively. In the latter, plant uptake of mineralized N was minimized. The comparison between core and fresh samples denoted by the same number provided an estimate of nett accumulation in mineralized N associated with that incubation period.

### 6.2.2.3 Measurement of Air and Forest Floor Mean Temperature

Daily air temperature at Granville forest was continuously monitored by New Zealand Forest Service with a thermo-hygrograph from July 1976 to June 1978 at a local meteorological station located about 1km from the two stands studied. No air temperature recordings were obtained after the dismantling of the station in June 1978.

Forest floor mean temperature was determined by the sucrose inversion method (Pallman et al., 1940; Berthet, 1960; Jones and Court, 1980). This method is based on the measurement of the rate of inversion of sucrose in acidified solution, viz.



This rate of inversion is a function of temperature and the  $\text{H}^+$  ion activity. If pH is kept constant in a buffer solution, the rate of inversion is then a function only of temperature.

#### 6.2.2.3.1 Preparation of Solution (pH 2.92)

The buffer solution was prepared by dissolving 10.5 g citric acid hydrate crystals (AR) in 50 ml of 2M  $\text{CO}_2$ -free NaOH and diluted to 250 ml; 202 ml of this solution was then made to 500 ml with 0.2M HCl.

The sucrose solution was prepared by dissolving 386.2 g of sucrose (LR) in water with 10.3 ml of 35% formaldehyde Merck and made to 500 ml.

Equal volumes of buffer solution and sucrose solution were mixed and the pH of the final solution adjusted to pH 2.92 with 0.2M HCl, if necessary.

### 6.2.2.3.2 Calculation of Mean Temperature

Angles of rotation of exposed and unexposed sucrose solutions were used to calculate the velocity constant  $K_T$ , where

$$K_T = \frac{1}{t} \log \frac{\alpha_0 - \beta_0}{\alpha - \beta_0}$$

where,

$$\beta_0 = -9^{\circ} 10$$

$\alpha_0$  = initial angle of rotation

$\alpha$  = final angle of rotation

$t$  = number of days of exposure

The absolute mean temperature (T) in that period of days (t) is given by the equation :

$$T = \frac{5854.0}{18.2878 - \log K_T}$$

The mean temperature in Celcius is  $^{\circ}\text{C} = T - 273.2$

### 6.2.2.3.3 Field Measurement

Aliquots (20 ml) of the prepared sucrose-buffer solution were dispensed into polythene tubes and frozen immediately. These tubes were thawed out only at the sites, shaken to mix the solutions well before inserting into the forest floor. Thereafter, during every sampling period, each of the exposed tubes was replaced by a fresh one. Exposed tubes were transported frozen in dry ice back to the laboratory where the contents were eventually thawed out, shaken well and read on the polarimeter. Unexposed solutions, treated similarly (i.e. frozen and thawed) were used to determine the initial angle of rotation.

#### 6.2.2.4 Moisture Content

Humus and soil moisture contents were determined on both fresh and incubated samples collected for N mineralization study. Moisture content is expressed as percent of oven-dried weight of sample.

### 6.3 RESULTS AND DISCUSSION

#### 6.3.1 Site Temperature and Moisture Index

Weekly mean air temperature (AT) increased steadily from about September to about February or March of each year (Figure 6.3.1.1). Highest AT recorded occurred at about early March in the first year ( $19.5^{\circ}\text{C}$ ) and about early February in the following year ( $26.6^{\circ}\text{C}$ ). Thereafter, the decline appears to be more abrupt and fell dramatically to a low value in the winter months of June, July and August. The lowest AT recorded in winter was  $4.2^{\circ}\text{C}$ , although there were marked fluctuations between weeks. For example, during July 1978, AT recorded during the first and second week was  $10.4^{\circ}\text{C}$  and  $5.3^{\circ}\text{C}$  respectively. Temperature measurements were only available for one complete winter because of the dismantling of the meteorological station in June 1978.

Periodic mean forest floor (8cm depth) temperatures (FT) were significantly higher in the radiata pine site than beech site during the summer months, and lower during the winter months for a corresponding time period (Figure 6.3.2.1 ). This effect is attributed to the more open

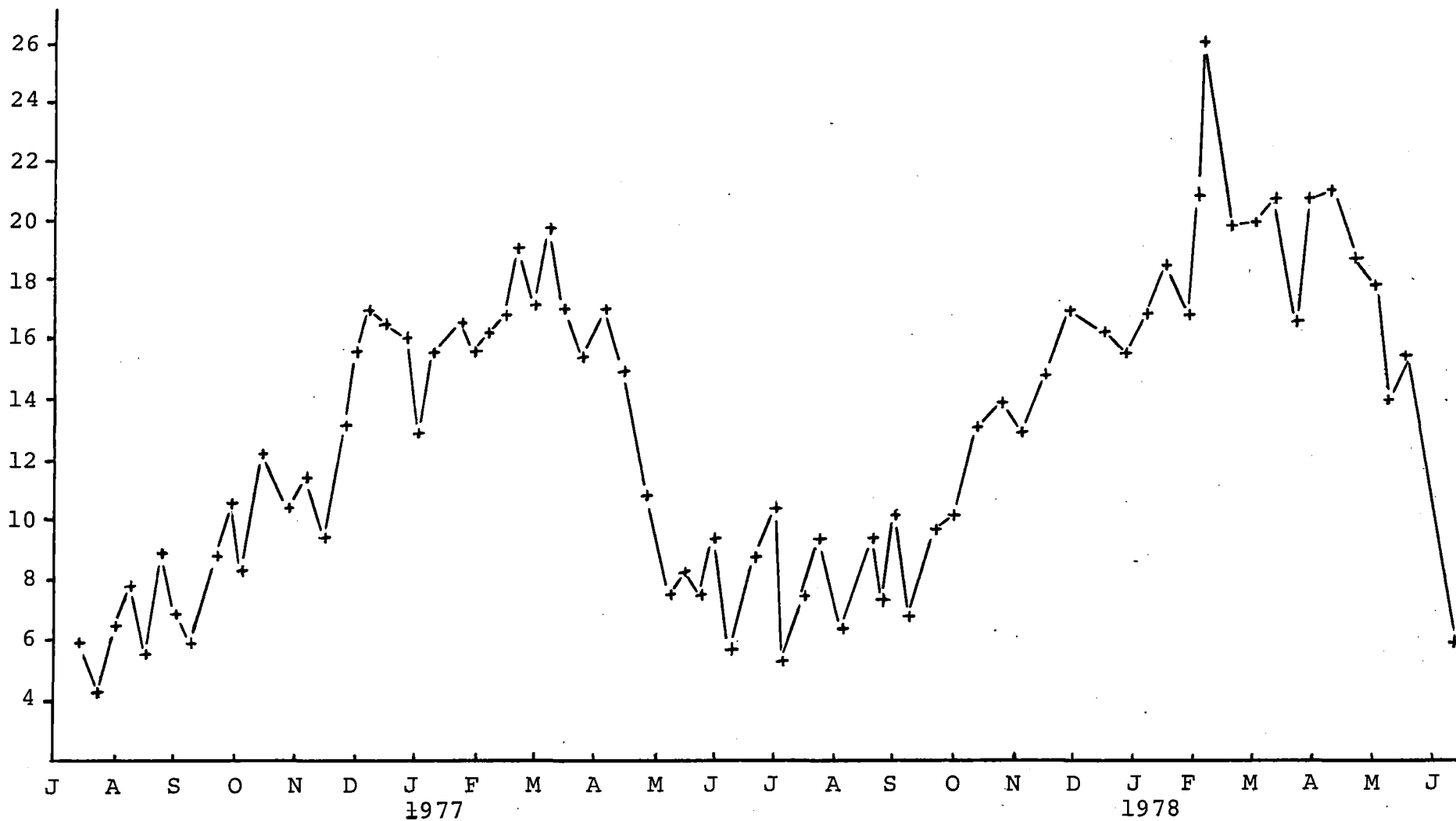


FIGURE 6.3.1.1 Weekly mean air temperature at Granville forest



canopy of the radiata pine stand compared to that of the beech stand, thereby exposing the forest floor in the radiata stand to greater insolation during summer and frosty conditions during winter. Light frosts were observed in the more exposed areas of the radiata pine stand in the early mornings during winter.

On comparison, AT and FT showed closely similar patterns (beech site,  $r = 0.921^{***}$ ; radiata site,  $r = 0.911^{***}$ ), except that the highest FT was recorded in the first year which was in a reverse order to that shown by AT (Appendix IV). However, this is probably the result of dissimilar period in which FT was measured during the first and second year. In the second year, measurements of FT were extended into early April when temperatures, as shown by AT, had already begun to decline (Figure 6.3.1.1). Therefore, measurements made in a similar time period would probably eliminate such a discrepancy. There was no indication that FT was either consistently higher or lower than AT calculated for a corresponding period in which FT was measured (Appendix IV). It is difficult to offer an explanation since several factors such as frequency of frosts in winter, precipitation and length of time of insolation interact in a complex manner to alter temperature (see Reiners, 1968).

Results (Figure 6.3.1.2) show that soil moisture contents were consistently higher in beech than radiata pine site, and these differences were frequently significant. Fluctuations in moisture contents of both humus and soil samples were more pronounced in beech than radiata site. However, no definite pattern was observed in the humus

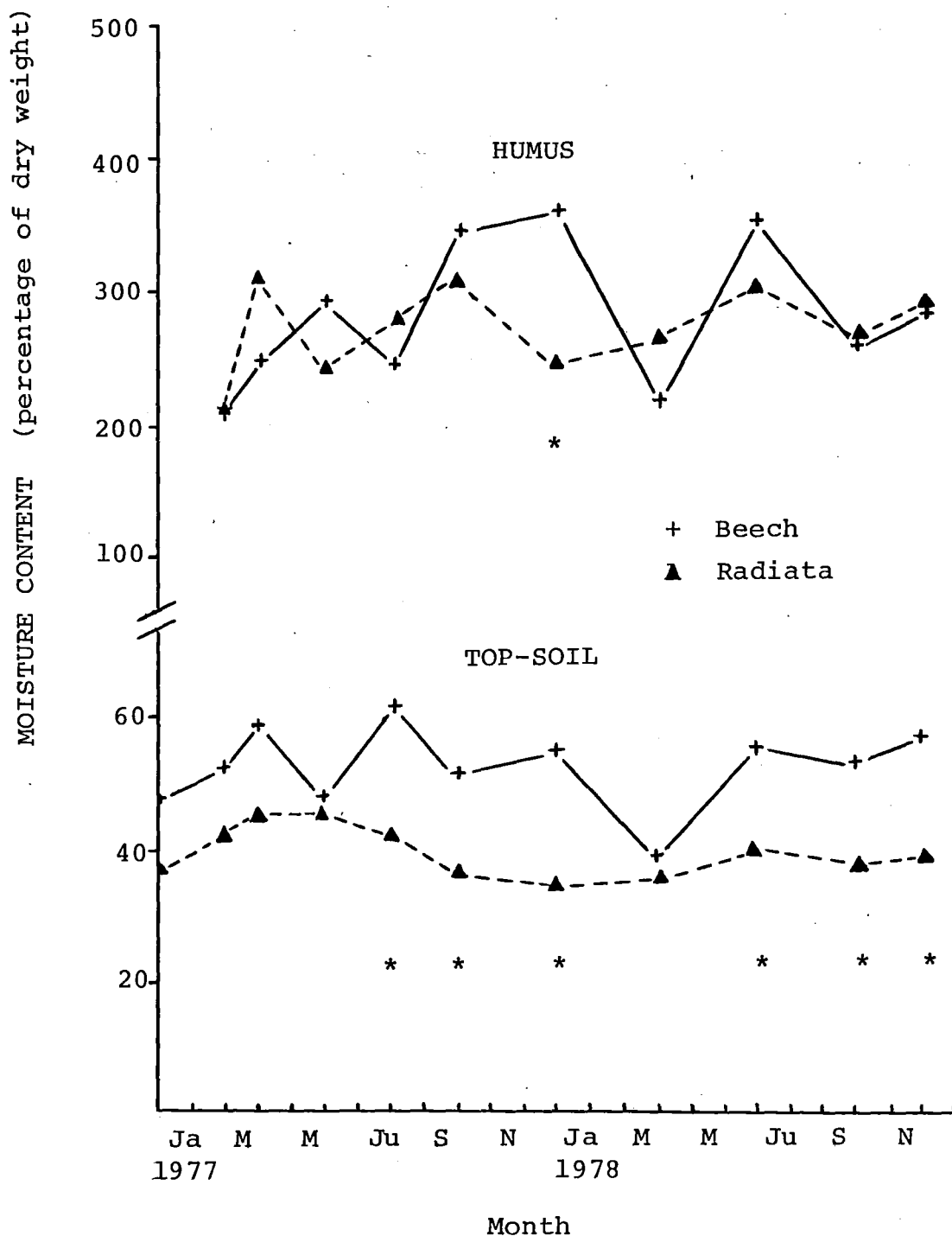


FIGURE 6.3.1.2 Humus and top-soil moisture contents in beech and radiata forest stands at Granville ( \* denotes significantly different at  $p = 0.05$ )

moisture contents between the two sites. Variability in the humus moisture contents within a sampling period was comparatively greater in radiata (C.V. range, 15 to 30%; mean, 26%) than beech site (C.V. range, 10 to 22%; mean, 17%). Variability in soil moisture contents were about the same in both sites (beech: C.V. range, 12 to 31%; mean 21%, and radiata: C.V. range, 12 to 45%; mean, 21%). The levels of moisture content in humus and soil samples of both sites were all well above the critical moisture values reported by Wiant (1967b). The favourable levels of moisture could be attributed to the effects of continuous canopies and the southerly aspects of the sites which effectively reduced moisture losses from excessive insolation and wind currents, together with the high annual precipitation this area receives ( $> 2000\text{mm}$ ).

There was no indication to suggest that the differences in soil moisture contents between the two sites were due to differences in soil properties such as the content of hydrophobic substances. The ether extract content of the soil in these sites used were found not to differ significantly (Table 5.3.1.9).

### 6.3.2 Carbon Mineralization

Results of  $\text{CO}_2$  evolution monitored at Granville forest and Larry's Creek Experimental Area are considered separately.

#### 6.3.2.1 Granville Forest

Daily rates of  $\text{CO}_2$  evolution found at the beech and radiata pine stands are shown in Figure 6.3.2.1. Detailed

results are given in Appendix IV.

#### 6.3.2.1.1 Seasonal Variation in CO<sub>2</sub> Evolution Rates

There was definite seasonal variation in the rates of CO<sub>2</sub> evolution in both sites. Peak rates occurred in summer (January to March) and low rates in winter (July and August). This pattern was found in both years although less frequent measurements of CO<sub>2</sub> evolution rates made it difficult to ascertain the rates obtained during the summer in the second year.

Rates of CO<sub>2</sub> evolution in both sites were highly correlated only with air temperature but not with other variables examined (Table 6.3.2.1). Multiple linear regressions using humus and soil moisture contents in addition to air temperature improved the correlation obtained with air temperature alone by 9 percent and 2 percent respectively, in beech and radiata site. These results therefore indicate that the seasonal variation in CO<sub>2</sub> production was mainly controlled by temperature changes. Such an influence of temperature on CO<sub>2</sub> production has also been found by other workers (e.g. Witkamp, 1966a; Anderson, 1973c; Edwards, 1975).

In general, under conditions where moisture is not limiting, such as those found in the sites used in the present study, temperature becomes the predominant factor in controlling CO<sub>2</sub> evolution rates. Moisture limits CO<sub>2</sub> production only when it is too low thus depressing microbial activity (Alexander, 1977), or too high thus possibly reducing aeration and O<sub>2</sub> supply necessary for aerobic decomposition. Carbon

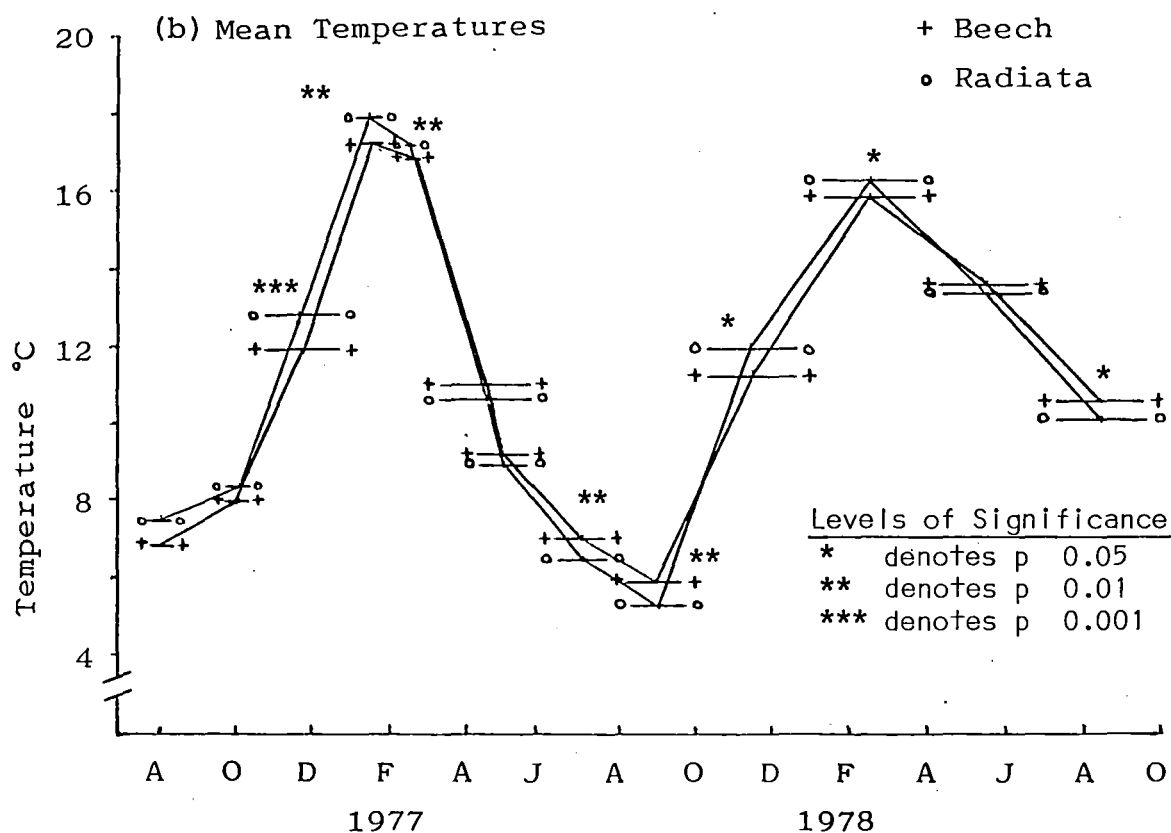
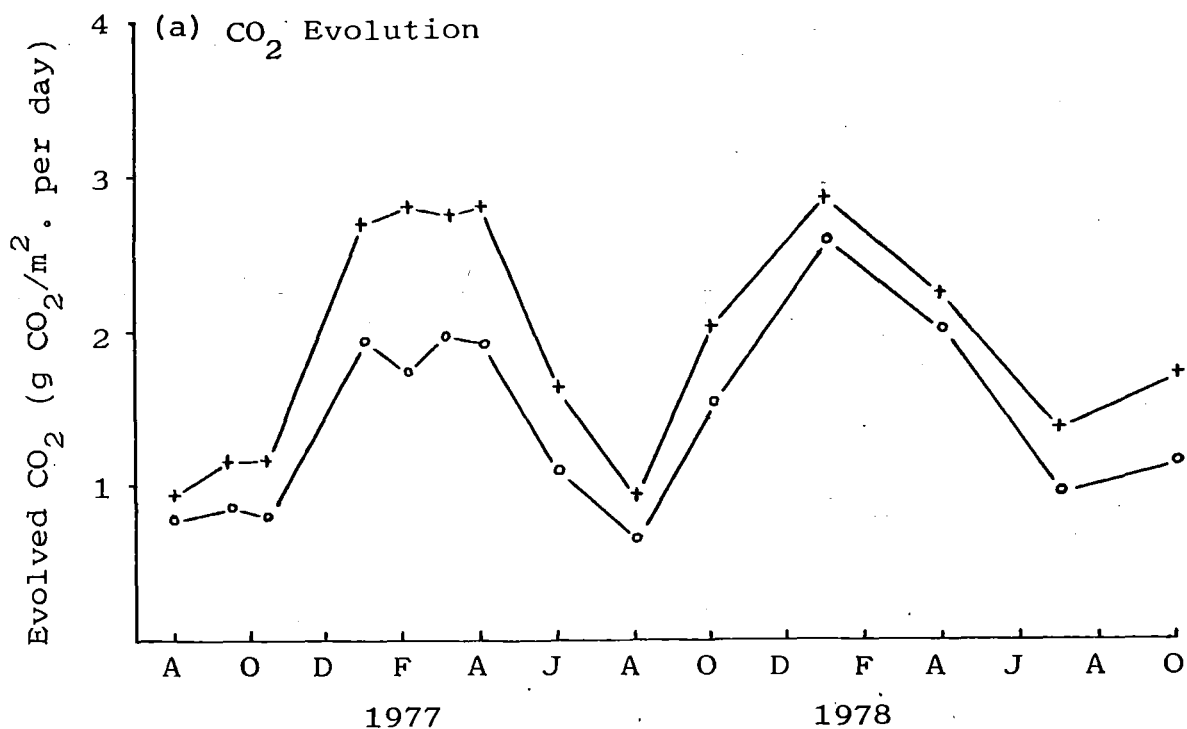


FIGURE 6.3.2.1 Carbon dioxide evolution and forest floor mean temperature recorded, in beech forest and radiata plantation at Granville

TABLE 6.3.2.1 Correlation coefficient and level of significance for the relationship between carbon dioxide evolution and either air temperature or humus and/or soil moisture content

	Beech Site	Radiata site
Air temperature	0.864***	0.897***
Humus moisture content	0.090	0.220
Soil moisture content	0.185	0.220
Humus and soil moisture content	0.192	0.344

\*\*\* Denotes significant statistically,  $p < 0.001$ ; otherwise not

dioxide production generally does not respond closely to changes in moisture content above the critical moisture level (Bartholomew and Norman, 1946; Wiant, 1967b; Platt, 1973). On this basis, it is apparent that temperature alone could be adequately used to predict  $\text{CO}_2$  production in both the sites of the present study.

The predicted patterns are very similar to those obtained from measurements in the field and they clearly show that the highest rates of  $\text{CO}_2$  evolution would normally be found in February and March (Figures 6.3.2.2 and 6.3.2.3).

Rainfall data was not considered as adequate or satisfactory as moisture content data in relating to effects on  $\text{CO}_2$  evolution. This is probably even more so in the present study where  $\text{CO}_2$  measurements were completed in a day, and were not made during rainy days. Additionally, under closed canopy, through-fall is too variable to be of importance in its correlation with  $\text{CO}_2$  evolution. Furthermore,  $\text{CO}_2$  evolution observed immediately after rain may not reflect increased respiration as  $\text{CO}_2$  in soil air may also be displaced by the percolating water (De Selm, 1952).

Although microbial activity and decomposition is commonly related to the available supply of nutrients and energy substrates (Hu et al., 1972; Behera and Wagner, 1974; Van Cleve, 1974), no apparent relationship between rates of  $\text{CO}_2$  evolution and litter-fall was observed in the sites studied. For example, high litter-fall during the autumn months was not followed by any increase in  $\text{CO}_2$  evolution rates. On this basis, it is therefore considered not unreasonable to suspect that the dramatic increase in  $\text{CO}_2$  evolution rates

found in spring primarily reflects the on-set of more favourable climatic conditions for microbial activity and  $\text{CO}_2$  production.

Although it may be questionable to derive any definite conclusions on litter-fall effect on  $\text{CO}_2$  production on the basis of the few measurements undertaken in the present study, several other workers have also noted the absence of litter-fall effect on  $\text{CO}_2$  production (e.g. Reiners, 1968; Ellis, 1969; Anderson, 1973c). It is possible that litter-fall has no immediate effect on  $\text{CO}_2$  production, but long term effects may be different. Carbon dioxide production could increase with increased accumulation of organic matter through continuous addition of litter provided steady state conditions have not been attained. In this respect, total forest floor  $\text{CO}_2$  evolution rates may be related to the amount of annual litter-fall, as suggested by Romell (1932) and Hilger (1963).

#### 6.3.2.1.2 Carbon Dioxide Evolution Rates in Beech and Radiata Pine Sites

Daily  $\text{CO}_2$  evolution rates in the beech site were consistently higher than those in the radiata pine site throughout the year (Figure 6.3.2.1 ). Rates of  $\text{CO}_2$  evolution ranged from 914 to 2855  $\text{mg CO}_2 \text{ per m}^2 \text{ per day}$  (mean 1929  $\text{mg CO}_2 \text{ per m}^2 \text{ per day}$ ) in the beech site and from 641 to 2596  $\text{mg CO}_2 \text{ per m}^2 \text{ per day}$  (mean 1427  $\text{mg CO}_2 \text{ per m}^2 \text{ per day}$ ) in the radiata site. The rates found in the present study are low when compared to those reported for other forest ecosystems (Witkamp, 1966a; Reiners, 1968; Anderson, 1973c; Edwards, 1975). Absolute comparison, however, is complicated by many



factors such as field method used and duration of measurements (see Review Section 2.5.2.2).

The maximum and minimum differences between the rates recorded in the two sites were 1068 mg CO<sub>2</sub> per m<sup>2</sup> per day (recorded in summer, AT = 16.1°C) and 140 mg CO<sub>2</sub> per m<sup>2</sup> per day (recorded in winter, AT = 8.8°C) respectively.

However, there was no appreciable seasonal pattern in the magnitude of these differences in rates of CO<sub>2</sub> evolution between beech and radiata site. In addition, most of the differences were not statistically significant (Figure 6.3.2.1 ), as a result of large variation in CO<sub>2</sub> production rates within each site (beech C.V., 27 to 49% and radiata C.V., 36 to 62%).

Large variation in CO<sub>2</sub> evolution rates of a forest floor is attributed to differing microsite properties of the forest floor horizons directly under each "respirometer". Some of these properties include pH and nutrient status of humus and soil, and organic matter content of the mineral soil (see Table 6.2.1 for description of main properties of the beech and radiata site used). These factors could interact to affect microbial population inhabiting the forest floor. Furthermore, the total CO<sub>2</sub> production rate in a forest floor is a composite of CO<sub>2</sub> production rates in litter, humus, root material and mineral soil (Edwards and Harris, 1977).

Organic matter accumulation (L+F+H) on the mineral soil surface differed substantially between the beech and radiata site used in the present study (Section 5.3.1). Accumulation in the beech site was about 25 times greater than

that recorded in the radiata site (mean values are 380 tonnes/ha in beech site and 15 tonnes/ha in radiata site). During the entire study, respiration rates found in the beech site did not, on any occasion, reflect such a large contrast. The ratios of  $\text{CO}_2$  evolution rates in beech to radiata site ranged from only 1.1 to 1.6.

In order to account for such a deviation between  $\text{CO}_2$  evolution rates in beech and radiata sites, it would be necessary to assume that a major proportion of the total  $\text{CO}_2$  evolved must have originated from the soil compartment (including root respiration), while organic residue decomposition and respiration of associated micro-organisms in the organic residue accounted for only a small proportion. Contribution to the total  $\text{CO}_2$  production by root respiration could be considerable (Macfadyen, 1970; Coleman, 1973; Minderman and Vulto, 1973; de Boois, 1974; Edwards and Harris, 1977), and as estimated by these workers, could range from 17% to 69% of the total  $\text{CO}_2$  production.

In this connection, the thickness of the L+F+H layer may be responsible for the higher rates of  $\text{CO}_2$  evolution in the beech site. For example, abundant fine roots were found within the thick humus of the beech site while hardly any fine roots were found in that of the radiata site. Since humus is less compact than mineral soil, such an effect would therefore allow a comparatively less restricted movement of  $\text{CO}_2$  from root respiration in beech site than would be the situation in the radiata site, where all the roots were found in the mineral soil.

A previous examination of differences in soil and humus

moisture contents and soil temperature between sites suggested that these abiotic factors may not be important in the explanation of dissimilarities in  $\text{CO}_2$  production found between the two sites. Differences in mean forest floor temperatures (beech  $\geq$  radiata) were generally very small, with a maximum difference recorded of only about  $0.9^\circ\text{C}$  (appendix IV).

Although differences in soil moisture contents (beech  $>$  radiata) were more frequently significant (8 out of 10 occasions) than those in the humus moisture contents (beech  $\geq$  radiata; 1 out of 10 occasions) there was no significant correlation between  $\text{CO}_2$  evolution rates and soil moisture contents (Table 6.3.2.1) to indicate that moisture had any significant effect on  $\text{CO}_2$  production rates in these sites. In addition, although greater fluctuations in moisture contents of humus and soil samples occurred in the beech site, there is little evidence to suggest that such fluctuations in moisture contents in these sites studied had approached a situation that could be considered as a drying-rewetting cycle. Birch (1958) and Sørensen (1974) have reported that such a condition has a stimulating effect on  $\text{CO}_2$  production.

The effect of plant litter chemical composition on its subsequent decomposition rates has been reported by a number of workers (e.g. Bockock, 1964; King and Heath, 1967; Hu et al., 1972; Platt, 1973; Van Cleve, 1974; Alexander, 1977). Accordingly, the rates of  $\text{CO}_2$  evolution may be influenced by the chemical composition of the different species studied. However, as the present field study did not allow the separate effect of chemical composition of

litter on  $\text{CO}_2$  evolution rates to be examined, a laboratory incubation experiment was undertaken to determine the effect of differences in chemical composition (e.g. water-soluble carbohydrates and water-soluble polyphenolic compounds) of beech leaves and radiata pine needles on soil respiration rates (Section 7.3.1).

#### 6.3.2.1.3 Carbon Inputs and Losses in Beech and Radiata Stands

Annual total carbon inputs were calculated from quarterly litter-fall. The carbon weight losses from litter were calculated using regression equations of carbon rate loss determined from litter-bag decomposition study (Section 4.3.2.2). Annual values were derived at using cumulative quarterly input and loss (Table 6.3.2.1.1). For beech, an assumption was made that the decay rates for combined leaf and twig litter found could be applied to "other" litter. This is a reasonable assumption since a considerably large proportion of the miscellaneous litter actually comprised of fragmented leaf and twig litter.

Annual total carbon losses (as  $\text{CO}_2$ ) were estimated by integrating the area under each curve of  $\text{CO}_2$  evolution rates (Figures 6.3.2.2 and 6.3.2.3), predicted from regression equations of  $\text{CO}_2$  evolution rates and air temperature. These values obtained were compared with those obtained by integrating the area under the curve of measured  $\text{CO}_2$  evolution rates. Additionally, total carbon losses in the summer quarter (January, February and March) and winter quarter (June, July and August) were also estimated.

TABLE 6.3.2.1.1 Calculation of annual carbon loss (kg/ha) from quarterly litter-fall<sup>@</sup>

SITE	Q1	Q2	Q3	Q4	Quarterly C loss	Annual C Loss
BEECH	770 <sup>#</sup>	30.8%;	10.5 <sup>#</sup>		→ 237.2	
		1088	26.2%;	7.5	→ 285.0	
			283	21.3%;	4.5	→ 60.3
				979	16.1%; 1.5	→ 157.6
						740.1
RADIATA	482	27.3%;	10.5		→ 131.6	
		1024	22.9%;	7.5	→ 234.5	
			192	18.3%;	4.5	→ 35.0
				777	13.4%; 1.5	→ 104.1
						505.2

# percentage loss; the period of decomposition in months

@ excluding branch and female cone litters

≠ quarterly litter input

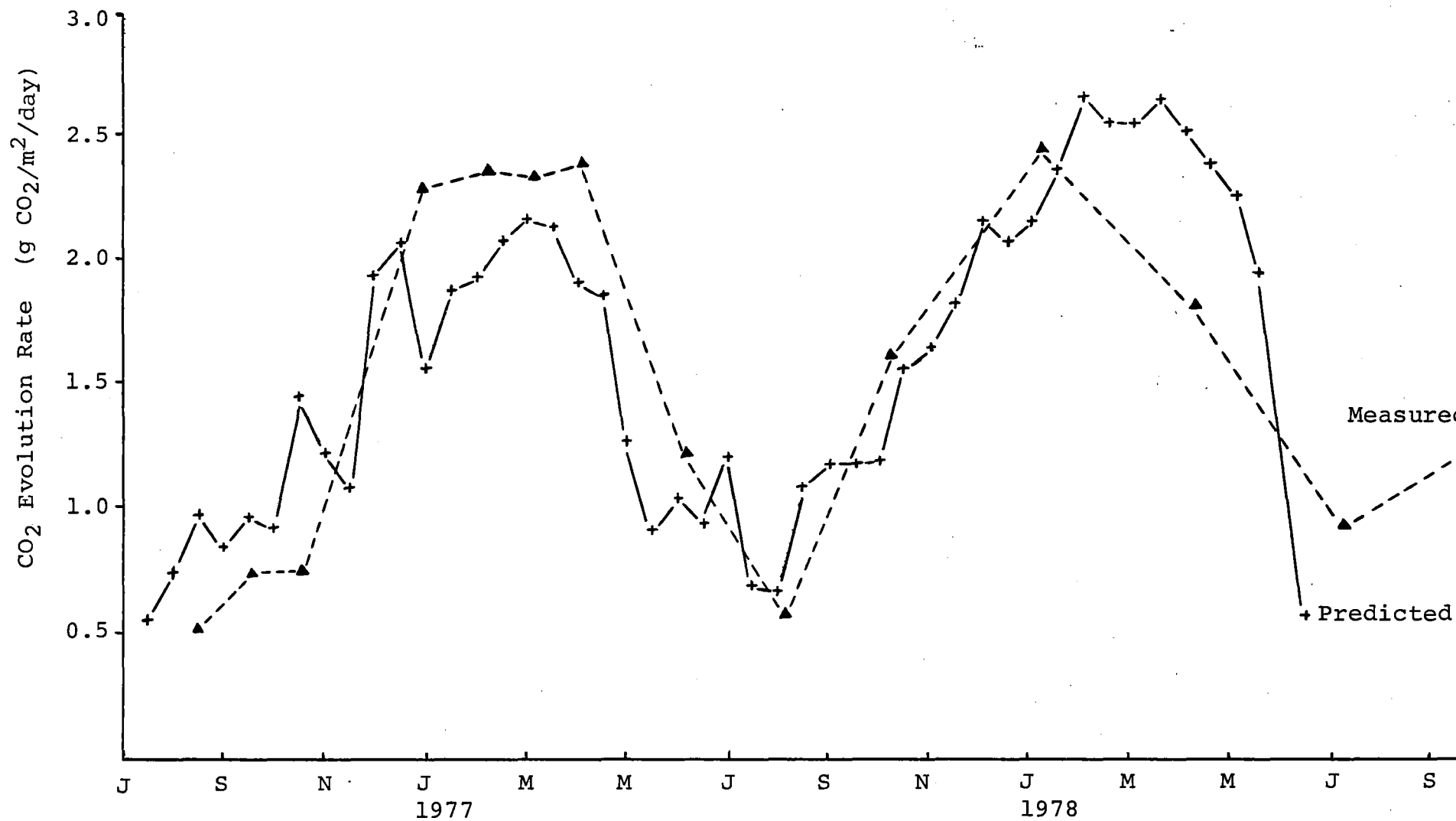


FIGURE 6.3.2.2 Seasonal variation in CO<sub>2</sub> evolution rates of beech stand at Granville



TABLE 6.3.2.1.2 Carbon input, mineralization and accumulation<sup>‡</sup> in beech and radiata pine forest stands at Granville

	Beech	Radiata pine
Carbon mineralized as CO <sub>2</sub>		
In summer (January+February+March)	581 <sup>#</sup>	448
In winter (June+July+August)	335 <sup>#</sup>	232
Annual (December 1976 to November 1977)		
From measured CO <sub>2</sub> evolution rates	2,094	1,470
From predicted CO <sub>2</sub> evolution rates	1,893	1,395
Annual input from litter-fall	3,120	2,474
Annual loss from decomposition of litter	740 (35) <sup>@</sup>	505 (34)
Amount in forest floor (L+F+H)	160,000	5,100
Amount in top-soil (0-20cm)	67,700	43,700

# Obtained from predicted CO<sub>2</sub> evolution rates

‡ All values given in kg/ha, unless otherwise stated

@ Data in parenthesis refer to annual loss as a percentage of input from litter-fall



The results (Table 6.3.2.1.2) show that both measured and predicted  $\text{CO}_2$  evolution rates did not differ markedly. This is notable considering the fact that direct measurements of  $\text{CO}_2$  evolution rates were obtained for only a few occasions throughout the year.

Based on predicted rates of  $\text{CO}_2$  evolution in a one-year period (December 1976 to November 1977), the total amounts of carbon lost as  $\text{CO}_2$  from beech and radiata forest floor were estimated to be 1893 and 1395 kg/ha respectively. More than 30 percent of the annual total carbon was estimated to be lost in each site during the summer. This result clearly indicates that decomposition rates were considerably greater in summer, an observation generally not evident in results of decomposition studies using litter weight loss measurements.

The annual loss of carbon from the litter-fall amounted to 740 and 505 kg/ha from beech and radiata forest floor, respectively. These losses accounted for about 35 percent of the annual total carbon released as  $\text{CO}_2$  in each of the two sites used (Table 6.3.2.1.2). These estimated values represent maximum values since carbon losses from litter-bags may include carbon losses from comminution and some leaching which may not be completely mineralized. In the present study, estimates of litter contributions of carbon to the total loss of carbon as  $\text{CO}_2$  are about double that estimated by Edwards and Harris (1977) for a mixed deciduous forest floor. However, these authors based their result on oxygen uptake of cut-up pieces of litter which do not include carbon losses by other natural processes

(e.g. comminution and leaching) associated with our litter-bag carbon losses. Nevertheless, the result of the present study is in accordance with those of Edward and Harris (1977) and others (Witkamp and Frank, 1969; Garrett and Cox, 1973) and indicates that litter decomposition makes only a small contribution to the total carbon lost as  $\text{CO}_2$ .

The above result suggests that a very large proportion of losses measured as  $\text{CO}_2$  must have come from other compartments such as humus and soil, or possibly root respiration. Based on the relative amount of carbon accumulated on the forest floor in the two sites studied (Table 6.3.2.1.2), the results clearly implicate both soil compartment and root respiration as major sources of  $\text{CO}_2$  evolution. The rate of loss of carbon as  $\text{CO}_2$  from the forest floor of the beech site must be extremely small in order to reconcile with the disproportionality found in the amount of carbon accumulated (160 tonnes/ha in beech site versus 5 tonnes/ha in radiata site). As the decomposition results of the present study indicated small differences in the rates of decomposition between beech and radiata litter (Section 4.3.1), the importance of humus contributing to  $\text{CO}_2$  release is insignificant.

The factors causing the discrepancy in the amounts of carbon loss measured from litter decomposition and  $\text{CO}_2$  evolution are obscure but possible explanation must focus on the contributions made by root respiration. Reiners (1968) also found that the total  $\text{CO}_2$  evolution from the forest floor was over three times higher than expected from an equivalent amount of carbon released from annual litter-fall. He attributed the disparity partly to tree root respiration.

According to Edwards and Harris (1977), more than 77 percent of the annual total carbon efflux was accounted for by root respiration and root decay. Therefore it is evident that in order to obtain a better appreciation of the difference in decomposition rates between the beech and radiata sites, it would be necessary to partition the carbon losses from decomposition could be isolated and compared. At present, such attempt is complicated by the inability to quantify the contribution to the total  $\text{CO}_2$  evolved from root respiration.

#### 6.3.2.2 Larry's Creek Experimental Area

Rates of  $\text{CO}_2$  evolution in forested (FS), clearcut (CS) and burned (BS) sites at Larry's Creek, and their mean floor temperatures, are shown in Figure 6.3.2.4 . Further data on  $\text{CO}_2$  evolution rates are also given in Appendix IV.

##### 6.3.2.2.1 Rates of $\text{CO}_2$ Evolution

Highest rates of  $\text{CO}_2$  evolution found in the three sites were 3.48 (FS), 4.84 (CS) and 4.68 (BS)  $\text{g CO}_2$  per  $\text{m}^2$  per day. All these rates were recorded during measurements made at 8 days after selected clearcut sites were burned in March 1977 (see Phillips, 1980). These measurements also coincided with the first measurements taken following the installation of the "respirometers" (Section 6.2.2.1). Differences between these rates in the three sites were not statistically significant.

Except for the high rates mentioned above, the range of rates of  $\text{CO}_2$  evolution observed during the study period

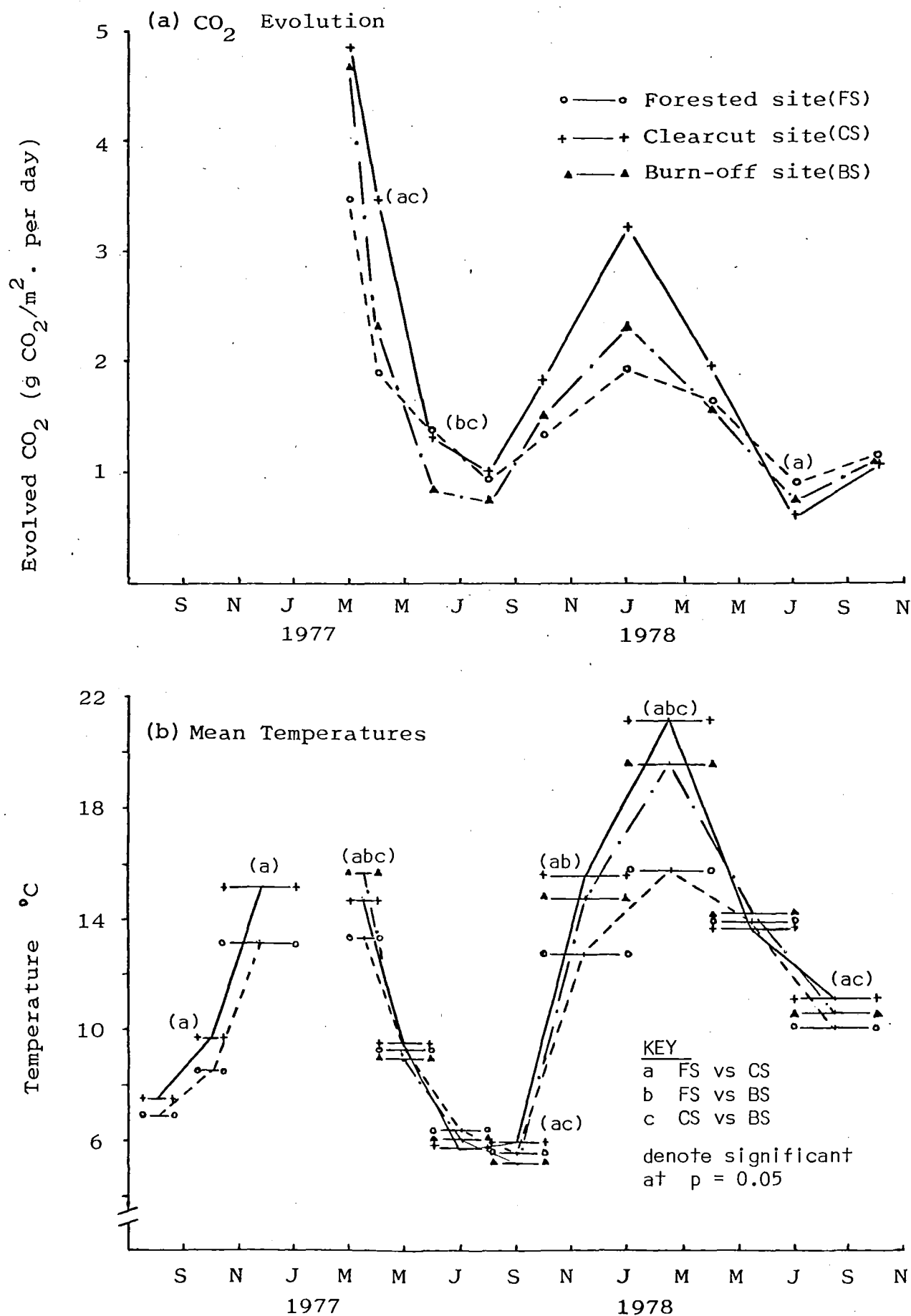


FIGURE 6.3.2.4 Carbon dioxide evolution and floor mean temperatures of sites at Larry's Creek Experimental area.

at Larry's Creek were within that found in the beech and radiata sites at Granville (Section 6.3.2.1.2). The mean rates determined for the entire study period at Larry's Creek were 1.63, 2.14 and 1.77 g CO<sub>2</sub> per m<sup>2</sup> per day respectively, in FS, CS and BS.

#### 6.3.2.2.2 Rates of CO<sub>2</sub> Evolution Between Sites

Generally, differences in CO<sub>2</sub> evolution rates between all sites (Figure 6.3.2.4) were not statistically significant as a result of large variation within sites (Appendix IV). However, for the greater part of the year, the magnitude of CO<sub>2</sub> evolution rates appeared to follow the order

$$CS > BS > FS .$$

These differences is attributed to the change in soil physical and chemical properties brought about by clearcutting and burning. The predominant effect of these two treatments was to alter the degree of influence of the abiotic factors in the clearcut and burned sites (e.g. insolation and precipitation reaching the soil surface). In comparison, the forest floor in the FS was buffered against dramatic changes in abiotic conditions by the presence of the tree canopy.

It is also probable that the dissimilar CO<sub>2</sub> evolution rates occurring in the CS and BS resulted from the differences in substrate quality of the organic matter remaining in the sites, in addition to the temperature and possibly moisture conditions. Comparatively lower rates of CO<sub>2</sub> evolution in BS could be due to the increased proportion of more resistant substances generated by the burn such as charcoal and lignified material. Phillips (1976) found that broadcast burning following a clearcut reduced the rate of carbon

mineralization of residual litter in the long term. He attributed the effect partly to a relative increase in resistant substances, particularly lignin and charcoal, in the burned sites. However, in the present study, no analysis was undertaken to determine the relative amount of charcoal and lignin in the sites used.

#### 6.3.2.2.3 Short and Long Term Effects on CO<sub>2</sub> Evolution Rates

It is difficult to attribute the relatively high rates of CO<sub>2</sub> evolution recorded immediately (24 hours) after the installation of respirometers, on a short term basis, directly to the effect of burning and clearcutting since these peak CO<sub>2</sub> evolution occurred at a time of the year (late summer, in early March) when high temperatures normally favour high rates of CO<sub>2</sub> production. Furthermore, the high values obtained may have coincided with a micro-peak in the fluctuations in the CO<sub>2</sub> production. As a result of the infrequent sampling, there is also no certainty that an even higher rate of CO<sub>2</sub> evolution rate could not have occurred during the following summer.

There is, however, a possibility that these high rates of CO<sub>2</sub> evolution could be due to disturbance effects caused during the installation of the "respirometers". The break-up of soil structures during installation increased the exposure of organic matter to microbial attack, which would otherwise be unavailable. Such a stimulating effect is partly related to that described by other workers (e.g. Birch, 1958; Soulides and Allison, 1961; Sørensen, 1974; Jager and

Bruins, 1975).

Results given in Table 6.3.2.2.2 show that rates of  $\text{CO}_2$  evolution recorded in corresponding months of the first and second year indicated a general decline in  $\text{CO}_2$  production in the BS and CS in the second year. This decline may be the result of several factors. In the CS, the decline was probably due to a decrease in the amount of oxidizable carbon substrates in the litter with time. Hu et al. (1972) found that the total  $\text{CO}_2$  evolved from decomposing plant material was indicative of the level of readily oxidizable carbon in the material and its state of decomposition. In the BS, however, the decline may have actually reflected the flush of  $\text{CO}_2$  released due to a plentiful supply of nutrients immediately after the burn. Lower coefficients of variation in the  $\text{CO}_2$  evolution rates in the BS than CS (Table 6.3.2.2.2) suggest that the rates of  $\text{CO}_2$  evolution was influenced by the nature and distribution of organic matter in the site. Burning effectively creates a more uniform distribution and availability of nutrients.

It is necessary to point out that the above view was based on the assumption that abiotic conditions (e.g. temperature and moisture) on the days in question were representative of the general conditions occurring during that time of the year so that a comparison in  $\text{CO}_2$  evolution rates between the two years is valid. This assumption is reasonable since there was only a relatively small decline in  $\text{CO}_2$  evolution rates in the FS, compared to those found in the CS or BS, thus suggesting a relatively similar abiotic condition.

In the present study, the possibility of  $\text{CO}_2$  uptake

TABLE 6.3.2.2.2 Rates of CO<sub>2</sub> evolution (mg/m<sup>2</sup>. day) in corresponding months of two consecutive years in forested, clear-cut and burned sites at Larry's Creek

Month	Forested	SITES Clear-cut	Burned
April 1977	1892(43) <sup>#</sup>	3471(46)	2327(34)
April 1978	1625(34)	1946(50)	1605(20)
October 1977	1305(41)	1810(50)	1525(27)
October 1978	1154(32)	1071(65)	1134(37)

# Data given in parenthesis refer to the coefficient of variation, n = 10



by microflora as a factor underlying the decline in  $\text{CO}_2$  evolution with time recorded cannot be discounted. Extensive areas of the BS, and to a lesser extent CS, were colonized by lichens during the later stages of the study. However, lichens found within the "respirometers" were removed to reduce such effects.

#### 6.3.2.2.4 Seasonal Variation in $\text{CO}_2$ Evolution Rates

A definite season pattern in the rates of  $\text{CO}_2$  evolution was observed at the three sites studied. High rates occurred in the summer and low rates in the winter (Figure 6.3.2.4). This seasonal pattern is closely similar to that found in the beech and radiata pine sites at Granville (Figure 6.3.2.1).

Regression analysis of mean floor temperatures (FT) and  $\text{CO}_2$  evolution rates was not undertaken since FT and  $\text{CO}_2$  evolution rates had been determined over dissimilar lengths of time. Nevertheless, the obvious relationship between FT and  $\text{CO}_2$  evolution rates could be clearly seen in Figure 6.3.2.4. The direct and close relationships between  $\text{CO}_2$  evolution rates and air temperatures, and air temperatures and floor temperatures in this region of heavy rainfall (where moisture contents were generally adequate) have been established (Section 6.3.2.1.1). Humus and soil moisture contents in the FS and CS, and soil moisture contents in the BS throughout the year (M.J. Phillips, pers. comm.) were within the range of levels which could be considered as substantially above the critical levels reported by Wiant (1967b) which dramatically reduced  $\text{CO}_2$  production.

### 6.3.2.3 Reliability of Method Used in the Measurement of CO<sub>2</sub> Evolution Rates

Results of maximum temperatures and light intensities recorded within the "respirometers" installed on the forest floor are shown in Table 6.3.2.3. Despite apparent dissimilarities in the maximum temperatures recorded between "respirometers", these differences were not statistically significant. This is due primarily to the wide variations in temperatures recorded. Nevertheless, the result suggests that the temperatures within the "respirometers" were not excessively increased over the prevailing air temperatures. The differences in temperatures between the "respirometers" with clear lids and those with translucent lids could be attributed to the thinner clear polythene sheet windows on the lids of the former kind of "respirometers". Presumably, heat insulation would be reduced in those with thinner lids.

As the above measurements were made on the forest floor, the results may not apply to burned surfaces which could act as heat absorbing "black bodies". However, it is suspected that as a result of shading, the temperatures within the "respirometers" on such surfaces may not be excessively increased over those at the burned surfaces under direct sunlight.

Results in Table 6.3.2.3 also show that there were significant differences in light intensities within the "respirometers" using different kind of lids. Even when there was no lid on, a 21 percent reduction in light intensity compared to that of the surrounding was recorded. The examination of this aspect of the method was necessary because

TABLE 6.3.2.3 Maximum temperature and light intensity recorded within "respirometers" used in measurement of CO<sub>2</sub> evolution rates

	Temperature (°C) in "Respirometer" <sup>@</sup>			Light <sup>‡</sup> Intensity (%)
	In Open Space (1)	(2)	Under Tree (1)	
Surrounding Space	18.7(0.5) <sup>#</sup>	18.3(1.1)	16.6(0.9)	100
Within "Respirometer"				
Without lid	-	-	-	79.3(3.3)
With clear lid	18.6(2.6)	18.7(2.6)	15.5(2.5)	54.0(1.1)
With translucent lid	19.3(2.6)	19.0(3.2)	17.8(4.3)	26.5(1.8)

# values given are mean ± 95 percent C.I.

@ mean of 3 replicates

‡ mean of 4 replicates

these "respirometers" were required to be left at the sites after installation for the entire study period. A reduction in light intensity within the uncovered "respirometer" may have a long term effect on subsequent  $\text{CO}_2$  evolution rates (De Santo and Alfani, 1975). Although there was greater reduction in light intensities in "respirometers" using lids (reduction by clear lid = 46 percent, translucent lid = 74 percent) than those without lids, the effect due to lids was considered to be critical on  $\text{CO}_2$  evolution rates only on a short term basis because measurements of  $\text{CO}_2$  evolution were taken within a day at different times throughout the year.

The concentration of the NaOH solution used in the present study (5 ml of 2.0M NaOH) was substantially higher than those used by other workers (e.g. Witkamp, 1966a; Phillipson et al., 1975) in order to increase the efficiency of  $\text{CO}_2$  absorption. Furthermore, as measurements of  $\text{CO}_2$  evolution were made over a longer time interval (24 hours) than those of other workers, the need to use a more concentrated NaOH solution was greater. According to Kirita and Hozumi (1966) and Kirita (1971a, 1971b), at least 80 percent of the initial amount of alkali must remain unused at the end of the measurement period in order to achieve an absorption rate greater than 90 percent of the potential rate. In the present study, it was found that the amount of NaOH remaining unused at the end of the 24-hour measurements ranged from 70 to 95 percent of the initial amount.

Other aspects of the method such as the effect of surface area of the absorbing solution and the height of this surface above the forest floor were not examined. However, diurnal effects were minimized by extending  $\text{CO}_2$  evolution

measurements over 24-hour periods (Witkamp, 1969).

The permanent situation of each "respirometer" was considered essential to provide isolation and examination of seasonal variation, by maintaining constant microsite properties. Shifting of "respirometers", while providing a better estimate of the variability of  $\text{CO}_2$  evolution rates, tends to be complicated by disturbance effects.

Thus, from the considerations given above, there is little reason to suspect that the method and apparatus used in the present study affected the results obtained.

### 6.3.3 Nitrogen Mineralization

Results of nitrate-N and ammonium-N concentrations in humus and top-soil (0-20cm) samples are shown in Table 6.3.3 and Figure 6.3.3.2 respectively. Additional data are given in Appendix IV.

#### 6.3.3.1 Nitrate Concentration

Nitrate-N was generally detected (limit  $0.01 \mu\text{g/ml}$ ) more frequently in radiata than in beech samples, either humus or top-soil of both fresh and core samples (Table 6.3.3). The mean concentration and maximum concentration were also considerably greater in radiata than in beech samples, particularly in the humus samples. Within a site, there was no apparent difference between fresh and core samples in the nitrate concentrations in both humus and top-soil.

The above results suggest that the forest floor conditions under radiata pines favour greater nitrification over the beech counterpart. In part, such a difference in nitrate

TABLE 6.3.3 Nitrate-N concentration ( $\mu\text{g/g}$ ) in humus (FH) and top-soil (0-20cm) of beech and radiata pine forest stand at Granville

	Forest Stand	Humus Sample		Top-soil Sample	
		Fresh <sup>#</sup>	Core <sup>@</sup>	Fresh <sup>#</sup>	Core <sup>@</sup>
Proportion of samples (% of total) with nitrate present	Beech	14	12	20	10
	Radiata	26	27	30	39
Mean nitrate-N concentration	Beech	0.46	0.40	0.36	0.33
	Radiata	2.21	3.33	1.35	1.00
Maximum nitrate-N concentration	Beech	0.8	0.4	0.8	0.4
	Radiata	13.3	15.6	4.8	4.0

# total number of samples in each site = 100 } collected between March 1977 and December 1978  
 @ total number of samples in each site = 90 }

concentration may be attributed to the dissimilar pH conditions . The pH values in L+F+H and top-soil were 3.3 and 4.2 respectively under beech but both were 4.5 under radiata pine. Low pH conditions are known to be unfavourable for nitrification (and ammonification), and according to Alexander (1977) nitrification decreases below pH 6.0 and becomes negligible at pH 5.0. The pattern of a general absence of nitrate in both the sites used in the present study is therefore consistent with that indicated by Alexander (1977). Furthermore, although nitrate was detected in samples with pH as low as 3.3 for humus and 4.2 for top-soils, such a result is not uncommon. High levels of nitrate and considerable populations of nitrifiers have also been found in soils of pH 4.0 and less (Weber and Gainey, 1962; Smith et al., 1968).

In the present study, most of the nitrate found in humus and top-soil in the radiata site was noticeably from samples collected within a specific area. . . Thus, it is possible that nitrification could have occurred in small pockets of samples with pH higher than those determined from the bulk samples.

It is also possible that tannins and other polyphenolic compounds contained in the organic matter and leached from the overlying litter could have inhibited nitrification. Rice and Pancholy (1974) presented evidence indicating that the presence of small amounts of tannins inhibited nitrification . In the present study, chemical analyses of litter showed both beech and radiata litters contained substantial amounts of polyphenols, with beech litter containing higher

levels than radiata litter (Section 3.3.7.1).

#### 6.3.3.2 Ammonium Concentration

Unlike nitrate, ammonium was detected in all humus and soil samples from both beech and radiata sites throughout the entire study period. In fresh top-soil samples, ammonium-N levels in beech site (range: 1.5 to 13.3, mean: 7.4  $\mu\text{g/g}$ ) were closely similar to those found in radiata site (range: 1.4 to 12.2, mean: 7.7  $\mu\text{g/g}$ ). This similarity is maintained throughout the experimental period in the top-soil samples (Figure 6.3.3.2). However, for humus, ammonium levels in radiata samples (range: 22.6 to 85.4, mean: 43.3  $\mu\text{g/g}$ ) were consistently greater than those found in beech (range: 11.0 to 63.1, mean: 29.8  $\mu\text{g/g}$ ). A similar pattern in ammonium levels in both humus and top-soil was also found in the core samples (Figure 6.3.3.2). Most of the differences found in ammonium levels between radiata and beech samples were generally not statistically significant. As with  $\text{CO}_2$  evolution rates, the within site variability in ammonium concentrations was too large to allow any significance to be detected.

The exact reason for the presence of considerable amounts of ammonium and negligible amounts of nitrate in both beech and radiata sites is uncertain. However, one probable factor is the pH, since the more complex ammonifying micro-organisms are less sensitive to pH effect (Alexander, 1977). Another probable explanation relates to the loss of nitrate by leaching, although incubation experiment under controlled laboratory conditions has shown no significant nitrate formation (Section 7.3.2.1). Such a disparity in ammonium and



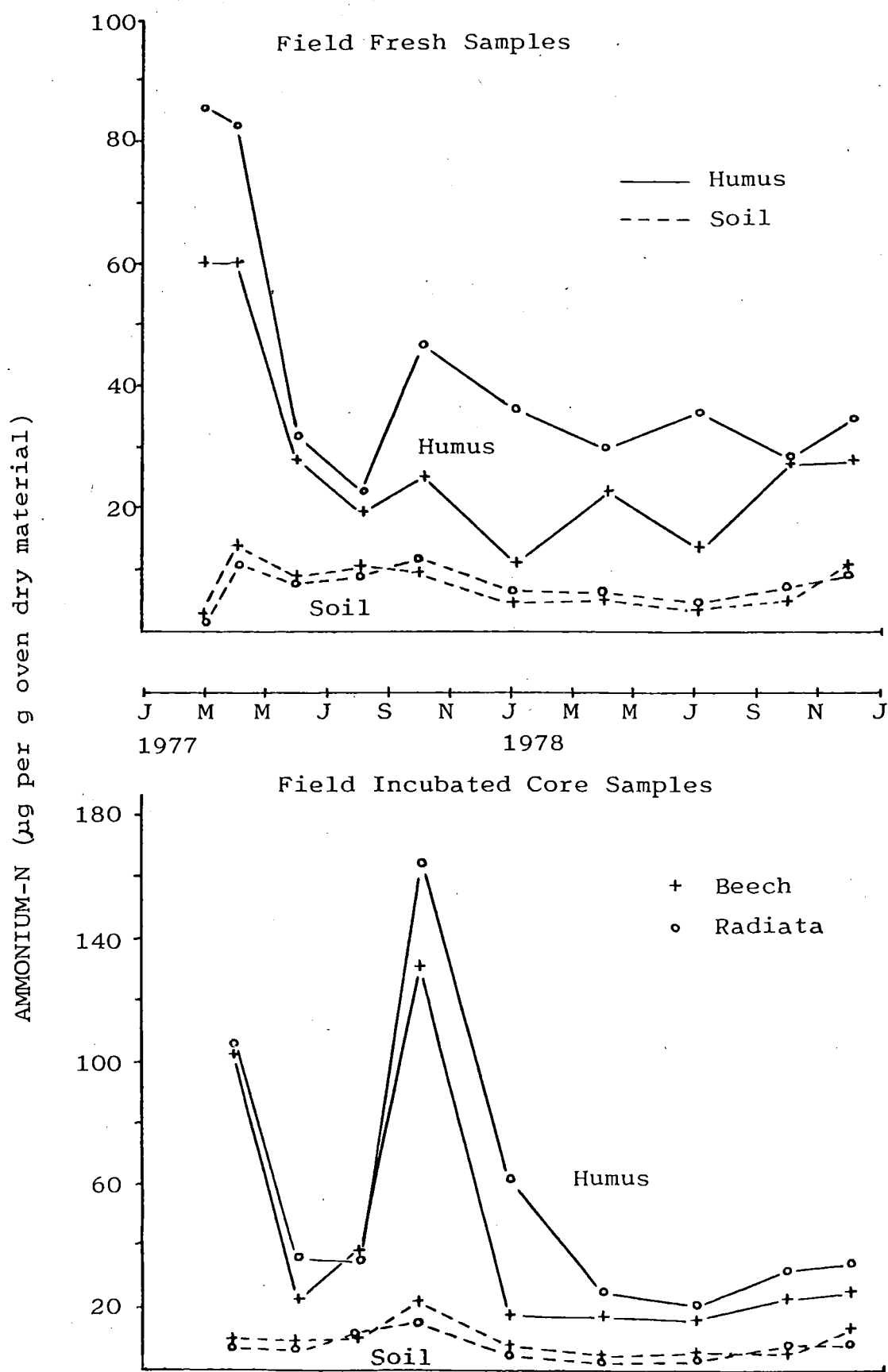


FIGURE 6.3.3.2 Seasonal variation in ammonium-N concentrations of humus and top-soil of beech forest and radiata plantation at Granville

nitrate levels is not unusual since several workers have also reported its occurrence (e.g. Viro, 1963; Lodhi, 1977). Rice and Pancholy (1972, 1973, 1974) found significant increases in ammonium concentrations and significant decreases in nitrate concentrations as succession progressed towards the climax in several types of vegetation. In the present study, although the beech stand may be considered a climax ecosystem, it is uncertain whether the same could be considered for the radiata pine stand (22 years old).

The nett change in ammonium levels (+ve for nett accumulation and -ve for nett depletion; see Section 6.2.2.2) could be reasonably regarded as an indication of the pattern of mineralization occurring in the period over which the sample was incubated *in situ*. However, part of the ammonium detected, particularly in the top-soil, would inevitably include those that became mineralized as a result of breaking-up of samples during core preparation. Waring and Bremner (1964) found that a decrease in soil mesh-size resulted in a marked increase in the amounts of N mineralized during incubation under aerobic and water-logged conditions. Basically, the breaking-up of soil samples would represent a similar kind of effect, although of a lesser degree than that of sieving.

Nett changes in levels of ammonium were generally variable (Figure 6.3.3.3). However, both beech and radiata samples appear to follow a similar pattern. For humus, maximum depletions of about 40 and 46  $\mu\text{g/g}$  ammonium-N were found in mid-autumn (about May) for beech and radiata samples respectively, while maximum nett accumulations of 111 and 142  $\mu\text{g/g}$  ammonium-N in the corresponding sites occurred in early spring (about September). Nett changes in ammonium

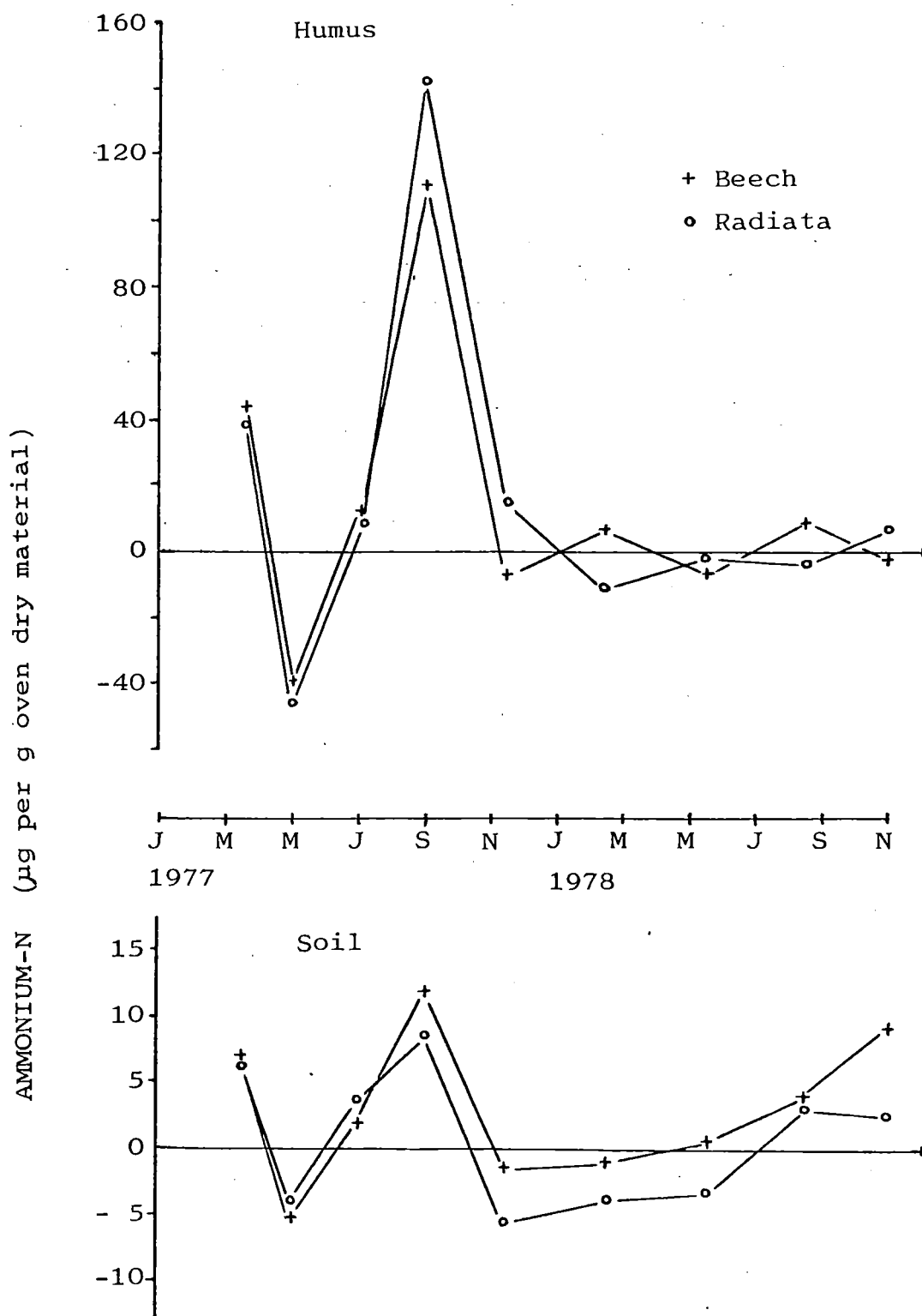


FIGURE 6.3.3.3 Seasonal variation in nett accumulation of ammonium-N in humus and top-soil of beech forest and radiata plantation at Granville

levels thereafter showed rather irregular fluctuations and the pattern in the first year was generally not repeated to any degree in the following year. Changes in the top-soil ammonium levels followed closely to those found for humus in the first year although the irregular fluctuations of values from humus samples were absent in the second year. Nett accumulations were recorded for both beech and radiata top-soil samples towards mid-spring. Overall, radiata top-soil samples showed a greater tendency to undergo depletion than those of beech. Depletion of N could have occurred through microbial immobilization, reduced N input from litter and possible denitrification.

#### 6.3.3.3 Seasonal Variation in Ammonium Concentration

Ammonium levels in all samples studied (humus and top-soil of both fresh and core samples) showed no apparent seasonal patterns. High ammonium-N levels (63  $\mu\text{g/g}$  in beech, 85  $\mu\text{g/g}$  in radiata samples) were recorded in fresh humus samples from the first sampling in March 1977. A smaller peak (47  $\mu\text{g/g}$ ) was also observed in radiata samples during October 1977. Ammonium concentrations in the humus of core samples followed a very much similar pattern as those of fresh humus samples except that the peak ammonium-N levels (130  $\mu\text{g/g}$  for beech and 164  $\mu\text{g/g}$  for radiata) were found in October 1977 as well as in March 1977.

No significant correlation was found between ammonium concentrations and mean forest floor temperatures recorded in the corresponding period in which the samples were being incubated *in situ*. Regression analyses also revealed no

significant relationships between ammonium concentrations and moisture contents in respective humus and top-soil samples. The seasonal variation in moisture contents was small and generally did not approach extreme levels (Figure 6.3.1.2). Multiple linear regression analyses also did not indicate any significant relationships between ammonium concentrations and both moisture contents and forest floor temperatures (Table 6.3.3.3). Thus, it would appear that both temperature and/or moisture content were insufficient to allow predictions to be made on N mineralization patterns in the beech and radiata sites.

It is doubtful whether any significant correlations could be obtained at all between the amounts of N mineralized and temperatures and/or moisture levels under the conditions prevailing in the two sites used in the present study. The mean floor temperatures recorded in these sites ranged from  $5^{\circ}$  to  $8^{\circ}\text{C}$  throughout the year (Figure 6.3.1.2) and were substantially below the reported optimum temperatures for nitrification and ammonification of about  $35^{\circ}\text{C}$  and  $50^{\circ}\text{C}$  respectively (Harmsen and Kolenbrander, 1965; Myers, 1975). Moisture contents of forest floor had remained relatively constant within sites throughout the year. Under these circumstances, it is possible that N mineralization patterns were governed by that of litter-fall.

In the first year, peak levels of ammonium-N were found in autumn and spring, and this pattern generally corresponded with that of litter-fall. However, such a pattern was not apparent in the following year, and overall, no significant correlation was obtained between the amounts of N mineralized

TABLE 6.3.3.3 Correlation coefficients and levels<sup>#</sup> of significance for the relationship between ammonium concentrations and either moisture contents and/or forest floor temperatures

Variables	BEECH		RADIATA	
	Soil	Humus	Soil	Humus
Floor Temperatures	0.15	0.39	0.14	0.42
Moisture Contents	0.36	0.60	0.17	0.03
Floor Temperatures and Moisture Contents	0.36	0.62	0.15	0.45

# not significant, unless otherwise stated.

in fresh samples and the amount of litter-fall recorded in the preceding month (beech: humus,  $r = 0.35$ ; soil,  $r = 0.35$ , and radiata: humus,  $r < 0.10$ ; soil,  $r = 0.52$ ). The lack of a clear relationship is probably the result of the combined effects of the many factors which influence N mineralization rates (Review Section 2.5.3.1), including microbial and plant uptake. The possibility of plant uptake cannot be discounted in the present study. Higher levels of ammonium in both humus and top-soil of core samples (where uptake was prevented) than those in fresh samples (where uptake was not prevented) were found. This was most evident in the spring season where plant uptake and plant growth was expected to be greatest. Similarly, microbial uptake of ammonium (and organic N) may be reflected by the increase in  $\text{CO}_2$  production during the spring season (Section 6.3.2).

#### 6.3.3.4 Factors Affecting Ammonium Accumulation

There were no significant correlations between ammonium concentrations and the total-N contents of the samples, as determined on samples collected from four sampling period (Table 6.3.3.4). Results of ammonium-N and total-N concentrations indicate that the former make up only a very small proportion of the total-N content, between an estimated 0.1% to 0.5%. These ammonium-N percentages in radiata were at least equal to or higher than the corresponding values in beech samples.

Several factors, including pH, the N and particularly polyphenol contents, are generally thought to be largely

TABLE 6.3.3.4 Ammonium-N ( $\mu\text{g/g}$ ) and total-N ( $\text{mg/g}$ ) concentrations in the humus (FH) and top-soil (0-20cm) of beech and radiata pine forest stand at Granville for different times of the year

SAMPLE	APRIL 1978		JULY 1978		OCTOBER 1978		DECEMBER 1978	
	$\text{NH}_4^+\text{-N}$	Total-N	$\text{NH}_4^+\text{-N}$	Total-N	$\text{NH}_4^+\text{-N}$	Total-N	$\text{NH}_4^+\text{-N}$	Total-N
HUMUS								
Beech	22.6	10.5	13.3	11.9	28.0	12.4	27.7	11.5
Radiata	29.9	11.5	35.5	10.3	27.8	12.0	34.4	11.1
TOP-SOIL								
Beech	5.3	2.3	3.2	2.3	4.6	1.9	10.2	2.1
Radiata	6.7	1.7	3.9	1.8	7.0	1.7	9.2	1.7



involved in differentiating the amounts of N mineralized in these two sites. The effect of pH has been discussed previously (Sections 6.3.3.1 and 6.3.3.2). The relationship between total N contents and amounts of N mineralized has also been discussed by several workers (e.g. Floate, 1970a; Vlassak, 1970). In the present study, however, such a relationship was not evident in humus and top-soil samples (fresh) from beech and radiata sites.

One possible reason for this relates to the presence of polyphenolic compounds. The effect of polyphenols is demonstrated in a separate part of this study (see Section 7.3.2.2). Earlier results (Section 4.4) show significant correlations between total-N and both polyphenol and lignin contents of litter during decomposition. Interactions between polyphenolic compounds and nitrogen (e.g. proteins) have been known to increase the resistance of the nitrogen to attack by heterotrophic micro-organisms (Basaraba and Starkey, 1968; Lewis and Starkey, 1968). Furthermore, evidence was obtained from a laboratory incubation experiment undertaken in the present study which showed that larger polyphenolic contents resulted in a smaller amount of N mineralized (Section 7.3.2.2). Thus, it is probable that lower ammonium levels as found in the beech site compared with those of the radiata site may be due to higher polyphenol content of beech litter. Chemical analysis revealed that the polyphenol concentration in beech leaf litter was about 3 times higher than that of radiata needle litter. A similar magnitude of difference in the annual polyphenol budget was also obtained by calculations from litter-fall data (Section 3.3.10.1).

Vallis and Jones (1973) recently linked differences in rates of N mineralization observed in laboratory studies of litter from two pasture legumes (*Desmodium* and *Phaseolus*) to polyphenol contents. *Desmodium* litter with higher polyphenol content than *Phaseolus* showed slower N mineralization rates. These workers also suggested that only a small proportion of the total polyphenols was involved since removal of 80 percent of the polyphenols did not enhance N mineralization.

#### 6.4 GENERAL DISCUSSION

A significant implication of the results obtained from the *in situ* carbon mineralization study is the effect related to the supply of exchangeable cations and leaching losses. A higher CO<sub>2</sub> production was associated with low pH and low levels of exchangeable cations, in the beech site. The reversed order was found in the radiata (Table 6.2.1).

The biological respiration by roots and soil biota introduces CO<sub>2</sub> into the soil atmosphere. This effect directly raises the concentrations of carbonic acid and its dissociation products which would act to maintain or even increase the supply of H<sup>+</sup> ions within the forest floor ecosystem. Eventually, in the soil solution, the acid dissociates and the H<sup>+</sup> ions can substitute the metallic cations on exchange sites within the forest floor and soil, consequently leading to the loss of these cations and associated anions from the ecosystem by leaching. These effects lower

the soil pH and levels of exchangeable cations in the beech site. In the radiata site, due to an apparently lower CO<sub>2</sub> production, these effects are observed at a lesser degree.

However, it is also necessary to add that other than carbonic acid effect, organic acids (Cronan et al., 1978) resulting from decomposition or root exudation (Smith, 1976) could also contribute to differences in pH and CEC status between the two sites.

An understanding of the pattern of N-mineralization in any forest ecosystem is important. In particular, there is a greater need for such information in temperate ecosystems where there is a marked short-term change in nett ecosystem productivity brought about by seasonal variation. There may be an excess of element uptake over element release during the growing season, yielding a seasonal cycle with a minimum in ecosystem outputs of important plant nutrients during the growing season. In this connection, the results obtained in the present study showing increased N mineralization, together with increased nutrient release due to peak litter-fall at about the time of spring has a certain degree of significance. It is clear that the peak periods of N mineralization in the two west coast sites are in phase with the period where maximum tree growth is normally occurring (in spring).

Another practical aspect of the results from the present study concerns the optimum time for the application of N fertilizers. The objective here would be to increase the effectiveness of the applied N fertilizer in terms of maximum uptake by the trees. As the results obtained suggest,

application in early spring would involve a time when maximum N mineralization is probably occurring. It would seem, therefore, that fertilizer application would be best done when maximum mineralization is on the decline and when both vegetation and microbial population are still in a period of rapid growth. Results of C and N mineralization patterns found in the sites studied indicate that the period for optimum effectiveness is early summer (about December). However, it is necessary to emphasise that this inference is based on the assumption that mineralized N levels which occur in spring in these sites are adequate for meeting the requirements of the existing vegetation.

It is unlikely that nitrate was being completely leached out of the forest floor (or soil) from the sites studied since incubation study in the laboratory (Section 7.3.2.1) has shown that negligible amounts of nitrate was produced. In certain respects, the lack of nitrate in these forest sites represents no serious disadvantage and may in fact be beneficial. Compared to ammonium, which is usually retained in soils, nitrate is easily leached. Furthermore, the leaching of nitrate can accelerate both cation and N losses and possibly rock weathering (Likens et al., 1969). In addition, the results of the present study suggest that both these forest stands at Granville have achieved an ecosystem level that is effectively reducing N and cations losses, a capability often associated with mature forest ecosystems (Rice and Pancholy, 1972, 1973, 1974)

Data obtained in the present study indicate no significant difference between levels of mineralized N in soils

under beech and radiata pine. These results therefore provide no conclusive evidence to suggest increased mineralization of N in the soil of one species over that of the other, although there appears to be higher ammonium levels in the humus layer of radiata than in that of beech. It would seem that the result of the present study cannot reconcile with that of Stone and Fisher (1968) which suggests that conifers increase N availability above their own requirements. These workers compared only N mineralization in soils between open field and conifer sites, and the N availability under beech was not studied.

The trend in the ammonium levels in top-soils appeared to reflect that of ammonium levels found in the overlying humus layer (Figure 6.3.3.3), particularly since there were considerably higher ammonium levels in the humus layer. If this is the case, then the present results suggest that N availability in radiata stands after clearcutting and replanting is likely to be affected by the prolonged absence of fresh litter during the early stages of stand development following replanting. Such an effect is made more critical since greatest demand by radiata pine for nutrients, including N, in the soil, appears to be during the first few years of its life (Will, 1964; Madgwick, 1979). It is possible that this effect may partly explain why second rotation radiata pine showed N-deficiency (Stone and Will, 1965). In such a stand, low levels of available N would be aggravated by the harvesting of the first rotation radiata pine.

## 6.5 CONCLUSIONS

Rates of  $\text{CO}_2$  evolution from forest floors of the beech and radiata pine stands at Granville were closely correlated with air and forest floor temperatures, but not with moisture contents of humus and/or top-soil (0-20cm). In areas of adequate moisture, such as forests with continuous canopy, temperature alone could sufficiently predict the  $\text{CO}_2$  evolution rates.

Annual total carbon efflux from the beech and radiata forest floors was 1893 kg/ha and 1395 kg/ha respectively. The rate of loss was greatest in summer (December to February) and amounted to about 31 and 32 percent of the annual total carbon efflux from beech and radiata sites respectively.

Annual total carbon losses (as  $\text{CO}_2$ ) from both sites were about 3 times higher than those expected from equivalent amounts of carbon released from decomposition of annual litter-fall. Respiration by tree roots and associated microbial populations were suspected as the major contributors to this disparity and that found in the daily rates of  $\text{CO}_2$  evolution between beech and radiata pine.

Clearcutting of a forest and burning of the forest floor apparently increased the rates of  $\text{CO}_2$  evolution from the forest floor when compared to that of the forest. Higher rates of  $\text{CO}_2$  evolution in clearcut site than those in burned site were attributed jointly to decrease in labile carbon substrates in the latter and greater amounts of decomposable organic matter in the former. Carbon dioxide evolution rates in these clearcut and burned sites were

predominantly influenced by temperature.

The present method used in the measurements of forest floor evolution rates adequately provided a reliable comparison between sites. However, due to large variations in the rates of  $\text{CO}_2$  evolution recorded between respirometers, it would be necessary to carry out more replications than that employed in the present study (10 per site).

Plant-available N accumulated (nett) in both humus and top mineral soil samples of beech and radiata stands studied was predominantly in the form of ammonium-N. Nitrate-N accumulation was generally negligible or undetectable. This result was attributed to the acidic conditions of the humus and top-soil in these two sites.

There was no clear seasonal variation in the levels of accumulated ammonium and nitrate in the humus and top-soil at both sites. These two forms of available N were not correlated with temperature, either moisture contents of humus or soil, and temperature and moisture contents.

Levels of ammonium-N accumulated in the soil were relatively similar between sites but those in humus were apparently greater in the radiata site (mean  $43.3 \mu\text{g/g}$ ) than in the beech site (mean  $29.8 \mu\text{g/g}$ ). This disparity was attributed to the relatively lower pH of the beech humus (pH 3.3) as compared to that of radiata (pH 4.5), and the higher polyphenol content of beech litter. This latter chemical property was also suspected as a factor responsible for the lack of correlation between concentrations of ammonium-N and total-N in humus and soil samples of both sites.

CHAPTER 7

EFFECTS OF WATER-SOLUBLE COMPONENTS OF BEECH AND RADIATA  
PINE LITTER ON SOIL CARBON AND NITROGEN MINERALIZATION.

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## CHAPTER 7

EFFECTS OF WATER-SOLUBLE COMPONENTS OF BEECH AND RADIATA PINE  
LITTER ON SOIL CARBON AND NITROGEN MINERALIZATION

## 7.1 INTRODUCTION

Plant litter generally varies in its chemical composition. Therefore, the change in vegetation following forest conversion inevitably leads to a change in the kind, amount and rate at which the different chemical compounds are released into the soil through the processes of leaching and decomposition.

Some chemical constituents of litter such as polyphenols and simple carbohydrates (see Review Section 2.2) are known to affect the rate of microbial decomposition of litter. Consequently, the change in vegetation may alter the rate of microbial respiration and mineralization of N which occur within the forest floors.

The objective of the present study was to examine the effects of water-soluble polyphenolic compounds and carbohydrates extracted from beech and radiata pine litter on the rates of  $\text{CO}_2$  evolution and levels of mineralized N in the soil under different forests. A laboratory incubation study was conducted under controlled conditions using chemical composition parameters (e.g. polyphenol fluxes) similar to those occurring under field conditions. This may provide

some information to account for part of the differences observed in carbon and N mineralization rates in the field between beech and radiata pine stands.

## 7.2 MATERIALS AND METHODS

### 7.2.1 Soils

The top-soil (0 - 20cm) of a Tekoa Hill silt loam at Hanmer was sampled from both under a beech (LOM) and a radiata pine (HOM) stand as described previously (Section 5.2.2). Soil samples were air-dried, passed through a 2mm sieve and stored. Methods used for characterizing the soils, except water-holding capacity (WHC) have been described earlier (Section 5.2.4). Some important properties of the soils are as follows:

LOM; C 2.2%, N 0.12%, pH 5.0, CEC 23.4 m.e.%, polyphenols 0.06 mg/g and WHC 55% DW.

HOM; C 3.7%, N 0.24%, pH 5.4, CEC 16.3 m.e.%, polyphenols 0.08 mg/g and WHC 68% DW.

### 7.2.2 Treatments

Five treatments were used for the CO<sub>2</sub> evolution (respiration) study. These included distilled water (C = control), beech leaf extract (B260), radiata pine needle extracts at two concentrations of polyphenolic compounds (RAD85 and RAD260), and pure catechin solution (CAT260).

Two additional treatments, one of glucose (GLU200) and the other of glucose with catechin (GLU200 + CAT260) were used in the N mineralization experiment. Treatments in the respiration study were carried out in duplicate while six replications were used in the N mineralization study.

Water-soluble materials were extracted separately from beech leaf and radiata pine needle litter, and analysed for contents of polyphenolic compounds and simple carbohydrates using the methods as described in Section 3.2.4.5 .

Volumes and concentrations of each extract solution were adjusted such that polyphenols were introduced at a rate of 260  $\mu\text{g}$  per g of soil for beech and at rates of 85  $\mu\text{g}$  and 260  $\mu\text{g}$  per g of soil for radiata pine; giving a final moisture content approximately equal to 60% of the water-holding capacity of the soils. The optimum moisture content for ammonification generally lies between 50 and 75 percent of the water-holding capacity of the soil (Alexander, 1977).

The rate of addition of polyphenols selected for beech litter extract (260  $\mu\text{g}/\text{g}$ ) was estimated from the rates of input of polyphenols to the fine soil ( $< 2\text{mm}$ ) in the top mineral soil (10 cm depth) of the beech stand at Granville, using data obtained from decomposition study (Section 4.3.3), litter-fall measurements (Section 3.3.2) and forest floor characterization study (Chapter 5). The calculated rates ranged from 67 to 345  $\mu\text{g}$  per g of soil. Although the actual rate used (260  $\mu\text{g}/\text{g}$ ) was based on a three-monthly period, it nevertheless represents a realistic rate, since additional contributions of polyphenolic compounds were also derived from accumulated organic matter in the forest floor which were

not included in the above rate calculations.

In Granville, it was found that the quantity of polyphenols returned in beech stand ranged between 2.4 and 4.8 times higher than those in radiata pine stand. This served as a basis for the selection of a rate of 85  $\mu\text{g}$  per g soil for the radiata pine litter extract treatment.

### 7.2.3 Experimental Procedure

The water-holding capacities of the soil samples were assessed by draining overnight-saturated samples for 24 hours. The moisture content of all soil samples used in the respiration and N mineralization experiments were adjusted to 60% of their water-holding capacities.

For the respiration experiment, a 100g soil sample was placed into each biometer flask (Bartha and Pramer, 1965) and then moistened with the appropriate volume of treatment solution. The rate of  $\text{CO}_2$  evolution was measured by placing 5.0 ml of 1.0M NaOH in the adjacent chamber. At each sampling time, the used-NaOH was removed and replaced by a fresh aliquot. The amount of  $\text{CO}_2$  absorbed was determined by titrating the excess NaOH with 0.2M HCl after precipitating the carbonates formed with excess 0.5M  $\text{BaCl}_2$  (about 5 ml). Rates of  $\text{CO}_2$  evolution were measured at different time intervals in a period of 16 days. Incubation was carried out at 30°C in an incubator.

For the N mineralization experiment, a 20g soil sample was placed into each incubation flask (200 ml), amended with the appropriate volume of treatment solution and then covered with a finely perforated lid. Ammonium-N and nitrate-N

were determined after a period of 14 days incubation using the method described in Section 6.2.2.2. Incubation conditions were identical to those used in respiration study.

### 7.3 RESULTS AND DISCUSSION

#### 7.3.1 CO<sub>2</sub> Evolution Rates

Soil mean CO<sub>2</sub> evolution rates recorded are shown in Figure 7.3.1. The mean CO<sub>2</sub> evolution rates given represent the quantity of CO<sub>2</sub> evolved divided by the time period (in hours) in which the CO<sub>2</sub> release occurred. Each point on the graph is placed in the mid-point of the time period in which the mean CO<sub>2</sub> evolution rate was determined. Detailed data are given in Appendix VI.

In both soils (LOM and HOM), CO<sub>2</sub> evolution rates were observed to increase markedly during the first 24 hours of incubation. These increases in HOM were generally more rapid than those in LOM for all treatments. In HOM, except for RAD260, broad peaks were observed in the CO<sub>2</sub> evolution rates. Sharp peaks in CO<sub>2</sub> evolution rates were common for all treatments in LOM, including RAD260 in HOM. At about 3 days, the rates of CO<sub>2</sub> evolution in both soils had declined appreciably. This pattern of CO<sub>2</sub> evolution rates is consistent with those described by other workers (e.g. Behera and Wagner, 1974; Alexander, 1977; Nannipieri et al., 1978, 1979).

In both soils, peak CO<sub>2</sub> evolution rates occurred between the 24th and 30th hour (shown as mean CO<sub>2</sub> evolution rates at

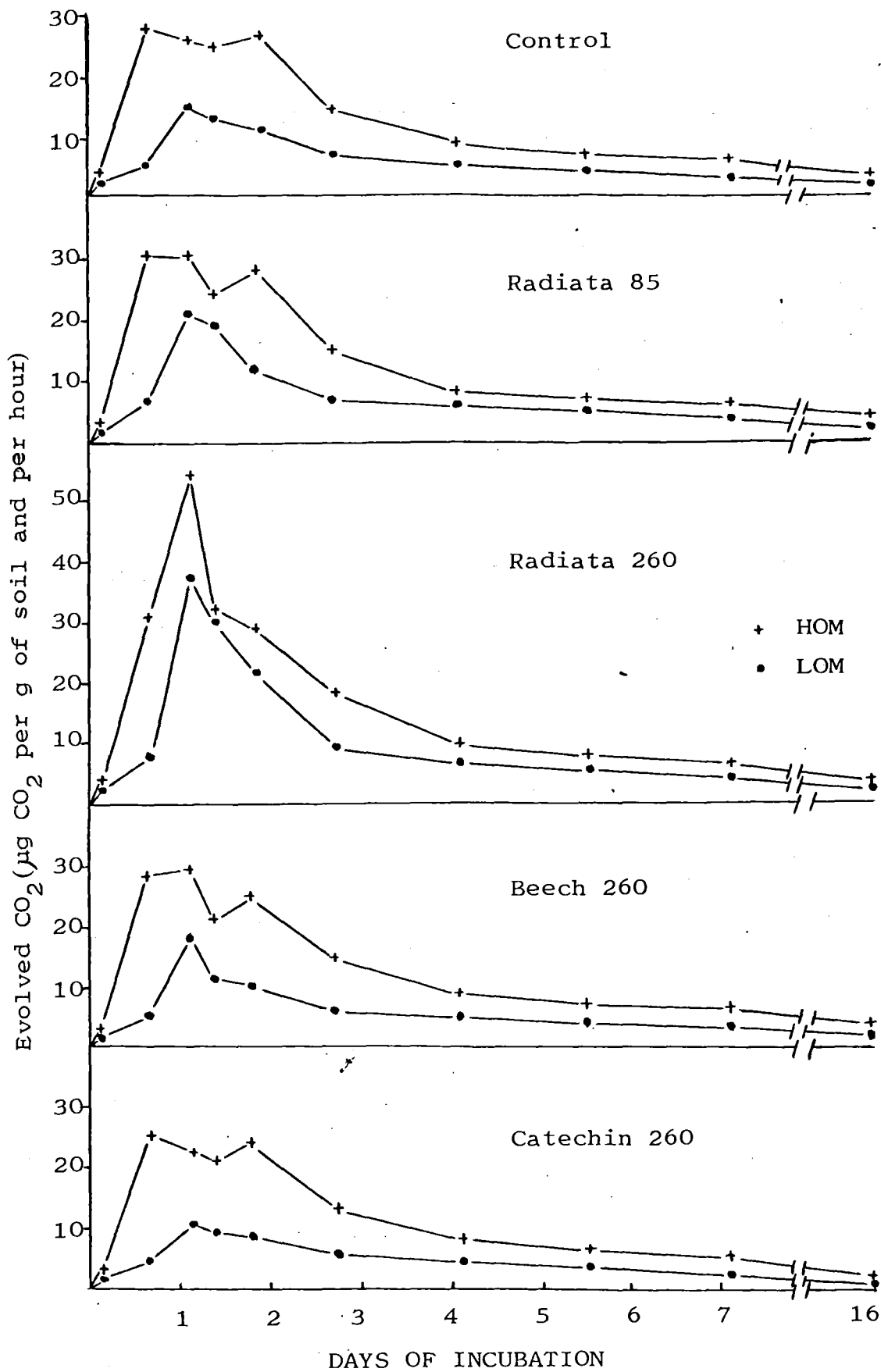


FIGURE 7.3.1 CO<sub>2</sub> Evolution rates of soils incubated with water extracts of beech and radiata litter, and catechin solution

TABLE 7.3.1 RESULTS OF DUNCAN'S MULTIPLE RANGE TESTS<sup>#</sup> FOR CO<sub>2</sub> EVOLUTION RATES BETWEEN SOILS INCUBATED WITH DIFFERENT SOLUTIONS<sup>‡</sup>

Sampling Period (hour)	HOM SOIL					LOM SOIL				
First 6	<u>CAT260</u>	<u>RAD85</u>	<u>B260</u>	<u>C</u>	<u>RAD260</u>	<u>C</u>	<u>CAT260</u>	<u>RAD85</u>	<u>B260</u>	<u>RAD260</u>
6th to 24th	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>
24th-30th	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>
30th-36th	<u>CAT260</u>	<u>B260</u>	<u>RAD85</u>	<u>C</u>	<u>RAD260</u>	<u>CAT260</u>	<u>B260</u>	<u>C</u>	<u>RAD85</u>	<u>RAD260</u>
36th-52nd	<u>CAT260</u>	<u>B260</u>	<u>C</u>	<u>RAD85</u>	<u>RAD260</u>	<u>CAT260</u>	<u>B260</u>	<u>C</u>	<u>RAD85</u>	<u>RAD260</u>
52nd-79th	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>	<u>CAT260</u>	<u>B260</u>	<u>C</u>	<u>RAD85</u>	<u>RAD260</u>
79th-118th	<u>RAD85</u>	<u>C</u>	<u>CAT260</u>	<u>B260</u>	<u>RAD260</u>	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>
118th-148th	<u>CAT260</u>	<u>C</u>	<u>RAD85</u>	<u>B260</u>	<u>RAD260</u>	<u>CAT260</u>	<u>C</u>	<u>B260</u>	<u>RAD85</u>	<u>RAD260</u>

# at  $p=0.05$

‡ see Table 7.3.3

TABLE 7.3.2 TOTAL CARBON (mg/100g soil) RELEASED AS CO<sub>2</sub> FROM INCUBATED SOILS UNDER DIFFERENT TREATMENTS IN A PERIOD OF 6 DAYS

Soils	Control	CAT260†	RAD85	B260	RAD260
HOM	58.4	54.0	61.7	58.8	72.4
LOM	24.6	21.1	26.1	25.8	42.4

†: CAT = catechin solution; RAD = water extract of radiata needles;  
B = water extract of beech leaves; Control = distilled water

TABLE 7.3.3 RATES OF ADDITION OF POLYPHENOLS (µg/g) AND CARBOHYDRATES (µg/g) FOR HOM AND LOM SOILS

Compounds	CONTROL	CAT260†	RAD85	RAD260	B260	GLU200	GLU+CAT
POLYPHENOLS	NIL	260	85	260	260	NIL	260
CARBOHYDRATES	NIL	NIL	81	247	109	200	200

† as for TABLE 7.3.2 , and GLU = glucose solution .



the 27th hour). In this period,  $\text{CO}_2$  evolution rates for CAT260, Control, B260, RAD85 and RAD260 were 23.0, 26.6, 29.2, 30.3 and 54.4  $\mu\text{g CO}_2$  per g soil per hour respectively for HOM, and 10.3, 14.6, 18.6, 21.1 and 37.2  $\mu\text{g CO}_2$  per g soil per hour respectively for LOM. The relative order in the rates of  $\text{CO}_2$  evolution between the treatments was similar in both soils, being:

RAD260  $\gg$  RAD85 > B260 > Control > CAT260 .

In addition, results (Table 7.3.1) indicate that the mean  $\text{CO}_2$  evolution rates in this period were significantly different.

The total amount of carbon released as  $\text{CO}_2$  in 6 days of incubation when apparent steady state conditions occurred under different treatments (Table 7.3.2), decreased in the order:

RAD260  $\gg$  RAD85 > B260 > Control > CAT260 .

This trend reflected that observed in the peak  $\text{CO}_2$  evolution rates occurring at about the 27th hour. The total amounts of carbon released from HOM soils under the different treatments were about double those released from LOM soils under corresponding treatments.

From the results obtained in the present experiment, it is evident that:

- (1) Catechin solution added to HOM or LOM soils led to a significant depression of the rates of  $\text{CO}_2$  evolved from the treated soils, compared to those added with distilled water (at the 27th hour: HOM 14% and LOM 30% depression).
- (2) Water extracts of radiata pine needles (RAD85 and RAD260) appear to promote greater rates of  $\text{CO}_2$  evolution than either

water extracts of beech litter or distilled water (HOM: RAD85 14%, RAD260 105% increase; LOM: RAD85 44%, RAD260 155% increase). However, in comparison, addition of RAD260 led to a substantially greater rate of  $\text{CO}_2$  evolution than that resulting from the addition of RAD85 (HOM 80% and LOM 77% greater), despite a larger amount of polyphenolic compounds in RAD260. It is probable that this disparity was associated with the larger amount of water-soluble carbohydrates added in the RAD260 treatment (Table 7.3.3).

(3) Despite equal concentrations of polyphenols, RAD260 added to both soils resulted in considerably greater rate of  $\text{CO}_2$  evolution than B260 (HOM 87% and LOM 101% greater), thus suggesting that  $\text{CO}_2$  evolution rates were promoted by the carbohydrates present in the water extracts.

(4) Although RAD85 contained a slightly smaller quantity of carbohydrates than B260 (Table 7.3.3),  $\text{CO}_2$  evolution rates recorded in soils added with RAD85 were generally greater than those from soils added with B260 (HOM 4% and LOM 13% greater). This disparity may be attributed to the larger content of polyphenolic compounds in B260, since  $\text{CO}_2$  evolution rates were apparently depressed in the presence of catechin.

(5) The carbon content of the soil is an important factor influencing the rate of  $\text{CO}_2$  evolution. Such an effect of carbon content is suggested by the higher  $\text{CO}_2$  evolution rates obtained in HOM soils (%C = 3.7) than those in LOM soils (%C = 2.2).

On the basis of these observations, it is therefore valid to infer that opposite actions were being exerted on

the rates of CO<sub>2</sub> evolution by the carbohydrates (increasing the rates) and the polyphenolic compounds (depressing the rates). However, the present results appear to suggest that the amount of carbohydrates has a greater influence than that of polyphenolic compounds. Other workers (e.g. Hu et al., 1972; Alexander, 1977) have also indicated that the magnitude of carbon mineralization is directly related to either the source of readily metabolizable substrates in the soil, or influenced by the addition of organic matter.

The inhibitory effect of polyphenols on decomposition, and thus CO<sub>2</sub> production, have been reported by a number of workers. For example, Benoit and Starkey (1968) found that the decomposition of cellulose and some hemicelluloses were much slower in the presence of tannin. The inhibitory effects were ascribed to both the inactivation of the microbial exoenzymes involved in the hydrolysis of such substrates and a chemical combination. In the present experiment, the inhibitory effect of polyphenolic compounds was observed to be more apparent in LOM than HOM.

It is unlikely that the trend in CO<sub>2</sub> evolution rates was an artefact of the elapsed time between each measurement carried out during the incubation, since this effect cannot account for the absence of double peaks in LOM soils, where sampling times and frequency were kept similar to those carried out for HOM soils. Moreover, other major factors governing the rate of CO<sub>2</sub> production such as temperature, moisture, pH and aeration (see Review Section 2.5.2.1) were all kept similar within each soil. Although drying and storing of soil may influence subsequent microbial growth on

rewetting (Spailing and Cheshire, 1979), this factor may not seriously undermine the results (showing differences) between treatments.

In the present study, although the differential  $\text{CO}_2$  evolution rates found were attributed primarily to the interactions of carbohydrates and polyphenolic compounds, it is also necessary to add that the importance of other substances present in the water extracts of litter in influencing  $\text{CO}_2$  evolution rates should not be ignored.

Of possible significance is the observation that  $\text{CO}_2$  evolution rates in HOM appeared to show two peaks (Figure 7.3.1). This seems to be consistent with the pattern of  $\text{CO}_2$  evolution rates reported by Nannipieri et al. (1979) for soil amended with glucose and sodium nitrate. However, these workers did not account for the above observation.

In the present study, it is possible that microbial growth was initially promoted by the sudden introduction of solutions, sustained temporarily by the readily metabolizable carbohydrates added and then shortly subsided upon the depletion of this very small energy source. These effects include those resulting from the rewetting of the soil described by Birch (1958). This view is consistent with the results showing apparently higher  $\text{CO}_2$  evolution rates in HOM soils added with RAD85 and B260 than those in HOM soils added with only distilled water. The second peak may be attributed to the microbial activity brought about by organic substrates and other secondary products in the soil which became solubilized by the solutions and made available to micro-organisms.

Although the above explanation is speculative, several observations appear to support this view. Firstly, RAD260 which contained the highest concentration of carbohydrates showed only one large peak in the rate of  $\text{CO}_2$  evolution. With a larger quantity of metabolizable substrates, a depletion was delayed thereby masking an apparent decline in the  $\text{CO}_2$  evolution rates. Furthermore, the  $\text{CO}_2$  evolution rate recorded after this peak at about the 27th hour of incubation was relatively similar in magnitude to those of the second peaks found with the other treatments, thus suggesting a similar effect due to substrates. This effect is likely to be related to the soil rather than the extracts, since there was a definite absence of second peaks in LOM soils.

The relatively lower  $\text{CO}_2$  evolution rates found with LOM soils may be ascribed to lower organic matter content and smaller microbial population present. However, this contention could only be confirmed by actual determinations of bacterial numbers in the soil.

### 7.3.2 Nitrogen Mineralization

Ammonium-N and nitrate-N levels found in LOM and HOM soils under the different treatments are shown in Table 7.4.1, together with their respective soil moisture contents at the end of the incubation period (14 days).

#### 7.3.2.1 Nitrate

Nitrate-N was not detected (limit  $> 0.1 \mu\text{g/g}$  soil) in LOM soil (under beech) and very low levels were found in HOM (under radiata pine). Regardless of treatments, nitrate-N

TABLE 7.4.1 MEAN AMMONIUM-N CONCENTRATION ( $\mu\text{g/g}$ ), NITRATE-N CONCENTRATION ( $\mu\text{g/g}$ ) AND MOISTURE CONTENT (% DW) OF SOILS INCUBATED WITH DIFFERENT SOLUTIONS TOGETHER WITH RESULTS OF DUNCAN'S MULTIPLE RANGE TESTS<sup>#</sup>

AMMONIUM-N							
HOM	RAD260(128.8) <sup>@</sup>	<u>RAD85(135.8)</u>	<u>B260(136.6)</u>	<u>CAT260(139.2)</u>	GLU+CAT(143.1)	CONTROL(156.2)	GLU200(163.2)
LOM	GLU+CAT(60.6)	<u>CAT260(66.1)</u>	<u>B260(67.4)</u>	RAD260(69.8)	RAD85(78.8)	GLU200(88.5)	CONTROL(91.6)
MOISTURE							
HOM	<u>B260(40.3)</u>	<u>RAD260(40.4)</u>	<u>CAT260(40.7)</u>	<u>GLU200(41.2)</u>	<u>GLU+CAT(41.4)</u>	<u>RAD85(41.7)</u>	CONTROL(42.4)
LOM	<u>CAT260(33.9)</u>	<u>RAD85(34.0)</u>	<u>B260(34.6)</u>	<u>RAD260(34.6)</u>	<u>GLU200(34.7)</u>	<u>GLU+CAT(35.3)</u>	CONTROL(36.2)
NITRATE-N							
HOM	GLU+CAT(0.7)	CONTROL(0.9)	RAD85(1.0)	GLU200(1.0)	B260(1.2)	CAT260(1.2)	RAD260(1.5)
LOM	<u>ALL &lt; 0.1</u>						

<sup>#</sup> at p = 0.05  
<sup>@</sup> solutions (see TABLE 7.3.3); data in parenthesis refer to mean value

was detected in 40 out of a total of 42 HOM soil samples and none was found in any of the LOM soil samples. All treatment solutions used had been previously analysed for ammonium- and nitrate-N, and both were not present in the solutions.

Although soils used for the incubation experiment were from Hanmer forest, the frequency and magnitude of nitrate levels were similar to those found in the field for soils from Granville forest (Section 6.3.3.1). At Granville, soil samples under radiata pine plantation frequently contained relatively higher levels of nitrate compared to those of soil samples from the beech site. This disparity in the field results has been attributed to the differences in soil pH and polyphenolic content of beech and radiata pine litter (Section 6.3.3.1). The pH of the soils used in the present incubation study was 5.4 for HOM and 5.0 for LOM. Although the pH of these soils were higher than those of the corresponding soils under radiata pine (pH 4.5) and beech (pH 4.2) in Granville forest, the relative order in pH magnitude between these incubated soils was reflective of that found in nitrate levels. This result is also consistent with reports that nitrification becomes almost negligible at pH 5.0 (Alexander, 1977).

There was no significant difference in the levels of nitrate produced when water extracts of beech and radiata pine litter were used. This result suggests that nitrification in these soils may be largely reflective of the soil properties such as quality and quantity of organic matter present (in addition to pH effect), rather than that due to the kind of litter extracts added.

### 7.3.2.2 Ammonium

Ammonium levels in LOM soil samples were consistently lower than those found in HOM soil samples under the same treatment. Levels of ammonium-N found after incubating the soils for 14 days ranged from 128.8 to 163.2  $\mu\text{g}$  per g soil in HOM and from 60.6 to 91.6  $\mu\text{g}$  per g soil in LOM (Table 7.4.1). Ammonium-N levels were observed to follow the order:

HOM, GLU200 > Control > GLU+CAT > CAT260 > B260 > RAD85 > RAD260

LOM, Control > GLU200 > RAD85 > RAD260 > B260 > CAT260 > GLU+CAT

The above orders bear no relationship to those of moisture contents (Table 7.4.1). For example, HOM soils treated with GLU200 showed the highest ammonium levels, but did not contain highest moisture content. Furthermore, moisture content was adjusted to about 60 percent of the water-holding capacity of each soil before incubation to be within the range for optimum ammonification (Alexander, 1977).

Both HOM and LOM soil samples treated with solutions containing polyphenols showed lower levels of ammonium at the 14th day of incubation when compared to those treated with distilled water or glucose (Table 7.4.1). For example, soils treated with GLU+CAT showed significantly lower ammonium levels than soils treated with GLU200; the difference was comparatively greater in LOM (difference = 27.9  $\mu\text{g/g}$ ) than in HOM (20.0  $\mu\text{g/g}$ ) soils. This result clearly suggests that catechin caused a reduction in the amount of ammonium produced.



Data obtained also indicate that both HOM and LOM soils treated with RAD260, which contained more than three times the amount of carbohydrates in RAD85 (Table 7.3.3), did not have higher ammonium levels than those in corresponding soils treated with RAD85. In addition, LOM soils treated with glucose did not show increased ammonium levels compared to those in soils treated with distilled water. These results, therefore, suggest that the amount of carbohydrates present in the treatment solutions did not have a noticeable effect on ammonium levels in the soils. Thus, it would appear that the influence due to carbohydrates is of lesser importance than that of polyphenols on ammonium levels in the soil.

There are several possible reasons for a lower ammonium level produced in the presence of polyphenols. One is associated with the apparent interaction between polyphenols and nitrogenous substrates. Polyphenols and proteins have been shown to react and form complexes (Handley, 1954, 1961). These reactions are favoured by a high ratio of polyphenol to protein (Basaraba and Starkey, 1966), and low pH conditions (Basaraba and Starkey, 1966; Benoit et al., 1968). In the present study, a close examination of the conditions existing in the soils during incubation suggests that polyphenol-nitrogenous substrate interaction may be a major factor responsible for the differential ammonium levels observed between soils and between treatments. The acidic soils (LOM pH 5.0; HOM pH 5.4) and water extracts of litter (beech pH 4.1; radiata pine pH 4.6) used may favour complex formation. This would be consistent with results obtained

in the present study indicating higher ammonium levels in HOM soil than in LOM soil which had a lower pH and N content (LOM N = 0.12%; HOM N = 0.24%).

It is possible that the concentrations of polyphenols in the water extracts used in the present experiment produced only a small inhibitory effect on the overall mineralization of N. The total amounts of polyphenols used (260  $\mu\text{g/g}$  max.) were considerably lower than the amounts of the estimated soil nitrogenous substrates. For example, based on 'crude protein' (total N  $\times$  6.25; see Allen, 1974), the amount of nitrogenous materials was 1.5 percent. This amount would also include a proportion of N materials which may be already in complex with polyphenols and lignin-like substances (Waksman and Iyer, 1932, 1933). According to Basaraba and Starkey (1966), the inhibitory effect of protein-tannin complexes increased with increase in the ratio of tannin to protein from 1:4 to 4:1.

It is also possible that any protein-polyphenol precipitates formed may have impregnated decomposable substrates such as hemicelluloses and cellulose, thereby possibly rendering these carbohydrates less susceptible to microbial decomposition (Handley, 1954, 1961). In the present study such an effect may lead to a deprivation of energy precursors for the microbial population, thus affecting N mineralization. These interactions may be more significant in soils of low than high organic matter contents.

Inhibition of decomposition of litter substrates and N mineralization have also been attributed to direct inactivation of microbial exoenzymes by tannins. Inactivation of

diverse enzymes by polyphenolic compounds have been reported (Goldstein and Swain, 1965; Hathaway and Seakins, 1958; Pollard et al., 1958; Porter and Schwartz, 1962; Pridham, 1963). A similar effect has been reported for nitrification (Basaraba, 1964). Extracts of leaves have also been reported to inhibit development of the free-living *Azotobacter* (Bukatsh and Saurig, 1963) and nitrifying bacteria (Hesse, 1957). According to Benoit and Starkey (1968), cellulase and urease activities were reduced or even almost completely prevented at certain tannin concentrations. These workers found that the enzyme urease was almost completely inactivated where the tannin-enzyme ratio was 1:10.

Probably, more than one specific process was interacting to produce the results observed in the present study. However, regardless of the nature of these processes, the results obtained seem to suggest that both carbonaceous and nitrogenous substrates were protected against microbial decomposition and mineralization. Thus, it is not unreasonable to believe that differences in vegetation cover and overlying tree litter may play a major role in dictating the status of soil N availability. What is more notable is the fact that the concentration of polyphenols needed to lower ammonium production in soils is extremely small (260  $\mu\text{g}$  per g soil). Compared to the polyphenol concentrations in beech leaf litter of 14.8 percent (Section 3.3.7.1), the apparently effective concentration found in the present study constituted only a negligible fraction (0.2%) of that in leaf litter.

It is necessary to state that the arguments offered to account for the differences in ammonium levels in soils

between treatments had been based on the assumptions that the relative magnitude in the levels of ammonium accumulation in soils under the different treatments were at a steady state and that fluctuations, if any, were in phase. For example, the ammonium concentrations determined at the 14th day of incubation reflected the overall relative levels in ammonium concentrations. Such a view appears to be supported by  $\text{CO}_2$  evolution rates which also showed a steady state condition at the 14th day (Figure 7.3.1), thus indicating that the pattern of microbial activity in the soils was in phase.

Radiata litter extracts were observed to be less favourable to ammonium production in HOM soil (radiata origin) than beech litter extracts, and vice versa in LOM soil (beech origin). A possible explanation of this result relates to the ability of the microbial population associated with one vegetation to mineralize N in the soil which had previously been unavailable to microbial populations associated with another vegetation. However, no firm conclusions on such a postulation could be drawn from the present results without further study. Such an effect suggested above may be related to that described by Stone and Will (1965) to account for N-deficiency in second generation radiata pine.

## 7.4 CONCLUSIONS

The results obtained in the present study showed that  $\text{CO}_2$  evolution rates and levels of ammonium produced in soils were depressed by the addition of litter extracts containing polyphenolic compounds and also catechin solution. Only a low concentration of polyphenolic compounds, approximately equivalent to 0.2 percent of that in fresh beech leaf litter, was sufficient to produce this inhibition.

Carbon dioxide production was stimulated by the addition of water-soluble plant carbohydrates (in litter extracts). The magnitude of this effect was greater than that produced by polyphenol inhibition. Generally, there was no apparent effect of carbohydrates, with and without the presence of polyphenols, on the levels of ammonium produced.

Higher rates of  $\text{CO}_2$  evolution and levels of ammonium produced were related to higher organic matter content in the soil. The trend in the relative rates of  $\text{CO}_2$  evolution from the soils after addition of different water extracts of litter and catechin solution was not affected by the organic matter content of the soils, although this effect was shown by the ammonium levels observed.

Nitrate production was generally negligible or absent in these acidic forest soils used. Neither the addition of carbohydrate solution (glucose), polyphenol solution (catechin) nor water extracts of both beech and radiata litters containing these two compounds affected the levels of nitrate produced.

## CHAPTER 8

AN ALTERNATIVE METHOD FOR THE EXTRACTION  
OF LIPID COMPONENTS OF LITTER SAMPLES

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## CHAPTER 8

AN ALTERNATIVE METHOD FOR THE EXTRACTION OF LIPID  
COMPONENTS OF LITTER SAMPLES

## 8.1 INTRODUCTION

Fats, waxes and resins (frequently referred to as lipids) are probably the least studied of plant organic components. This may be the result of difficulties in fractionating the lipids into definite chemical entities. These compounds form a convenient analytical group rather than a structural group, having perhaps only the common property of being variably soluble in numerous organic solvents. Some of the widely used solvents include acetone, benzene, chloroform, ethanol, ether, methanol, petroleum ether and mixtures of these solvents. The best solvent will depend on the nature and kind of lipids, and conversely, the yield and type of extract will depend on the solvent used. For example, lipids linked in combination with protein and carbohydrates are largely insoluble in non-polar solvents such as ether (Braids and Miller, 1975).

One of the conventional apparatus used in the extraction procedure involves the use of the Soxhlet extractor (see Allen, 1974; Stevenson, 1965), which provides a continuous and efficient solvent extraction of samples. However, a

problem associated with the use of this apparatus is the difficulty encountered in performing large numbers of analyses which are usually required for ecological studies.

The objective of the present study was to examine the feasibility of an alternative method of extraction to that using Soxhlet extractors in order to accommodate the large number of samples. To achieve this aim, the extraction was performed using extraction bottles (200 ml capacity) into which plant samples were placed with the solvent. In addition, the reliability of the alternative method, together with the effects of temperature, duration of extraction and the reproducibility of results between sample batches were examined. This was done in order to ensure that the results obtained will be reliable and acceptable.

## 8.2 MATERIALS AND METHODS

### 8.2.1 Solvent Used

Petroleum ether (40 - 60°C) was selected for the extraction of non-polar lipids primarily for its relatively less hazardous nature compared to other solvents. This solvent should satisfactorily extract most non-polar lipids including hydrocarbons (Allen, 1974).

The resins, which are more polar than fats and waxes, were removed from the residue after petroleum ether extractions with 75% aqueous ethanol extraction. This solvent also removes the water-soluble carbohydrates and polyphenolic compounds, the latter being extracted most efficiently by this solvent (Swain, 1965).



As the above extractions are basically exhaustive rather than selective extractions, it will be more appropriate to refer to them as ether extracts (EE) and aqueous ethanol extracts (AE) respectively.

### 8.2.2 Sample Preparation

Only air-dried litter samples were used for the EE and AE extractions since oven drying (105°C) of litter may result in losses of some volatile organic substances (Allen, 1974). Subsamples were used to determine litter moisture content for moisture correction of results obtained. All samples were ground to pass through a 40 mesh (0.4 mm) sieve to ensure homogeneity of tissues, particularly with twig litter which contains large amounts of bark material.

### 8.2.3 Experimental Procedure

The extraction vessels used in the alternative method consist of basically pop-top glass bottles (200 ml capacity). The solvent:sample (v/w) ratio used was approximately 50:1. This high solvent:sample ratio is favourable as it reduces problems associated with solvent saturation. These vessels were kept in a constant temperature (49°C for petroleum ether extraction and 62°C for aqueous ethanol) water bath to provide uniform temperature.

Tissue samples, about 1g size, were first exhaustively extracted with petroleum ether. On completion, the solutions were filtered through a #540 Whatman filter paper into drying tubes (100 ml capacity). Each bottle and filter paper was then rinsed out with small volumes of fresh

warm petroleum ether. After air-drying, the ether-extracted residue and filter paper were placed back into their respective bottles and extracted with a volume of 75% aqueous ethanol. On completion, the solutions were filtered and washed with fresh warm aqueous ethanol into 100 ml volumetric flasks, and made up to volume with aqueous ethanol. A large aliquot (50 ml) of each of these solutions was removed and placed into another set of drying tubes.

The aqueous ethanol extracted residues were finally oven-dried ( $105^{\circ}\text{C}$ ) for 24 hours and subsamples taken for holocellulose (HOL) and residual lignin determinations (see Section 3.2.4). The isolation of HOL and quantification of residual lignin (by difference) did not form part of the present examination of the alternative extraction method. However, HOL was included in the results only to provide a measure of the effect the preceding extractions had on the values of HOL obtained.

Polyphenol concentration in the aqueous ethanol solutions was determined by diluting suitable aliquots (2 ml) so that the final ethanol content was less than 2% . Higher ethanol content produces high blank values during the colorimetric determination of polyphenols by the method described in Section 3.2.4.5 .

Drying of both petroleum ether and aqueous ethanol solutions for weight determinations of the respective extracts were achieved with jets of warm air. It is essential to use drying tubes with vertical walls to prevent creeping of the solvent-extract front over the mouth of the tubes. Commonly, the solutions (entire volume for petro-

leum ether and 50 ml for aqueous ethanol) were reduced to dryness within 2 hours. These extracts were then dried further at 70°C for 2 hours before weighing.

#### 8.2.4 Treatments Used in Examination of the Alternative Method

To examine the method, separate plant standards of leaf, twig and needle tissues (see Section 3.2.4.1) were used. Twenty-four samples of each tissue were extracted with petroleum ether at 50°C. Four samples of each tissue were removed after 1, 3, 6, 14, 22 and 40 hours of extraction. All samples were then extracted with 75% aqueous ethanol at 60°C and removed accordingly after each prescribed duration as was done in the petroleum ether extraction.

After the optimum extraction duration was established, the effect of temperature (at 20, 30, 40, including 50°C) on the amount extracted at this duration (22 hours) was examined.

Batch reproducibility and comparison in the amount extracted by the alternative method and Soxhlet method were eventually examined at the optimum duration and temperature.

Blanks were carried through concurrently with each experimental run .

### 8.3 RESULTS AND DISCUSSION

Weights of extracted material from litter samples using different extraction times are shown in Figure 8.3.1.1 and Table 8.3.2.1. Results of comparisons for amounts extracted between different sample batches and using different temperatures and extraction methods are given in Tables 8.3.3.1, 8.3.4.1 and 8.3.5.1 respectively.

#### 8.3.1 Duration of Extraction

The extraction of both EE and AE were largely completed by the 22nd hour. Further extraction beyond this time did not appear to increase the amount extracted. Except for EE of leaf and twig litter, the amount extracted within the first hour did not differ markedly from that extracted in the 40-hour duration. For AE, these amounts removed in the first hour accounted for approximately 84, 84 and 67 percent of those removed after 40 hours from needle, leaf and twig litter respectively. A similar pattern in the amounts of polyphenols removed from litter samples was also observed.

For some unknown reasons, EE in leaf and twig litter showed a somewhat irregular pattern. Twig litter exhibited a marked increase in the amount extracted from the 3rd to the 6th hour. Leaf litter showed increases in amount extracted from the 1st to the 3rd hour, and again from the 14th to the 22nd hour. Discounting the possibility of contamination, this could have resulted from some kind of delay due to perhaps a protective layer of more difficult to extract or wet material.

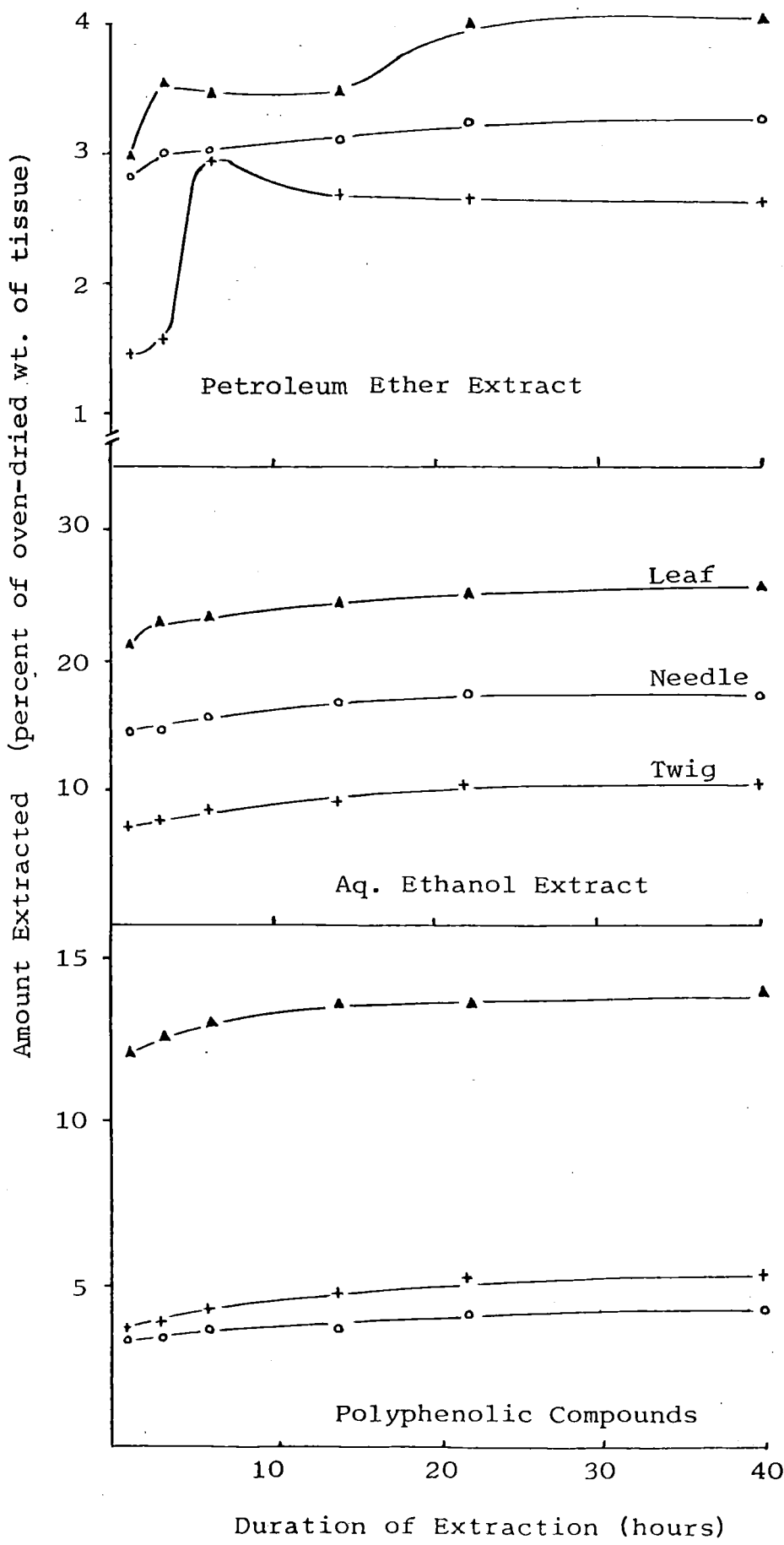


FIGURE 8.3.1.1 Effect of duration of extraction on yield of extracts from litter tissues

### 8.3.2 Batch Consistency and Sample Variability

No statistically significant difference was found in the amounts of EE, AE, polyphenols and HOL obtained from litter between two batches of samples using the alternative extraction method with a duration of 22 hours (Table 8.3.3.1).

Coefficients of variation for the 22 hour duration extraction in all tissues ranged from 1 to 7 percent. Variability was generally greater for twig than either leaf or needle litter. For the purposes of the present study, this range of coefficient of variation could be reasonably regarded as within an acceptable limit.

### 8.3.3 Temperature Effect

Only needle litter was used to examine the effects of temperatures at 20<sup>o</sup>, 30<sup>o</sup>, 40<sup>o</sup> and 50<sup>o</sup>C on the amounts of EE, AE and polyphenols extracted (Table 8.3.4.1). The amounts of these fractions extracted increased with increasing temperatures. Thus it is clear that temperature has a strong influence on the amount of these substances extracted from litter.

For EE, the amount extracted did not decline at the highest temperature (50<sup>o</sup>C) that could be satisfactorily operated in, using the particular petroleum ether. The measured temperature of the petroleum ether condensate was 49<sup>o</sup>C. The corresponding temperature found for 75% aqueous ethanol was 62<sup>o</sup>C.

TABLE 8.3.2.1 Effect of duration of extraction on yield of extracts, polyphenols and holocellulose from litter tissues using the alternative method

Extraction duration (hrs)	Ether Extract	Aq.Ethanol Extract	Poly-phenols	Holo-cellulose
<u>Needle</u>				
1	2.82 (3) <sup>#</sup>	14.56 (2)	3.28 (2)	54.81 (1)
3	2.99 (1)	14.62 (2)	3.29 (2)	55.00 (1)
6	2.91 (5)	16.86 (1)	3.76 (4)	52.67 (3)
14	3.11 (9)	17.03 (2)	3.74 (1)	53.16 (2)
22	3.22 (2)	16.96 (1)	3.82 (1)	53.84 (2)
40	3.21 (6)	17.37 (1)	4.12 (2)	52.17 (2)
LSD	0.19	0.36	0.12	1.32
<u>Leaf</u>				
1	2.99 (11)	21.43 (2)	12.08 (1)	55.28 (2)
3	3.56 (2)	23.35 (2)	12.65 (2)	54.17 (2)
6	3.45 (8)	23.78 (1)	12.91 (1)	54.55 (1)
14	3.48 (4)	24.66 (1)	13.60 (1)	55.11 (1)
22	3.96 (3)	25.70 (1)	13.58 (2)	55.25 (1)
40	4.05 (1)	25.56 (1)	13.95 (1)	52.28 (2)
LSD	0.26	0.40	0.42	1.23
<u>Twig</u>				
1	1.97 (17)	7.20 (4)	3.40 (2)	56.42 (1)
3	2.04 (8)	7.92 (2)	3.76 (1)	57.14 (3)
6	2.96 (23)	8.78 (3)	4.18 (3)	54.02 (1)
14	2.66 (16)	9.36 (3)	4.58 (3)	54.74 (4)
22	2.47 (7)	9.80 (5)	4.77 (5)	55.40 (1)
40	2.56 (12)	10.70 (3)	5.28 (5)	53.16 (3)
LSD	0.51	0.45	0.19	1.99

LSD = least significant difference,  $p = 0.05$

# amount extracted in % ; coefficient of variation is given in parenthesis

TABLE 8.3.3.1 Batch consistency and variability in the amount of ether extract (EE), aqueous ethanol extract (AE), polyphenols (P) and holocellulose (HOL) obtained using the alternative method @

Sample	EE	AE	P	HOL
Needle				
Batch A	3.22(2) <sup>#</sup>	16.96(1)	3.82(1)	53.84(2)
B	3.14(2)	17.41(1)	4.04(3)	51.75(1)
Leaf				
Batch A	3.96(3)	25.70(1)	13.58(2)	55.25(1)
B	4.02(2)	25.36(1)	13.37(5)	52.85(1)
Twig				
Batch A	2.47(7)	9.80(5)	4.77(5)	55.40(1)
B	2.61(5)	10.66(3)	5.09(2)	53.28(3)

# as for TABLE 8.3.2.1

@ duration of extraction 22 hours

TABLE 8.3.4.1 Effects of temperature on amount of EE, AE and polyphenols extracted using the alternative method for needle litter after 22 hours extraction

Temperature, °C	EE <sup>@</sup>	AE	P	HOL
20	1.96(7) <sup>#</sup>	14.19(1)	3.25(1)	57.22(1)
30	2.53(4)	13.97(2)	2.99(5)	56.20(1)
40	2.33(13)	15.89(1)	3.62(1)	55.98(1)
50	3.99(6)	16.52(1)	3.83(3)	54.41(1)
LSD	0.31	0.26	0.14	0.66

LSD = least significant difference at  $p = 0.05$

# as for TABLE 8.3.2.1

@ as for TABLE 8.3.3.1



TABLE 8.3.5.1 Comparison of amounts of ether extracts (EE), aqueous ethanol extracts (AE), polyphenols and holocellulose (HOL) obtained using the Soxhlet and alternative methods

Tissue/Method	EE	AE	Polyphenols	HOL
Needle				
Soxhlet	3.64 (5) <sup>#</sup>	14.33 (4)	2.92 (5)	51.84 (2)
Alternative	3.22 (2)	15.69 (1)	3.52 (1)	53.84 (2)
Levels of significance	*	*	***	*
Leaf				
Soxhlet	3.86 (13)	20.96 (4)	10.98 (5)	53.63 (4)
Alternative	3.96 (4)	25.70 (1)	13.58 (2)	55.25 (1)
Levels of significance	ns	***	***	ns
Twig				
Soxhlet	2.36 (5)	7.77 (6)	3.27 (3)	55.96 (1)
Alternative	2.47 (7)	9.80 (5)	4.77 (5)	55.40 (1)
Levels of significance	ns	***	***	ns

# as for TABLE 8.3.2.1

extraction duration in both methods was 22 hours

\* Denotes  $P < 0.05$ ; \*\*\* Denotes  $p < 0.001$ ; ns Denotes not significant

#### 8.3.4 Comparison of Results Obtained by the Alternative and Soxhlet Methods

Comparisons were made between results obtained by these two methods using amounts of EE and AE extracted from leaf, twig and needle at the prescribed duration (22 hours) and temperatures (EE at 49°C; AE at 62°C).

The results (Table 8.3.5.1) show that except for EE of needle litter, the alternative method gave values that were significantly higher than those obtained from the Soxhlet method, especially in the AE of leaf litter. This disparity may be partly caused by the extraction process occurring within the Soxhlet extractor. It was observed that the solvent solution in the boiling flask became progressively concentrated with organic substances extracted from the litter samples with each successive Soxhlet cycle. On account of this, the turnover time for a constant volume of solvent became longer, probably brought about by the resultant higher boiling point of the solvent-extract mixture. This effect occasionally gave rise to a certain amount of charring of the extracts on the walls of the boiling flask, thus leading to a lower amount of extracts recovered. The charring effect was more prominent when the volume of the solvent in the boiling flask was at its lowest in the solvent cycle.

The number of cycles of constant volume turnover are expected to vary between each Soxhlet set, although this may become less important over a longer duration of extraction. It may very well be that the greater variability of replicate samples obtained in the Soxhlet method (Table 8.3.5.1),

compared to those obtained in the alternative method, reflected the greater variability in operating temperatures between Soxhlet sets. However, it needs to be emphasized that these comparisons cannot allow a distinction to be made between an over-estimation or an under-estimation of the true value of the extracted materials by any of the methods studied.

By comparison, the alternative method, besides providing a reasonably precise and rapid determination of large number of samples, also offer other advantages including lower cost of apparatus and its replacements. However, some factors associated with the alternative method may require further consideration. The method of filtering the extracted solution is relatively tedious and also may cause some extracts to be left behind in the filter paper. Although the latter was overcome by a light washing with fresh warm solvent, both these problems can be eliminated by performing the extraction in Pyrex centrifuge tubes followed by centrifugation. In the Soxhlet method, coloured substances were also observed to collect around the neck of the cellulose thimbles during extraction.

#### 8.4 CONCLUSIONS

The data obtained in the present study indicate that apart from minor limitations discussed, the alternative method offers many advantages over the Soxhlet method. A larger number of samples can be extracted with much less demand on apparatus. For example, it is easier to extract

samples using 80 bottles or tubes at one time in a constant temperature water bath using the alternative method than to set up and operate 80 Soxhlet extractors. Cost-wise, the alternative method is also more favourable. In addition, less variability in results was obtained in the alternative method. Due to the unknown nature of the organic substances present in the litter samples studied it is not possible to evaluate and compare the efficiency of extraction between the two methods.

## CHAPTER 9

## GENERAL SUMMARY

The literature related to litter production, litter decomposition, organic matter accumulation in the forest floor, and carbon and nitrogen mineralization in forest ecosystems was reviewed. Some relevant aspects relating to chemical composition of plant materials and their effects on ecological processes were emphasized.

In order to compare the addition, decomposition and accumulation of organic matter between native beech (*Nothofagus* spp.) forests and radiata pine (*Pinus radiata*) plantations, pairs of adjacent beech and *Pinus radiata* stands in three major forest areas (Granville, Hanmer and Golden Downs) located in the South Island of New Zealand were used. These included the following:

- |                                    |   |
|------------------------------------|---|
| Granville forest:                  | hard beech ( <i>Nothofagus truncata</i> ) and<br>1955-planted <i>Pinus radiata</i> stand,   |
| Hanmer forest                      | : mountain beech ( <i>Nothofagus solandri</i> var<br><i>cliffortioides</i> and 1960-planted <i>Pinus</i><br><i>radiata</i> stand, and   |
| Golden Downs<br>forest<br>(Nelson) | : mixed beech (dominant species: <i>Nothofagus</i><br><i>solandri</i> var <i>solandri</i> and <i>Nothofagus solan-</i><br><i>dri</i> var <i>cliffortioides</i> ) and 1956-planted |

*Pinus radiata* stand. An additional 1956-regenerated *Pinus radiata* stand was used in this forest.

Field measurements involving litter-fall and litter-bag decomposition were conducted in the above forest stands over a period of two years.

Three additional pairs of adjacent native (beech and podocarp-hardwood) and *Pinus radiata* forest stands were used in another part of the present study aimed at quantifying the accumulation of organic matter in the forest floor and top mineral soil (0-20cm). These were:

- Hanmer forest : mountain beech and 1926-planted *Pinus radiata* stand,
- Hochstetter forest : podocarp-hardwood and 1967-planted *Pinus radiata* stand, and
- Peel forest : podocarp-hardwood and 1937-planted *Pinus radiata* stand.

This study also included another two *Pinus radiata* stands (1967-planted and 1947-planted) in the Golden Downs forest.

Dynamics of organic matter decomposition were studied in Granville forest (hard beech and 1955-planted *Pinus radiata*) by measuring directly in the field the rates of mineralization of carbon and nitrogen over a period of two years.

In each of the forest stand at Granville, Hanmer and Nelson, the experimental area used for the above field measurements of litter addition (litter-fall), litter decomposition, and carbon and nitrogen mineralization (at Granville

only) was 50 x 30m, each subdivided into 5 experimental plots (10 x 30m). This was done to facilitate direct statistical comparisons of litter addition and decomposition results between adjacent beech and radiata pine stands. Using annual litter-fall data, plot and sample variances between adjacent beech and radiata pine stands of each forest were analysed and found to be homogeneous. This facilitated valid statistical comparisons on a pooled sample and plot basis of experimental data within each forest.

Litter-fall in each of the forest stand studied at Granville, Hanmer and Nelson was estimated by field measurement using 2 litter-traps ( $0.38 \text{ m}^2$  collection area) per plot. All litter-fall samples collected monthly were separated into leaves, twigs, wood (> 1cm diameter) and "others" component for beech, and needles, pollen cones, female cones and wood for radiata. These litter components collected monthly were bulked over a three-month period on a plot basis for chemical analyses which included nitrogen (N), carbon (C), phosphorus (P), potassium (K), magnesium (Mg), Calcium (Ca), the water-soluble components of carbohydrates (WSC), polyphenols (WSP) and total materials (WSF), and the organic constituents of ether-extractable substances (EE), aqueous ethanol-extractable fraction (AE), holocellulose (HOL) and residual lignin (RLIG)

Annual litter-fall in beech stands were generally greater than those occurring in the adjacent radiata stands. Annual litter-fall values obtained ranged from 3915 to 7471 kg/ha (mean 5921 kg/ha) in the beech stands, and from 1445 to 5522 kg/ha (mean 3932 kg/ha) in the radiata stands. Peak litter-fall during the year occurred in spring (October-

November) for both types of forest at Granville, Hanmer and Nelson. Leaf material accounted between 36 and 67 percent of the annual total litter-fall in beech forests, while needle litter accounted between 72 and 96 percent of those in radiata pine plantations.

In these forest stands, except for K, seasonal variation in the concentration of the macro-nutrient elements studied and the relative distribution of the water-soluble and organic constituents was not observed. At Hanmer and Nelson, peak K concentrations in leaf and needle litter were found to occur in autumn (March-April).

In general, radiata pine needles had higher concentrations of N and P than beech leaves in each of the three forests studied. However, the "others" litter components of beech stands had the highest concentrations of N and P among all the litter components. Differences in nutrient concentrations were found between litter components and also between forests. Such differences were attributed mainly to climatic and site differences.

Relative distributions of the water-soluble and organic constituents varied according to litter components studied. Marked differences were found in the WSP concentration between beech leaf and radiata pine needle (range of 3-monthly mean values: beech 10.4-18.2 percent, radiata 2.9-9.2 percent). A lower RLIG concentration in beech leaves as compared to that in radiata pine needles was apparent. In general, branchwood contained high HOL content (>70 percent) although the distribution values for the other constituents were usually very low (e.g. WSC < 2 percent, EE < 0.6 percent).



Three-monthly and annual litter-fall budgets for the macro-nutrient elements, carbon and water-soluble components in beech forests were greater than those in their adjacent radiata pine stands. Amounts of total macro-nutrients ( $N + P + K + Mg + Ca$ ) returned annually in the two year period (1976/77 and 1977/1978) in radiata pine stands accounted between 35 and 65 percent of those returned in their adjacent beech stands. These differences were attributed primarily to a larger litter-fall biomass in beech stands.

In the three forests at Granville, Hanmer and Nelson, spring (October-November) and summer (December-January) were the periods when large differences occurred in the amounts of macro-nutrients and the other plant constituents returned to the forest floor between beech and radiata pine stands. These differences between stands were most pronounced in the amounts of WSP.

An apparent relationship was observed between macro-nutrient levels and the distribution of organic constituents in plant litter, especially N and WSC. This relationship was explained in terms of the relatively slow N release from litter in connection with results found in the Hanmer radiata stand where stand thinning had taken place previously.

The decomposition of litter in the beech and radiata pine stands was followed for about 26 months using litter-bag technique. Twenty-five nylon mesh bags (25 x 25cm, 1mm aperture) containing known amounts of beech (leaf+twig) litter and a similar number containing radiata (needle) litter were placed in each of the 5 plots of the respective stands at Granville, Hanmer and Nelson at about October 1976.

Two bags were withdrawn from each plot after different periods of decomposition (Granville: after 3, 5, 8, 10, 15, 21 and 26 months; Hanmer: 4, 8, 10, 15, 21 and 26 months; Nelson: 2, 4, 7, 9, 11, 14, 20 and 25 months) and the weight of litter remaining determined. Litter-bags from each plot were bulked, and for beech litter, separated into leaf and twig litter components. Chemical analyses were done separately on leaf, twig and needle litters of each plot for N, P, K, Mg, Ca, carbon, water-soluble components (WSC, WSP, WSF) and the organic constituents (EE, AE, HOL, RLIG).

Losses in weight of beech and radiata litter at the end of the 26-month period ranged from 46 to 54 percent and from 37 to 54 percent of the initial weight of litter used, respectively. Large weight losses occurred in the first few months ( $< 5$  months) of decomposition. These rapid losses in weight were attributed to the loss of water-soluble materials. Only marginal differences were observed in decomposition rates between the two species of litter in all the three forests. First-year weight loss rates of litter (k values) computed from logarithmic regression analysis ranged from 0.40 to 0.47 for beech and 0.33 to 0.48 for radiata.

Except for N and RLIG, the concentrations of the nutrients and relative distributions (or concentrations) of water-soluble components and organic constituents generally declined with time. Those of K and the water-soluble components, especially polyphenols, declined rapidly in the early stages of decomposition. In Granville, significant correlations were obtained between N and RLIG concentrations in

both beech and radiata litters during decomposition. Significant correlations were also obtained between N and WSP, and between WSP and RLIG concentrations in beech litter. These results were ascribed to polyphenol-nitrogenous substrates complex formation.

First-year weight loss rates (k values) for the elements, water-soluble components and organic constituents ranged from a low value for N (0.10 to 0.27) and RLIG (0.05 to 0.17) to a high value for K (0.43 to 1.47) and WSP (0.91 to 1.55). Loss rates of P, K, EE and HOL were generally greater for radiata pine litter than beech, although the reverse order was found for Mg, carbon and RLIG. Nitrogen, Ca, AE and the water-soluble components showed no consistent differences in loss rates.

Generally speaking, despite greater returns of litter-fall biomass and nutrients in beech stands than radiata pine stands, the radiata pine stands apparently recycled greater amounts of P and K than beech. Using data obtained from litter-fall measurements (Section 3.3.8) and nutrient loss rates determined (Section 4.3.2.2), the amounts of P and K released from litter-fall during the two-year study period were estimated. In the beech stands the values ranged from 0.5 to 3.6 kg/ha (mean 2.2 kg/ha) for P and from 8.6 to 17.5 kg/ha (mean 12.1 kg/ha) for K. The corresponding values for the radiata pine stands were 1.5 to 4.8 kg/ha (mean 2.9 kg/ha) for P and 11.6 to 28.3 kg/ha (mean 18.3 kg/ha) for K. On the other hand, larger amounts of Mg and Ca were recycled by beech than by radiata pine while no consistent differences were apparent for N.

It was not possible to develop a general model for the prediction of first-year decomposition rates of litter in the three forests studied (Granville, Hanmer and Nelson) using linear regression equations based on initial chemical composition parameters. This was attributed to climatic variation and changes in the relative control by the different litter organic constituents on litter decomposition rates with time. Data obtained showed that litter decomposition occurring in the first year was governed to different extent by HOL, AE and RLIG. In the extended period of 26 months, the weight change during decomposition in HOL alone accounted for more than 43 percent of the weight change in litter recorded at various stages of decomposition. In the same period, contributions from AE declined from 28 percent to 9 percent while those from RLIG increased from 9 percent to 34 percent.

In quantifying the organic matter accumulation in the forest floor, the forest floor (L+F+H depths) and top-soil (0-20cm) in 6 pairs of adjacent native and radiata stands (at Granville, Hanmer, Nelson, Hochstetter and Peel forest) were sampled using a  $0.025 \text{ m}^2$  guide frame. Forest floor and top-soil samples, at least 1 meter apart, were obtained along a line of predominant slope and as far removed from trees as possible. Macro-nutrient concentrations and total contents in these samples were determined. In addition, cation exchange capacity and levels of exchangeable cations for top-soil were determined.

Data obtained showed that, except for the forest floors in the native stands at Granville and Hochstetter, no significant differences were found in forest floor weights between

adjacent native and radiata pine stands. Total weights of the forest floors ranged from 25 to 464 tonnes/ha (mean 173 tonnes/ha for native stands, and from 9 to 79 tonnes/ha (mean 32 tonnes/ha) for radiata pine stands. The litter (L) layers accounted for 11 percent and 22 percent of the total weights of the forest floor in beech and radiata pine stands respectively. The above results were discussed with respect to forest management practices.

No significant differences were found in the nutrient concentrations between native and radiata pine stands in both forest floors and top-soils. In the beech stand at Granville, concentrations of K, P and Ca in the relatively thick ( $> 25\text{cm}$ ) forest floor were found to decrease with depth while Mg and N remained about constant.

In general, native stands accumulated greater amounts of nutrients in the forest floor than radiata pine stands. However, these differences were smaller in the top-soil and in some cases radiata pine stands accumulated apparently greater amounts of nutrients. This result suggests that the nutrient status of the top-soil in the radiata pine stands studied were more favourable for tree growth compared to those of the top-soil in their native counterparts. Other properties of top-soil such as levels of exchangeable cations and Bray-P were also found to be more favourable in radiata pine stands.

Forest floor carbon dioxide evolution rates in the beech and radiata pine stand at Granville were measured in the field from August 1976 to October 1978. The effects on  $\text{CO}_2$  evolution of clearcutting a forest stand and burning of the forest floor were also examined at Larry's Creek Experimental

Area in the period from March 1977 to October 1978. Rates of  $\text{CO}_2$  evolution (over 24 hours) were measured *in situ* using the technique employing open-ended plastic containers. Some aspects of the apparatus used, including the temperature and light intensity within these "respirometers" were examined. The reliability of this method for estimating  $\text{CO}_2$  evolution rates in the field was evaluated.

Rates of  $\text{CO}_2$  evolution in both beech and radiata pine stands were significantly correlated with air temperatures (beech:  $r = 0.846^{***}$  ; radiata pine:  $r = 0.897^{***}$ ) but not with soil and/or humus moisture contents. A relationship was also observed between temperatures and rates of  $\text{CO}_2$  evolution in the forested, clearcut and burned sites at Larry's Creek. Peak  $\text{CO}_2$  evolution rates recorded for both stands at Granville and the three sites at Larry's Creek occurred in late summer (about February).

At Granville, forest floor  $\text{CO}_2$  evolution rates in the beech stand were apparently higher than those recorded in radiata pine stand. This disparity was attributed mainly to root respiration. At Larry's Creek, it was found that clear-cutting a forest stand and burning of the forest floor apparently increased the rates of  $\text{CO}_2$  evolution, compared to those of the forest site. Higher rates of  $\text{CO}_2$  evolution of the clearcut site compared to those of the burned site was attributed jointly to a decrease in labile carbon substrates in the burned site and more decomposable organic matter in the clearcut site.

At Granville, between December 1976 and November 1977 (a period of one year), amounts of carbon lost as  $\text{CO}_2$  from

the beech and radiata pine forest floors estimated by integrating predicted  $\text{CO}_2$  evolution curves were found to be 1893 kg/ha and 1395 kg/ha respectively. These amounts were about than three times higher than expected from carbon released from annual litter-fall in the respective stands. This disparity was attributed to root respiration as an important contributor to the  $\text{CO}_2$  produced at these stands.

Mean forest floor temperatures at the beech and radiata pine stands at Granville were determined using the sucrose inversion method. In this method, tubes of sucrose solution were placed in the forest floor (8cm depth) . Mean temperatures were determined from the angles of rotation of exposed and unexposed sucrose solutions.

Results obtained showed significantly higher mean forest floor temperatures occurred at the radiata pine stand compared to those at the beech stand during summer (December-February). The reverse situation was found in winter (June-August). This pattern was attributed to the effect of forest canopy and micro-climatic conditions due to frosts and insolation. Air temperatures were significantly correlated with forest floor temperatures.

Dynamic changes in the nitrogen levels of forest floor (F+H) and top-soil (0-20cm) were studied in the beech and radiata pine stands at Granville. Nitrogen mineralization was measured in the field using fresh samples and field incubated core samples. Core samples were prepared by coring fresh top-soil (0-20cm) and placing it in nylon mesh (0.045mm) tubes to a depth of 20cm, together with humus materials placed on top of it (6-8cm depth). These prepared core samples were

then incubated *in situ* over a time period ranging from one to three months. Ammonium-N and nitrate-N levels in freshly collected humus and top-soil samples and those in the incubated samples were determined.

In all humus and top-soil samples, either fresh or incubated, nitrate levels were generally not detected ( $< 0.1 \mu\text{g/g}$ ) or were present in negligibly low levels. This was found for both beech and radiata pine stands although, in comparison, radiata pine appeared to favour a greater nitrate accumulation than beech. These above results were attributed largely to pH effects.

In contrast, ammonium was found in all humus and top-soil samples, either fresh or incubated, from both beech and radiata pine stands. For fresh samples, it was observed that ammonium levels in humus (beech: range 11.0 to 63.1  $\mu\text{g/g}$ , mean 29.8  $\mu\text{g/g}$  and radiata pine: range 22.6 to 85.4  $\mu\text{g/g}$ , mean 43.3  $\mu\text{g/g}$ ) were considerably higher than those found in top-soils (beech: range 1.5 to 13.3  $\mu\text{g/g}$ , mean 7.4  $\mu\text{g/g}$  and radiata pine: range 1.4 to 12.2  $\mu\text{g/g}$ , mean 7.7  $\mu\text{g/g}$ ). Furthermore, these results also indicated the conditions in humus layers under radiata pine favoured an apparently greater ammonium accumulation than those under beech.

No seasonal variation was observed in the levels of ammonium for either humus or top-soil samples. These ammonium levels were not correlated with temperature and/or moisture content. No relationship was found between ammonium levels and N content in either humus or top-soil samples. This result was attributed to the effects of polyphenols as demonstrated by the results obtained from a laboratory



incubation experiment described below.

Laboratory experiments were designed to examine the effects of polyphenols on carbon and nitrogen mineralization. For this purpose, water extracts of beech and radiata litter at known concentrations of polyphenolic compounds and carbohydrates, and standard catechin solutions were used to examine their effects on  $\text{CO}_2$  evolution rates and mineralization of nitrogen in soils from beech and radiata pine stands at Hanmer. The N mineralization study also included the effects of glucose and glucose+catechin. The soils used were amended with appropriate volumes of the above solutions to give a moisture content equivalent to 60 percent of the water-holding capacity and incubated at  $30^\circ\text{C}$ . In the experiments, rates of  $\text{CO}_2$  evolution were monitored continuously while ammonium levels were determined only once, after 14 days of incubation.

The results showed that rates of  $\text{CO}_2$  evolution were depressed by the addition of catechin solution and also litter extracts containing high concentrations of polyphenolic compounds but were stimulated by addition of litter extracts containing high concentrations of carbohydrates. The stimulatory effect of carbohydrates in the litter extracts, however, was greater than the inhibitory effect of polyphenolic compounds.

Ammonium levels were also depressed by the addition of litter extracts containing polyphenolic compounds and also catechin solution, but no apparent effect of carbohydrates on ammonium levels was observed, with or without the presence of polyphenols. The effect of polyphenols on  $\text{CO}_2$

evolution rates and ammonium levels was explained in terms of polyphenol complex formation.

It was also found that differences between soils in the rates of  $\text{CO}_2$  evolution and levels of ammonium were related to the organic matter content in the soil. Nitrate accumulation was either absent or present in negligibly low levels, and this was attributed to the low pH values of the soils used.

A method was developed for the extraction of lipid components of plant materials, capable of handling a large number of samples. This method is an alternative to that offered by the conventional Soxhlet method. In the alternative method, plant materials and solvent were placed in extracting bottles and kept in a constant temperature water-bath for 22 hours. Samples were initially extracted with petroleum ether (at  $49^\circ\text{C}$ ) and then on completion, the residues were extracted with 75% aqueous ethanol (at  $62^\circ\text{C}$ ). Effects of temperature and the duration of extraction on the amount of substances extracted, and the reproducibility of results of sample batches were examined. In addition, results obtained by the alternative method were compared with those of the Soxhlet method.

Under the conditions of the experiments carried out the best results obtained involved extracting the samples with petroleum ether at  $49^\circ\text{C}$  and with 75% aqueous ethanol at  $62^\circ\text{C}$  for a duration of 22 hours. In terms of amounts of organic substances extracted and variability of results between samples, the values obtained by the alternative method were comparable or better than those using the Soxhlet extractors. Furthermore, the alternative method facilitated

the extraction of a larger number of samples at any one time and at a lower cost of apparatus.

From a consideration of the results obtained in the present study, it is possible to reach an overall conclusion that the *Pinus radiata* ecosystems are functioning as well as their adjacent native beech ecosystems, especially on sites where their native counterparts had grown previously.

There is ample data in the present study to suggest that the *Pinus radiata* ecosystem is recycling some macro-nutrients and organic constituents more rapidly, and probably more efficiently, than the beech ecosystem, in spite of what appears to be a relatively smaller pool of nutrients in the organic matter present.

In practical terms, the above results suggest that the conversion of native forest to *Pinus radiata* was not detrimental to the subsequent productivity of the soil under *Pinus radiata*, at least, not during the life of the first rotation *Pinus radiata* and depending upon the nature of the forest management practices carried out during forest conversion. It was evident that management practices during and subsequent to forest conversion had a dramatic effect on the organic matter accumulated in the forest floor in the *Pinus radiata* stands, and therefore on the short-term supply of nutrients and energy substrates, and the nutrient status of the soil.

In qualitative terms, the results of the present study on the dynamics of the water-soluble components and organic constituents in litter-fall together with those of the macro-nutrients demonstrated the importance of the

relationships between these constituents and the macro-nutrients, such as those of lignin, nitrogen and polyphenols, and also that between carbohydrates and nitrogen. Furthermore, the carbohydrates and polyphenols in litter were found to be important chemical compounds affecting the dynamics of the mineralization processes, and thus the release of nutrients to the trees. This emphasizes the usefulness of including such an aspect in studies on the ecological processes occurring within ecosystems.

It is also apparent from the present results that complex interactions between chemical constituents of plant litter and other biotic and abiotic components of the soil environment are important in determining the dynamics of organic matter transformations. For example, the relative distribution of the organic constituents in litter appears to determine the rate of its disappearance, while temperature emerges as an important variable affecting the dynamics of carbon mineralization in the field. It follows on that the study of any of these factors in isolation from the others is not expected to provide a reliable method of predicting organic matter turnover or allow a reasonable comparison of the functioning of any two ecosystems in the field.

Generally speaking, the present study emphasizes the need for any comparative study of this kind to cover a variety of aspects of ecological processes over longer periods ( $\geq 2$  years) and also over a wide range of climatic conditions and soil types before a generalization and application of the results obtained can become valid. Further-

more, in such a study, it is necessary to account for the micro-site variability within each forest stand studied in order to facilitate a comparison.

There is little doubt that many areas in the present study deserve further research, including those related to the influence on the relative resistance of humic substances to microbial decomposition arising from differences in the litter substrate quality between beech and radiata. Possibly, this will provide an insight into the long-term changes in organic matter quality, and also perhaps on the influence of substrate quality on some soil physical properties such as soil structure and stability resulting from the incorporation of organic matter.

Some future work which will be facilitated by results obtained on the present study includes experiments to examine the role of polyphenolic compounds in the transportation of sesquioxides and other cations from organic matter and soil surface to the lower soil horizons, and its role in the differential forest floor accumulation between beech and radiata stands. The present study has clearly shown that larger amounts of polyphenolic compounds were produced in and released from beech litter compared to those for radiata pine. This disparity has clearly placed some significance in the relative effects which may result from the ecological processes mentioned above.

In general, considerable empirical work, including the modeling of individual ecological processes, is needed to increase our understanding of the functioning of any ecosystem. In this respect, the present study therefore

makes a significant contribution to the efforts aimed at achieving this goal. Hopefully, the present study will stimulate, if not, forms a useful basis for future work in this region and field of research, and also for any future ecosystems modeling of energy flow or of mineral element cycling.

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## APPENDIX I

### Site and Soil Descriptions

For all the forest sites studied, forest floor and top-soil (0-20cm) physical and chemical properties obtained in the present study are given in Chapter 5.

## GRANVILLE FOREST

Site Used: Hard beech

Soil Name: Mahoney Steepland Soil

Location: Hills to the south of the end of Burma road

Topography: Slight terracing; slope 25° ; aspect S-W ; altitude 210 m

Vegetation: Hard beech (*Nothofagus truncata*), some kamahi (*Weinmannia racemosa*) and miro (*Podocarpus ferrugineus*), with light understorey vegetation consisting of tree ferns (*Cyathea smithii*, *Blechnum discolor* and *Metrosideros diffusa*).

Soil Profile<sup>a</sup>:

18 cm	yellowish brown (10YR 5/4 - 5/6) slightly stony gravelly sandy loam; very friable; moderately developed fine nut and crumb structure.
26 cm	yellowish brown (10YR 5/4 - 5/6) slightly stony gravelly sandy loam; friable; moderately developed medium to coarse, medium to fine nut structure.
26 cm	yellowish brown (10YR 5/6) slightly stony gritty fine sandy loam, friable, moderate fine nut with some coarse nut and indurated sandstone and granite stones.
23 cm	as above; weakly developed very coarse and coarse block breaking to moderately developed coarse and medium nut structure.
17 cm	yellowish brown and dark yellowish brown (10 YR 4/4) gritty fine sandy loam; friable; weakly developed coarse and medium fine nut structure.
20 cm	brownish yellow-olive yellow (1Y 6/6) matrix of Old Man Gravels with abundant coarse continuous dark brown humus inclusions.
on	light yellowish brown (2.5Y 6/4) medium weakly compacted sandstone.

## GRANVILLE FOREST

Site Used: Radiata pine (1955)  
 Soil Name: Granville Steepland Soil  
 Location: About 7 km inwards from the main highway on the slope east of Teviot Creek.  
 Topography: convex surface, on lower mid-slope; slope 25° ; aspect S ; altitude 170 m.  
 Vegetation: *Pinus radiata* planted 1955, with some understorey vegetation including gorse (*Ulex europaeus*), wineberry (*Aristotelia serrata*) and tree fern (*Dicksonia squarrosa*). There is a light canopy; stand thinned to waste to 580 stems/hectare in 1968.

Soil Profile<sup>a</sup>:

22 cm	dark brown (7.5YR 3/2) fine sandy loam; very friable; moderately developed medium nut structure.
3 cm	light brown (7.5YR 6/3) silt loam; very friable; weakly developed medium nut structure.
<1 cm	dusk red (10R 2/3) strongly cemented iron pan.
20 cm	yellow (10YR 7/8) silty clay loam; very friable; moderately developed medium nut structure.
22 cm	bright yellow (2.5YR 7/6) silty clay loam; very friable; moderately developed medium and coarse nut structure.
32 cm	light grey (7.5Y 7/2) fine sandy clay loam; firm; weakly developed coarse vertical plate-like structure.
on	light olive grey (2.5GY 7/1) coarse sandy loam; firm; weakly developed coarse vertical plate-like structure.

## HOCHSTETTER FOREST

Soil Name: Arahura Hill Soil  
(sandy loams, silt loams and stony loams)

Parent Material: Greywacke, schist, and granite gravels  
and glacial till

Rainfall: > 2000 mm annually.

Soil Profile<sup>@</sup>:

5 cm	brown to dark brown (7.5YR 4/2) slightly gravelly, gritty silt loam; friable; moderately developed medium and fine nut structure.
5 cm	dark brown (7.5YR 5/4 and 5/8); slightly gravelly, gritty silt loam; friable; moderately developed fine, medium and coarse nut structure.
20 cm	yellow brown (10YR 5/4 and 5/8) slightly gravelly. gritty heavy silt loam; friable; weakly developed coarse block breaking to moderately developed medium and fine block structure.
45 cm	brownish yellow (10YR 6/6) with some yellow brown (10YR 5/4) slightly gravelly and gritty heavy silt loam; friable; moderately developed coarse and medium block breaking to fine block structure.
28 cm	brownish yellow (10YR 6/6) stony gravelly slightly gritty heavy silt loam; friable; weakly developed medium and fine nut and block structure.
on	brownish yellow (10YR 6/6) stony silt loam matrix; weakly developed medium and fine nut and crumb structure.

@ from Levett (1978)

Site Used: Podocarp

Location: 7.3 km up main Callaghan's Ridge road from junction with State Highway 7.

Topography: Near ridge crest; slope  $25^{\circ}$  ; aspect S; altitude 250 m.

Vegetation: rimu (*Dacrydium cupressinum*), rata (*Metrosideros umbellata*, *M. robusta*) and quintinia with understorey of *Coprosma* spp.

Site Used: Radiata pine (1967)

Location: Along Callaghan's Ridge about mid-way between the podocarp site and the main highway.

Topography: Near ridge crest; slope  $20^{\circ}$  ; aspect S ; altitude 200 m.

Vegetation: *Pinus radiata* planted 1967; discontinuous canopy; abundant understorey vegetation comprising mainly of bracken (*Pteridium esculentum*).



## HANMER FOREST

Soil Name: Tekoa Hill Soil  
(silt loams and stony silt loams)

Parent Material: Greywacke detritus, some Greywacke gravels and loess.

Rainfall: 1400 mm annually.

## Soil Profile: #

13 cm	dark grey brown silt loam; very friable; soft; strongly developed fine and very fine crumb structure.
50 cm	yellow brown silt loam; friable; nutty and blocky structure.
40 cm	brown yellow stony heavy silt loam; friable-firm; block structure.
on	fragmented Greywacke.

Site Used: Mountain beech

Location: East of Compartment 90

Topography: slightly convex surface; slope  $10^{\circ}$  ; aspect S-W ; altitude 450 m; situated beside a stream.

Vegetation: dominated by mountain beech (*Nothofagus solandri* var *cliffortioides*), manuka (*Leptospermum scoparium*); with a light understorey vegetation of *Coprosma* spp.

Site Used: Radiata pine (1960)

Location: Compartment 94

Topography: concave surface; slope  $25^{\circ}$  ; aspect S-W ; altitude 580 m.

Vegetation: *Pinus radiata* planted 1960; thinned to waste from 500 st/ha to 250 st/ha in 1974; a discontinuous canopy.

Site Used: Mountain beech  
Location: Sawyer's Gully, in Compartment 32  
Topography: Flat; altitude 490 m.  
Vegetation: mountain beech (*Nothofagus solandri cliffortioides*) with a very light understorey vegetation of *Coprosma* spp.

Site Used: Radiata pine (1926)  
Location: Near Sawyer's Gully, in Compartment 32  
Topography: Easy rolling; slope 5° ; aspect S-W ; altitude 490 m.  
Vegetation: *Pinus radiata* planted 1926; very little understorey vegetation of mainly ferns; some parts of discontinuous canopy due to relatively open crowns.

## GOLDEN DOWNS FOREST

Soil Name: Spooner Hill Soils  
(silt loams and stony loams)

Parent Material: Greywacke gravels (weathered)

Rainfall: 900 mm annually

## Soil Profile: #

10 cm	dark grey brown silt loam; firm; nutty structure.
18 cm	yellow brown stony silt loam; firm; blocky structure.
on	gravels on silt and clay matrix.

Site Used: Mixed beech

Location: Compartment 128b

Topography: slight convex surface; slope  $10^{\circ}$  ;  
aspect S ; altitude 570 m

Vegetation: dominant species: mountain beech (*Nothofagus solandri* var *cliffortioides*) and  
black beech (*Nothofagus solandri* var *solandri*); partially open canopy.

Site Used: Radiata pine (1967)

Location: Compartment 147

Topography: plane surface; slope  $20^{\circ}$  ; aspect S-W;  
altitude 400 m.

Vegetation: *Pinus radiata* planted 1967; stand not  
thinned before, 1850 stems/ha; closed  
canopy with some gorse (*Ulex europaeus*).

Site Used: Radiata pine (1956)  
 Location: Compartment 102  
 Topography: plane surface; slope  $15^{\circ}$  ; aspect S-W;  
 altitude 430 m.  
 Vegetation: *Pinus radiata* planted 1956; closed canopy  
 with 870 stems/ha; light understorey  
 vegetation mainly gorse (*Ulex europaeus*).

Site Used: Radiata pine (1947)  
 Location: Compartment 102  
 Topography: slight convex surface; slope  $20^{\circ}$  ;  
 aspect S-W ; altitude 220 m.  
 Vegetation: *Pinus radiata* planted 1947; 600 stem/ha;  
 closed canopy with no understorey  
 vegetation.

Site Used: Radiata<sub>reg.</sub> pine (1956)  
 Location: Compartment 102  
 Topography: plane surface; slope  $25^{\circ}$  ; aspect S-W;  
 altitude 460 m.  
 Vegetation: *Pinus radiata* regenerated in 1956;  
 not pruned before; some understorey  
 vegetation mainly of dead gorse (*Ulex*  
*europaeus*).

## PEEL FOREST

Soil Name: Peel Forest Soils  
(silt loams to sandy loams; some stony loams)

Parent Material: Greywacke alluvium

Rainfall: 1000 mm annually.

Soil Profile: #

25 cm	very dark greyish brown silt loam; very friable; granular structure.
30 cm	yellowish brown silt loam; friable; weakly mottled orange nutty and blocky structures.
on	pale yellowish brown silt loam; friable-firm; blocky and nutty structures.

Site Used: Podocarp

Location: About 100 metre from roadside, approximately 3 km from Peel Forest Information Centre.

Topography: Flat

Vegetation: dominated by totara (*Podocarpus totara*) and matai (*Podocarpus spicatus*) with some white pine (*Podocarpus dacrydioides*), site unmilled before; closed canopy.

Site Used: Radiata pine (1937)

Location: In farmland, about 2 km from Peel Forest Information Centre.

Topography: Flat

Vegetation: *Pinus radiata* planted approximately 1937; not pruned before; site forms part of pasture land.

## APPENDIX II

LITTER-FALL DATA FOR  
FOREST STANDS AT  
GRANVILLE, HANMER AND NELSON

## TABLE.

- A. Mean monthly and annual litter-fall weights.
- B. Mean chemical composition of quarterly litter-fall components.
- C. Mean quarterly litter-fall budgets for carbon, macro-nutrients and water-soluble and organic constituents.

Data given in parenthesis refer to 95 percent confidence intervals.

TABLE A.1 Mean monthly and annual litter-fall at Granville

GRANVILLE:		BEECH MEAN MONTHLY LITTERFALL			kg/ha
MONTH	LEAF	TWIG/STEM	OTHER	BRANCH	TOTAL
1976					
Dec.	236(87)	172(58)	109(23)		517(98)
Jan.	240(88)	237(172)	141(34)		618(106)
Feb.	133(57)	68(23)	81(36)		282(91)
Mar.	217(78)	30(17)	55(41)		302(110)
Apr.	204(78)	208(273)	238(370)		650(434)
May	429(138)	485(255)	161(118)		1075(342)
Jun.	213(45)	42(50)	60(25)		315(120)
Jul.	32(8)	13(3)	29(7)		74(15)
Aug.	47(14)	30(15)	50(33)		127(38)
Sep.	62(24)	59(30)	66(25)		187(35)
Oct.	317(110)	275(223)	133(13)	1073(2757)	1798(2348)
Nov.	445(186)	253(158)	99(29)		797(192)
Annual	2575(378)	1872(936)	1222(492)	1073(2757)	6742(2153)
Dec.	412(109)	206(95)	118(63)		736(186)
Jan.	108(26)	47(25)	66(23)		221(47)
Feb.	113(32)	42(17)	53(18)		208(18)
Mar.	210(61)	41(24)	143(148)	2073(5331)	2467(4629)
Apr.	194(45)	56(40)	51(54)		301(82)
May	224(54)	76(76)	84(29)	101(203)	485(224)
Jun.	308(41)	85(41)	87(29)		480(118)
Jul.	122(31)	62(44)	77(83)		261(91)
Aug.	72(24)	43(40)	122(143)	508(1197)	745(1089)
Sep.	285(32)	49(34)	93(23)		427(53)
Oct.	308(95)	89(21)	278(71)	48(122)	723(184)
Nov.	137(46)	36(14)	244(54)		417(76)
Annual	2493(297)	832(252)	1416(427)	2730(5021)	7471(3007)
Dec.					
	398(105)	177(56)	374(128)		949(157)
Jan.					

TABLE A.2 Mean monthly and annual litter-fall at Granville

GRANVILLE: RADIATA(1955) MEAN MONTHLY LITTERFALL kg/ha					
MONTH	NEEDLE	POL./CONE	CONE	BRANCH	TOTAL
1976					
Dec.	245(53)	31(17)			276(98)
Jan.	391(71)	49(13)		18(37)	458(73)
Feb.	185(18)				185(18)
Mar.	187(36)				187(36)
Apr.	462(115)				462(115)
May	1202(144)			10(25)	1212(164)
Jun.	165(32)				165(32)
Jul.	31(9)				31(9)
Aug.	153(23)				153(23)
Sep.	248(36)				248(36)
Oct.	572(109)	310(101)			882(136)
Nov.	244(52)				244(52)
Annual	4085(377)	390(77)		28(37)	4503(391)
Dec.	309(42)				309(42)
Jan.	207(55)				207(55)
Feb.	178(63)				178(63)
Mar.	186(33)				186(33)
Apr.	163(51)				163(51)
May	296(73)				296(73)
Jun.	151(59)				151(59)
Jul.	183(50)				183(50)
Aug.	252(59)				252(59)
Sep.	331(48)				331(48)
Oct.	583(74)	199(71)			782(110)
Nov.	187(30)	109(56)			296(53)
Annual	3026(453)	308(57)			3334(379)
Dec.					
Jan.	720(132)		371(636)		1091(633)



TABLE A.3 Mean monthly and annual litter-fall at Hanmer

HANMER:		BEECH MEAN MONTHLY LITTERFALL			kg/ha
MONTH	LEAF	TWIG/STEM	OTHER	BRANCH	TOTAL
1976					
Nov.	496(115)	58(23)	82(7)		636(113)
Dec.	400(58)	111(38)	100(11)		611(80)
Jan.	233(55)	117(61)	232(239)		582(290)
Feb.	152(34)	48(32)	24(18)		224(49)
Mar.	341(524)	64(32)	38(17)		443(78)
Apr.	456(197)	77(48)	37(18)		570(215)
May	220(64)	44(23)	46(32)		310(49)
Jun.	145(38)	24(7)	11(3)		180(35)
Jul.	46(17)	3(1)	4(2)		53(15)
Aug.					
	30(9)	12(1)	34(61)		76(49)
Sep.					
Oct.	131(46)	149(31)	48(18)		328(72)
Annual	2650(291)	707(111)	656(254)		4013(592)
Nov.	378(120)	76(53)	121(21)		575(120)
Dec.	492(63)	62(24)	110(33)		664(112)
Jan.	478(127)	82(23)	61(9)		621(124)
Feb.	152(63)	121(63)	47(18)		320(77)
Mar.	467(79)	122(40)	47(13)		636(77)
Apr.	35(7)	35(16)	12(4)		82(15)
May	121(59)	76(44)	35(40)		232(72)
Jun.	93(39)	26(21)	29(17)		148(41)
Jul.	19(8)	5(2)	5(1)		29(7)
Aug.	35(14)	37(15)	10(4)		82(29)
Sep.	38(18)	41(20)	10(4)		89(27)
Oct.	329(121)	41(18)	67(37)		437(79)
Annual	2637(246)	724(129)	554(64)		3915(390)

TABLE A.4 Mean monthly and annual litter-fall at Hanmer

HANMER: RADIATA(1960) MEAN MONTHLY LITTERFALL					kg/ha
MONTH	NEEDLE	POL./CONE	CONE	BRANCH	TOTAL
1976					
Nov.	55(25)	32(21)			87(37)
Dec.	82(34)	20(10)			102(41)
Jan.	98(30)	14(8)			112(25)
Feb.	43(10)				43(10)
Mar.	107(20)				107(20)
Apr.	305(84)				305(84)
May	242(53)				242(53)
Jun.	206(96)				206(96)
Jul.	6(3)				6(3)
Aug.	27(13)				27(13)
Sep.					
Oct.	208(104)				208(104)
	1379(309)	66(37)			1445(303)
Nov.	86(54)				86(54)
Dec.	51(21)				51(21)
Jan.	83(14)				83(14)
Feb.	173(40)				173(40)
Mar.	489(180)				489(180)
Apr.	170(66)				170(66)
May	252(116)				252(116)
Jun.	24(9)				24(9)
Jul.	16(10)				16(10)
Aug.	32(20)				32(20)
Sep.	55(30)				55(30)
Oct.	72(115)	60(11)			132(82)
	1503(397)	60(11)			1563(398)

TABLE A.5 Mean monthly and annual litter-fall at Nelson

NELSON:		BEECH MEAN MONTHLY LITTERFALL			kg/ha
MONTH	LEAF	TWIG/STEM	OTHER	BRANCH	TOTAL
1976					
Dec.	803(208)	179(61)	158(36)		1140(213)
Jan.	193(59)	125(61)	81(23)		399(73)
Feb.	152(48)	38(31)	51(13)		241(52)
Mar.	82(22)	18(13)	39(20)		139(28)
Apr.					
May	340(59)	118(39)	203(104)		661(161)
Jun.	188(15)	100(37)	67(38)		355(41)
Jul.	50(6)	14(15)	24(9)		88(17)
Aug.	54(15)	5(3)	31(16)		90(14)
Sep.	119(28)	26(10)	30(8)		175(29)
Oct.	722(124)	419(312)	156(54)		1297(268)
Nov.	999(201)	240(175)	161(21)		1400(203)
Annual	3702(408)	1282(377)	1001(104)		5985(592)
Dec.	443(146)	147(46)	109(17)		699(149)
Jan.	253(53)	345(309)	78(18)		676(209)
Feb.	283(104)	236(182)	192(198)		711(308)
Mar.	426(139)	60(52)	106(94)	801(1724)	1393(1770)
Apr.	144(56)	60(58)	47(24)		251(104)
May	64(10)	36(24)	64(56)		164(53)
Jun.	72(26)	25(17)	40(15)	825(2122)	962(1863)
Jul.	55(17)	87(69)	148(109)	76(136)	366(249)
Aug.	41(25)	50(32)	62(38)		153(97)
Sep.	186(71)	18(20)	35(11)		239(44)
Oct.	368(90)	170(151)	170(54)		708(163)
Nov.	663(94)	132(87)	284(62)		1079(159)
Annual	2998(635)	1366(459)	1335(289)	1702(2423)	7401(2558)

TABLE A.6 Mean monthly and annual litter-fall at Nelson

NELSON:		RADIATA(1956) MEAN MONTHLY LITTERFALL			kg/ha
MONTH	NEEDLE	POL./CONE	CONE	BRANCH	TOTAL
1976					
Dec.	388(87)	60(9)			448(60)
Jan.	506(55)	26(18)			532(51)
Feb.	238(26)			27(61)	265(91)
Mar.	237(127)				237(127)
Apr.					
May	1134(185)				1134(185)
Jun.	688(133)				688(133)
Jul.	60(11)				60(11)
Aug.	102(21)				102(21)
Sep.	122(37)				122(37)
Oct.	294(68)	670(163)		99(162)	1063(191)
Nov.	446(120)	82(30)	153(393)		681(354)
Annual	4215(313)	838(156)	153(393)	126(150)	5332(556)
Dec.	214(37)				214(37)
Jan.	338(56)				338(56)
Feb.	970(198)		630(1621)		1600(1323)
Mar.	461(240)			276(417)	737(482)
Apr.	364(105)				364(105)
May	595(92)				595(92)
Jun.	146(34)				146(34)
Jul.	320(85)				320(85)
Aug.	271(125)				271(125)
Sep.	69(24)				69(24)
Oct.	262(69)	156(22)			418(85)
Nov.	362(177)	52(7)		46(72)	460(174)
Annual	4372(491)	208(20)	630(1621)	322(421)	5532(1204)

TABLE A.7 Mean monthly and annual litter-fall at Nelson

NELSON: RADIATA(reg.1956) MEAN MONTHLY LITTERFALL					kg/ha
MONTH	NEEDLE	POL./CONE	CONE	BRANCH	TOTAL
1976					
Dec.	238(75)	79(28)			317(63)
Jan.	467(83)	51(38)			518(88)
Feb.	200(70)			32(82)	232(126)
Mar.	148(58)				148(58)
Apr.	588(67)				588(67)
May					
Jun.	692(173)			25(47)	717(168)
Jul.	67(12)				67(12)
Aug.	95(20)				95(20)
Sep.	146(30)				146(30)
Oct.	542(133)	434(164)			976(141)
Nov.	478(151)	59(31)	585(1504)		1122(1400)
Annual	3661(300)	623(120)	585(1504)	57(71)	4926(1354)
Dec.	178(44)				178(44)
Jan.	303(68)				303(68)
Feb.	642(68)			32(80)	674(94)
Mar.	256(22)		450(1157)		706(969)
Apr.	217(71)				217(71)
May	519(110)				519(110)
Jun.	158(56)				158(56)
Jul.	274(70)				274(70)
Aug.	192(31)				192(31)
Sep.	137(32)				137(32)
Oct.	304(158)	253(76)			557(91)
Nov.	285(136)	116(17)	479(1230)	29(74)	909(1182)
Annual	3465(580)	369(63)	929(1463)	61(95)	4824(1578)

TABLE B.1 Mean chemical composition of quarterly leaf litter-fall in beech stand at Granville

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	6.82(1.16)	5.38(1.55)	6.12(0.43)	7.78(1.95)	5.91(0.40)	5.02(0.63)	6.29(0.67)	5.60(0.43)
C, %	52.2(0.9)	50.7(0.5)	52.4(2.0)	50.0(1.2)	49.8(2.1)	52.5(2.3)	50.1(1.2)	50.6(2.3)
WSC,mg.g <sup>-1</sup>	60.1(15.9)	62.1(8.4)	70.9(10.6)	70.0(5.4)	79.2(2.5)	60.3(6.9)	66.7(7.8)	73.4(4.0)
WSP,mg.g <sup>-1</sup>	113 (4)	130 (12)	138 (17)	143 (13)	182 (1)	142 (7)	157 (29)	175 (6)
WSF,mg.g <sup>-1</sup>	283 (42)	295 (2)	289 (40)	297 (11)	384 (27)	317 (45)	323 (55)	356 (15)
EE, %	5.28(1.17)	5.01(0.31)	4.67(0.56)	4.16(0.40)	4.47(0.62)	5.53(0.16)	5.12(0.47)	5.13(0.32)
Aq. E, %	19.2(4.0)	21.1(1.2)	20.7(2.5)	22.2(3.8)	29.8(3.9)	19.1(2.4)	26.0(3.4)	26.1(8.6)
HOLO, %	43.6(3.2)	46.9(1.6)	46.7(1.8)	45.3(2.3)	42.3(0.5)	46.3(5.4)	45.6(3.1)	46.6(0.2)
R. LIG,%	31.9(1.0)	27.0(2.9)	27.9(2.3)	28.3(2.1)	23.4(4.3)	29.1(4.2)	23.3(0.9)	22.1(8.4)
P, mg.g <sup>-1</sup>	0.43(0.14)	0.24(0.01)	0.38(0.18)	0.49(0.51)	0.34(0.12)	0.28(0.07)	0.29(0.10)	0.29(0.07)
K, mg.g <sup>-1</sup>	1.61(0.21)	1.15(0.09)	1.33(0.27)	2.20(0.86)	2.41(0.62)	1.71(0.62)	1.92(0.09)	1.35(0.12)
Mg,mg.g <sup>-1</sup>	1.74(0.29)	1.46(0.18)	1.37(0.10)	1.55(0.34)	2.19(0.42)	2.09(0.80)	1.41(0.18)	1.26(0.20)
Ca,mg.g <sup>-1</sup>	8.08(2.26)	9.51(0.82)	7.26(3.18)	8.12(3.36)	8.60(2.45)	8.31(3.31)	7.46(1.73)	6.89(2.01)

TABLE B.2 Mean chemical composition of quarterly twig litter-fall in beech stand at Granville

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	5.10(0.96)	4.27(0.70)	4.36(1.80)	4.85(0.49)	5.06(0.78)	4.68(1.00)	5.33(1.06)	5.16(0.60)
C, %	51.8(1.2)	51.1(1.2)	50.5(5.1)	49.7(0.7)	49.3(0.5)	50.8(1.0)	50.4(3.2)	48.1(0.5)
WSC,mg.g <sup>-1</sup>	39.5(0.5)	43.0(1.0)	53.6(16.1)	35.6(6.2)	51.4(10.0)	44.7(3.4)	47.5(7.8)	36.4(11.8)
WSP,mg.g <sup>-1</sup>	60 (18)	67 (8)	82 (21)	54 (16)	110 (3)	106 (35)	83 (17)	48 (34)
WSF,mg.g <sup>-1</sup>	171 (19)	171 (11)	190 (42)	143 (34)	237 (6)	219 (44)	197 (21)	136 (69)
EE, %	2.65(0.45)	2.04(0.53)	2.33(0.98)	1.98(0.29)	2.07(0.31)	2.15(1.22)	2.43(0.64)	2.19(0.86)
Aq. E, %	9.6 (4.2)	10.3(1.8)	10.6(1.6)	7.8 (1.1)	14.3(3.1)	8.2 (4.6)	11.4(1.1)	9.9 (3.2)
HOLO, %	47.4(6.4)	49.2(7.6)	45.2(9.8)	49.6(4.2)	49.3(2.3)	50.6(9.3)	48.7(4.2)	54.9(9.3)
R.LIG, %	40.3(1.6)	38.5(5.6)	41.9(7.3)	40.5(4.2)	34.4(1.4)	37.8(2.9)	37.5(3.4)	34.4(8.6)
P, mg.g <sup>-1</sup>	0.32(0.07)	0.25(0.07)	0.24(0.12)	0.25(0.07)	0.30(0.12)	0.25(0.10)	0.29(0.07)	0.29(0.05)
K, mg.g <sup>-1</sup>	1.24(0.34)	1.44(0.09)	1.38(0.20)	1.25(0.10)	1.87(0.05)	1.44(0.98)	1.78(0.27)	1.28(0.87)
Mg,mg.g <sup>-1</sup>	1.72(0.31)	1.63(0.21)	1.72(0.60)	1.70(0.27)	1.92(0.49)	1.75(0.64)	1.90(0.34)	1.47(1.26)
Ca,mg.g <sup>-1</sup>	11.9(2.8)	11.3(5.5)	10.6(6.2)	13.4(6.4)	11.5(3.7)	10.1(3.5)	12.9(4.5)	10.4(8.0)

TABLE B.3 Mean chemical composition of quarterly "others" litter-fall in beech stand at Granville

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	10.36(1.12)	11.65(2.17)	11.21(2.71)	12.01(0.96)	12.66(1.28)	8.75(2.64)	10.69(0.59)	12.66(1.67)
C, %	51.2(1.4 )	51.9(2.9 )	52.1(0.7 )	51.5(2.3 )	51.3(0.3 )	48.9(2.04)	52.0(1.4 )	52.0(2.1 )
WSC,mg.g <sup>-1</sup>	51.1(21.7)	42.5(8.6 )	50.4(28.1)	41.9(9.8 )	51.7(15.1)	46.7(11.5)	54.0(8.2 )	48.7(9.6 )
WSP,mg.g <sup>-1</sup>	57 (34)	41 (12)	43 (26)	37 (11)	76 (32)	48 (25)	76 (33)	64 (20 )
WSF,mg.g <sup>-1</sup>	183 (97)	159 (2 )	143 (48)	139 (19)	213 (31)	177 (55)	221 (36)	190 (6 )
E.E. %								
Aq.E. %								
HOLO. %	The organic constituents of "others" litter-fall were not determined							
R.LIG %								
P, mg.g <sup>-1</sup>	0.99(0.32)	0.90(0.18)	1.08(0.07)	1.07(0.18)	1.08(0.31)	0.76(0.29)	0.85(0.29)	0.92(0.25)
K, mg.g <sup>-1</sup>	1.82(1.40)	1.69(1.29)	3.82(2.37)	2.07(0.80)	2.30(0.87)	2.37(1.04)	4.44(3.55)	2.09(1.37)
Mg.mg.g <sup>-1</sup>	1.58(0.53)	1.40(0.36)	1.54(0.12)	1.45(0.18)	1.50(0.10)	1.30(0.31)	1.38(0.10)	1.28(0.09)
Ca.mg.g <sup>-1</sup>	7.90(5.52)	8.06(2.81)	7.21(5.83)	6.33(1.31)	6.59(2.43)	9.63(3.53)	7.65(2.94)	7.50(0.64)



TABLE B.4 Mean chemical composition of quarterly needle litter-fall in radiata stand at Granville

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	8.87(2.36)	6.74(1.65)	7.48(1.43)	9.93(1.63)	9.16(1.31)	8.28(1.12)	7.03(2.18)	8.64(2.09)
C, %	51.9(2.9 )	53.6(0.7 )	53.0(0.9 )	52.0(1.6 )	50.9(0.7 )	53.4(1.2 )	53.2(0.5 )	51.3(2.7 )
WSC,mg.g <sup>-1</sup>	36.3(6.2 )	41.3(4.2 )	39.8(9.8 )	36.7(2.3 )	40.8(2.9 )	35.6(6.2 )	34.7(0.5 )	38.4(3.1 )
WSP,mg.g <sup>-1</sup>	38 (4 )	42 (8 )	36 (6 )	42 (12)	48 (4 )	44 (3 )	36 (2 )	42 (5 )
WSF,mg.g <sup>-1</sup>	169 (30)	188 (64)	139 (10)	163 (13)	193 (25)	167 (28 )	159 (8 )	173 (18 )
E.E. %	3.41(0.65)	4.81(0.91)	4.52(0.12)	3.94(0.43)	4.15(0.32)	5.08(1.28)	5.02(1.35)	4.82(1.22)
Aq. E. %	9.7 (2.5 )	11.9(1.6 )	12.3(2.1 )	11.2(3.0 )	14.6(0.8 )	10.5(2.2 )	10.4(1.4 )	11.8(2.0 )
HOLO, %	47.7(0.9 )	49.3(3.2 )	47.8(6.0 )	47.0(2.7 )	49.0(2.5 )	51.5(4.0 )	52.5(1.2 )	52.5(2.7 )
R. LIG. %	39.1(3.8 )	34.0(5.1 )	35.5(4.3 )	37.8(5.8 )	32.3(2.5 )	32.9(6.5 )	32.1(3.8 )	30.8(3.2 )
P, mg.g <sup>-1</sup>	0.59(0.23)	0.46(0.14)	0.45(0.05)	0.70(0.23)	0.67(0.01)	0.45(0.05)	0.40(0.10)	0.48(0.20)
K, mg.g <sup>-1</sup>	2.01(0.76)	1.78(0.47)	1.79(0.27)	2.47(0.18)	2.69(0.05)	3.09(1.07)	1.55(0.36)	1.54(0.65)
Mg,mg.g <sup>-1</sup>	1.24(0.32)	1.11(0.20)	1.11(0.34)	1.20(0.34)	1.36(0.18)	1.29(0.09)	1.06(0.27)	0.96(0.21)
Ca,mg.g <sup>-1</sup>	4.35(0.16)	4.39(0.76)	4.91(0.73)	4.47(1.62)	4.72(0.65)	4.74(1.33)	4.36(2.43)	4.00(1.88)

TABLE B.5 Mean chemical composition of quarterly leaf litter-fall in beech stand at Hanmer

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	4.58(0.48)	4.46(0.36)	4.72(0.73)	5.17(0.21)	4.80(0.33)	4.11(0.46)	3.86(0.23)	6.30(0.48)
C, %	50.3(1.4 )	47.0(6.2 )	49.5(1.4 )	47.2(4.3 )	49.3(2.9 )	46.8(1.0 )	49.2(1.6 )	51.4(2.7 )
WSC,mg.g <sup>-1</sup>	60.9(1.4 )	60.1(10.2)	63.5(7.6 )	65.1(5.8 )	75.5(4.7 )	70.3(5.6 )	62.9(7.8 )	53.8(3.6 )
WSP,mg.g <sup>-1</sup>	143 (9 )	114 (9 )	122 (13)	137 (22)	166 (4 )	158 (6 )	124 (4 )	112 (4 )
WSF,mg.g <sup>-1</sup>	306 (15)	249 (10)	269 (5 )	320 (23)	375 (16)	364 (61)	278 (22)	253 (10 )
E.E. %	5.47(0.51)	4.37(0.45)	4.93(1.24)	4.77(0.42)	5.12(0.58)	4.01(0.53)	4.89(0.42)	4.86(0.73)
Aq.E. %	24.6(1.6 )	27.9(1.9 )	24.4(5.5 )	18.5(1.4 )	24.6(1.1 )	29.4(2.9 )	25.5(3.1 )	19.3(4.3 )
HOLO, %	53.0(0.5 )	53.5(1.0 )	52.8(0.5 )	53.7(6.5 )	53.2(2.7 )	52.7(1.4 )	52.5(1.6 )	54.7(0.9 )
R.LIG %	16.9(1.4 )	14.3(2.5 )	17.9(4.9 )	23.1(7.5 )	17.1(1.2 )	13.9(1.4 )	17.1(4.3 )	21.1(3.2 )
P, mg.g <sup>-1</sup>	1.01(0.05)	1.04(0.84)	1.06(0.29)	0.65(0.07)	0.92(0.18)	1.38(0.71)	0.98(0.12)	0.66(0.25)
K, mg.g <sup>-1</sup>	2.38(0.47)	4.02(0.38)	2.91(0.60)	1.79(0.18)	2.46(0.84)	4.20(0.49)	2.94(0.07)	1.73(0.49)
Mg.mg.g <sup>-1</sup>	1.33(0.25)	1.40(0.10)	1.23(0.21)	1.12(0.07)	1.31(0.34)	1.29(0.07)	1.23(0.05)	1.15(0.20)
Ca.mg.g <sup>-1</sup>	9.06(1.18)	11.54(1.44)	10.11(1.64)	9.28(0.45)	9.69(1.06)	10.81(2.34)	10.49(0.65)	10.87(1.22)

TABLE B.6 Mean chemical composition of quarterly twig litter-fall in beech stand at Hanmer

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	5.51(1.35)	5.06(0.67)	4.55(0.36)	4.71(0.79)	4.23(0.86)	4.70(0.51)	5.04(0.29)	5.59(0.36)
C, %	52.8(2.7 )	50.0(4.2 )	51.1(0.9 )	50.7(1.2 )	51.8(1.8 )	50.9(1.2 )	50.5(0.9 )	50.2(1.8 )
WSC,mg.g <sup>-1</sup>	36.6(4.0 )	37.1(13.1)	29.9(5.4 )	28.9(3.1 )	41.7(9.1 )	41.6(3.6 )	32.0(6.0 )	32.5(2.9 )
WSP,mg.g <sup>-1</sup>	69 (13)	63 (9 )	30 (18)	59 (8 )	70 (23)	85 (3 )	64 (2 )	58 (4 )
WSF,mg.g <sup>-1</sup>	148 (23)	153 (23)	147 (27)	145 (22)	184 (8 )	187 (34)	150 (6 )	135 (10 )
E.E. %	3.11(0.84)	3.77(0.45)	3.67(0.76)	3.56(0.53)	3.45(0.58)	3.32(0.16)	3.51(0.31)	4.17(0.03)
Aq.E. %	13.7(1.0 )	16.2(3.5 )	12.5(2.0 )	11.7(0.3 )	13.7(0.3 )	17.2(4.5 )	12.3(0.9 )	11.6(0.3 )
HOLO. %	52.2(2.0 )	49.3(1.6 )	50.8(2.7 )	49.8(0.5 )	51.5(1.2 )	49.9(1.6 )	49.4(0.9 )	49.2(2.5 )
R.LIG %	31.0(2.3 )	30.8(4.7 )	33.0(1.0 )	34.9(0.7 )	31.3(1.4 )	29.5(3.1 )	34.8(1.2 )	35.1(2.7 )
P, mg.g <sup>-1</sup>	0.89(0.18)	0.90(0.75)	0.77(0.34)	0.65(0.12)	0.79(0.16)	0.93(0.14)	0.79(0.07)	0.59(0.05)
K, mg.g <sup>-1</sup>	2.47(1.61)	2.71(1.39)	1.86(0.84)	1.77(0.09)	2.19(0.64)	2.82(1.13)	2.05(0.31)	1.45(0.32)
Mg.mg.g <sup>-1</sup>	2.15(0.23)	2.13(0.34)	2.00(0.10)	1.91(0.09)	2.11(0.09)	2.10(0.31)	2.00(0.05)	1.86(0.09)
Ca.mg.g <sup>-1</sup>	10.46(1.83)	17.86(2.32)	11.94(3.82)	13.36(3.86)	11.76(2.12)	12.87(3.62)	13.55(3.11)	13.86(0.96)

TABLE B.7 Mean chemical composition of quarterly "others" litter-fall in beech stand at Hanmer

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	8.04(0.57)	8.07(0.23)	6.26(1.05)	8.76(1.04)	7.20(0.95)	8.51(0.96)	7.69(0.77)	7.66(0.14)
C, %	55.1(0.1 )	51.6(0.3 )	52.0(0.5 )	46.4(1.4 )	51.7(5.1 )	49.9(7.5 )	50.8(3.2 )	53.2(2.3 )
WSC,mg.g <sup>-1</sup>	35.5(2.9 )	45.6(9.8 )	34.7(19.9)	55.8(11.1)	55.1(12.9)	49.0(7.3 )	36.7(5.8 )	38.3(2.3 )
WSP,mg.g <sup>-1</sup>	82 (19)	64 (3 )	83 (20)	78 (5 )	115 (32)	83 (17)	73 (6 )	50 (7 )
WSF,mg.g <sup>-1</sup>	165 (61)	188 (7 )	241 (69)	233 (9 )	252 (32)	219 (34)	198 (27)	157 (6 )
E.E. %	The organic constituents of "others" litter-fall were not determined							
Aq.E. %								
HOLO. %								
R.LIG %								
P, mg.g <sup>-1</sup>	0.91(0.12)	1.06(0.43)	1.56(0.62)	1.32(0.86)	0.95(0.20)	1.10(0.10)	1.23(0.56)	0.90(0.21)
K, mg.g <sup>-1</sup>	2.14(1.73)	2.60(1.61)	2.67(0.32)	3.02(0.67)	2.37(1.26)	3.05(0.56)	2.77(0.47)	2.40(1.44)
Mg.mg.g <sup>-1</sup>	1.19(0.31)	1.58(0.87)	1.61(0.51)	1.85(0.10)	1.30(0.34)	1.66(0.67)	1.65(0.34)	1.38(0.65)
Ca.mg.g <sup>-1</sup>	9.64(0.25)	8.76(0.42)	7.60(2.92)	7.85(1.51)	8.80(0.96)	8.00(1.37)	8.13(0.98)	8.92(0.42)

TABLE B.8 Mean chemical composition of quarterly needle litter-fall in radiata stand at Hanmer

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	5.53(0.55)	5.79(0.94)	4.76(0.51)	5.69(0.40)	6.46(1.23)	7.62(1.36)	4.01(1.41)	5.51(0.19)
C, %	52.6(1.4 )	51.1(2.9 )	52.9(5.1 )	51.9(0.3 )	52.8(0.3 )	52.1(1.4 )	52.6(2.1 )	52.9(2.7 )
WSC,mg.g <sup>-1</sup>	57.7(1.6 )	62.6(9.1 )	68.5(11.7)	65.7(7.1 )	91.5(3.4 )	71.7(12.6)	66.2(7.3 )	44.0(8.9 )
WSP,mg.g <sup>-1</sup>	76 (3 )	64 (35)	91 (15)	85 (5 )	90 (8 )	92 (14)	73 (16)	50 (13 )
WSF,mg.g <sup>-1</sup>	265 (10)	261 (50)	325 (38)	295 (24)	347 (17)	319 (34)	268 (43)	208 (36 )
E.E. %	5.02(0.56)	5.30(0.62)	5.69(0.60)	5.20(0.40)	5.22(0.32)	5.35(0.27)	5.41(0.43)	5.12(0.87)
Aq.E. %	19.0(2.1 )	24.4(3.0 )	23.4(2.4 )	22.1(0.9 )	19.4(1.5 )	24.5(1.4 )	22.7(3.4 )	14.9(3.4 )
HOLO. %	52.2(2.3 )	47.7(2.1 )	50.0(1.2 )	49.9(1.8 )	51.6(2.1 )	46.0(3.2 )	48.6(0.1 )	50.7(2.3 )
R.LIG %	23.8(1.2 )	22.6(0.5 )	20.9(3.1 )	22.8(0.5 )	23.8(2.7 )	24.1(2.1 )	23.4(3.8 )	29.3(3.2 )
P, mg.g <sup>-1</sup>	1.09(0.21)	1.56(0.31)	1.20(0.21)	0.99(0.25)	1.12(0.14)	1.38(0.62)	1.21(0.01)	1.04(0.09)
K, mg.g <sup>-1</sup>	5.10(0.75)	6.37(0.32)	4.48(0.42)	3.17(0.69)	4.53(0.95)	5.97(1.68)	4.50(0.58)	2.85(0.65)
Mg.mg.g <sup>-1</sup>	0.94(0.18)	1.26(0.16)	1.31(0.42)	0.91(0.20)	1.06(0.20)	1.30(0.27)	1.18(0.23)	1.05(0.21)
Ca.mg.g <sup>-1</sup>	5.25(1.40)	5.99(0.86)	7.87(0.29)	6.80(2.03)	6.11(1.37)	6.37(2.69)	7.18(1.18)	7.50(1.20)

TABLE B.9 Mean chemical composition of quarterly leaf litter-fall in beech stand at Nelson

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	6.12(0.57)	6.76(0.67)	7.33(1.09)	7.97(1.09)	5.74(0.46)	7.56(1.64)	5.83(0.73)	8.24(0.75)
C, %	48.8(0.7 )	47.3(0.9 )	47.5(0.7 )	48.1(0.9 )	48.5(0.5 )	47.3(4.5 )	48.0(1.0 )	49.0(1.4 )
WSC,mg.g <sup>-1</sup>	54.3(3.6 )	57.0(6.0 )	53.0(10.9)	62.8(2.7 )	68.4(7.5 )	75.3(8.9 )	58.2(8.4 )	52.6(1.4 )
WSP,mg.g <sup>-1</sup>	121 (10)	127 (17)	104 (26)	112 (3 )	152 (22)	158 (12)	119 (27)	107 (7 )
WSF,mg.g <sup>-1</sup>	265 (24)	269 (14)	245 (39)	273 (20)	320 (77)	364 (15)	262 (27)	277 (16 )
E.E. %	4.53(0.82)	3.39(0.25)	3.81(0.21)	3.78(0.34)	4.34(0.40)	3.67(0.80)	3.80(0.32)	4.36(0.29)
Aq.E. %	19.5(1.5 )	27.5(0.7 )	15.8(3.4 )	18.6(5.5 )	19.6(0.9 )	29.2(1.8 )	17.9(3.5 )	19.1(1.4 )
HOLO. %	50.8(2.3 )	49.2(3.1 )	52.2(0.7 )	53.1(2.1 )	50.7(0.5 )	48.3(0.9 )	51.2(2.0 )	51.9(0.5 )
R.LIG %	25.2(0.7 )	19.8(3.4 )	28.2(2.5 )	24.6(3.8 )	25.3(0.9 )	18.8(1.2 )	27.1(4.9 )	24.6(1.0 )
P, mg.g <sup>-1</sup>	0.94(0.12)	1.13(0.14)	0.81(0.12)	0.81(0.05)	0.95(0.05)	1.02(0.09)	0.91(0.16)	0.81(0.14)
K, mg.g <sup>-1</sup>	3.07(0.16)	5.83(1.83)	3.26(0.86)	2.78(0.05)	3.11(0.07)	5.37(0.45)	3.12(0.71)	2.97(0.10)
Mg.mg.g <sup>-1</sup>	1.20(0.09)	1.28(0.18)	1.21(0.20)	1.09(0.23)	1.20(0.07)	1.23(0.07)	1.21(0.03)	1.20(0.23)
Ca.mg.g <sup>-1</sup>	12.62(0.78)	12.56(4.06)	12.73(1.11)	12.69(0.69)	12.58(0.20)	11.90(1.00)	12.65(0.51)	12.78(1.31)

TABLE B.10 Mean chemical composition of quarterly twig litter-fall in beech stand at Nelson

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	5.78(0.41)	5.89(1.56)	6.02(0.32)	5.46(0.25)	5.44(1.10)	5.09(1.06)	4.68(0.54)	7.51(1.15)
C, %	52.8(0.6 )	48.7(0.9 )	50.9(2.9 )	49.3(1.6 )	49.5(5.3 )	47.0(3.1 )	48.8(3.6 )	46.4(5.1 )
WSC,mg.g <sup>-1</sup>	31.7(3.1 )	37.6(9.3 )	33.3(1.8 )	37.6(2.7 )	40.3(7.1 )	38.7(17.2)	35.9(4.2 )	36.2(4.0 )
WSP,mg.g <sup>-1</sup>	72 (16)	97 (18)	65 (32)	79 (17)	91 (11)	73 (43)	74 (22)	66 (12 )
WSF,mg.g <sup>-1</sup>	141 (25)	183 (47)	154 (53)	169 (27)	185 (18)	173 (89)	164 (17)	178 (20 )
E.E. %	3.16(1.20)	2.61(0.16)	2.69(0.51)	3.17(0.65)	2.91(0.40)	2.29(0.53)	2.73(0.43)	2.74(0.25)
Aq.E. %	11.9(2.0 )	13.9(4.0 )	10.7(2.4 )	11.8(1.9 )	11.8(1.4 )	12.9(2.5 )	11.9(2.4 )	11.0(2.1 )
HOLO. %	49.8(3.1 )	49.5(2.1 )	50.2(3.8 )	49.5(4.2 )	49.7(1.4 )	52.5(1.6 )	49.9(2.0 )	48.9(1.0 )
R.LIG %	35.2(0.1 )	34.1(2.0 )	36.5(5.6 )	35.6(1.6 )	35.6(1.8 )	32.4(1.2 )	35.5(3.1 )	37.3(1.6 )
P, mg.g <sup>-1</sup>	0.80(0.10)	0.76(0.20)	0.73(0.12)	0.65(0.01)	0.77(0.05)	0.72(0.45)	0.74(0.03)	0.71(0.12)
K, mg.g <sup>-1</sup>	3.11(1.09)	2.43(1.17)	2.78(0.10)	3.17(1.66)	2.88(0.49)	2.79(2.36)	2.73(0.12)	1.99(0.12)
Mg.mg.g <sup>-1</sup>	1.86(0.10)	1.98(0.32)	1.78(0.42)	1.93(0.16)	1.86(0.14)	1.64(0.80)	1.82(0.16)	1.84(0.31)
Ca.mg.g <sup>-1</sup>	13.31(2.26)	16.44(3.25)	14.46(0.58)	13.74(3.55)	13.34(1.22)	12.34(3.78)	14.15(0.53)	15.79(6.45)

TABLE B.11 Mean chemical composition of quarterly "others" litter-fall in beech stand at Nelson

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	8,31(0,55)	9,53(1,65)	8,33(1,40)	7,49(0,33)	9,41(0,31)	10,85(2,08)	9,00(1,42)	9,17(1,42)
C, %	49.8(2.0 )	48.8(2,9 )	49,0(0,7 )	50,2(0,7 )	49,7(0,5 )	49,2(2,7 )	49,5(0,7 )	50,4(5,3 )
WSC,mg.g <sup>-1</sup>	40,9(4,9 )	40,6(19,2)	43,5(12,0)	78,3(5,3 )	56,2(2,3 )	67,3(31,0)	41,3(3,6 )	69,2(24,7)
WSP,mg.g <sup>-1</sup>	67 (24)	45 (17)	39 (13)	35 (19)	123 (28)	50 (25)	39 (2 )	26 (5 )
WSF,mg.g <sup>-1</sup>	148 (21)	135 (57)	143 (21)	157 (34)	264 (67)	201 (21)	147 (9 )	188 (38 )
E.E. %								
Aq.E. %								
HOLO. %								
R.LIG %								
P, mg.g <sup>-1</sup>	1.02(0.05)	0.97(0.18)	1.12(0.12)	1.19(0.01)	1.09(0.12)	1.11(0.45)	1.12(0.07)	1.05(0.51)
K, mg.g <sup>-1</sup>	3.25(0.69)	2.74(0.60)	3.59(0.86)	5.24(0.82)	3.38(0.29)	3.35(1.84)	3.58(0.42)	3.72(1.62)
Mg.mg.g <sup>-1</sup>	1.11(0.32)	1.16(0.32)	1.27(0.07)	1.15(0.07)	1.19(0.14)	1.39(0.07)	1.20(0.16)	1.11(0.36)
Ca.mg.g <sup>-1</sup>	13.56(5.16)	13.28(1.15)	14.92(0.14)	7.46(0.47)	13.97(1.84)	13.40(4.59)	14.60(0.65)	15.22(7.94)

The organic constituents of "others" litter-fall were not determined



TABLE B.12 Mean chemical composition of quarterly needle litter-fall in radiata stand at Nelson

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	8.42(1.86)	7.65(0.64)	5.98(0.98)	6.79(1.41)	7.79(0.83)	10.39(1.54)	7.80(1.71)	6.01(0.29)
C, %	51.5(0.9 )	50.8(2.1 )	51.3(2.5 )	50.4(0.5 )	51.0(0.9 )	50.4(2.9 )	50.9(0.9 )	51.8(2.0 )
WSC,mg.g <sup>-1</sup>	32.9(3.1 )	40.8(8.4 )	50.4(0.5 )	41.1(2.3 )	58.2(12.8)	53.1(6.2 )	47.5(5.8 )	39.4(2.9 )
WSP,mg.g <sup>-1</sup>	30 (6 )	51 (1 )	64 (2 )	41 (9 )	49 (12)	55 (3 )	60 (7 )	41 (3 )
WSF,mg.g <sup>-1</sup>	125 (38)	205 (20)	226 (27)	192 (9 )	207 (45)	239 (37 )	212 (23)	198 (20 )
E.E. %	4.17(0.65)	4.73(1.18)	5.54(1.39)	5.63(0.82)	5.20(1.00)	6.16(0.84)	5.44(0.75)	5.47(0.40)
Aq.E. %	10.2(1.3 )	20.3(1.8 )	15.8(2.0 )	12.1(0.7 )	12.6(4.9 )	19.1(1.1 )	16.3(0.8 )	13.6(1.2 )
HOLO. %	53.2(3.6 )	51.6(1.6 )	53.7(1.1 )	52.3(6.2 )	51.6(2.5 )	46.7(2.1 )	51.8(4.5 )	50.9(2.7 )
R.LIG %	31.9(5.4 )	23.5(1.8 )	25.0(3.1 )	30.0(5.4 )	30.5(2.9 )	28.1(2.9 )	26.5(3.8 )	30.1(1.2 )
P, mg.g <sup>-1</sup>	0.89(0.14)	1.32(0.21)	1.10(0.23)	1.00(0.14)	1.02(0.20)	1.34(0.29)	1.11(0.01)	0.98(0.31)
K, mg.g <sup>-1</sup>	2.83(0.32)	5.69(2.39)	3.90(0.64)	2.93(0.27)	3.19(0.45)	4.58(0.76)	3.98(0.27)	3.10(0.86)
Mg,mg.g <sup>-1</sup>	1.28(0.31)	1.52(0.20)	1.54(0.23)	1.39(0.21)	1.37(0.14)	1.40(0.10)	1.45(0.14)	1.39(0.12)
Ca,mg.g <sup>-1</sup>	7.26(1.79)	6.97(3.91)	8.71(1.51)	9.27(0.98)	7.41(0.38)	5.91(0.67)	7.89(1.04)	8.41(2.43)

TABLE B.13 Mean chemical composition of quarterly needle litter-fall in radiata<sub>reg.</sub> stand at Nelson

CONSTITUENTS	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8
N, mg.g <sup>-1</sup>	8.32(0.96)	8.47(1.18)	6.66(0.65)	5.71(0.87)	7.55(0.92)	12.71(1.52)	7.31(1.02)	5.31(0.62)
C, %	51.3(1.2 )	50.4(1.0 )	51.7(0.5 )	51.3(1.6 )	51.5(1.2 )	51.6(7.3 )	51.6(0.9 )	51.2(3.6 )
WSC,mg.g <sup>-1</sup>	31.0(2.0 )	32.4(6.9 )	52.0(7.3 )	39.2(2.9 )	72.5(9.1 )	40.4(8.7 )	47.6(8.2 )	39.3(1.4 )
WSP,mg.g <sup>-1</sup>	29 (5 )	36 (8 )	57 (13)	40 (7 )	56 (4 )	37 (9 )	56 (2 )	45 (3 )
WSF,mg.g <sup>-1</sup>	102 (2 )	171 (9 )	243 (52)	163 (26)	249 (15)	179 (26)	210 (56)	193 (12 )
E.E. %	4.51(0.51)	4.11(1.04)	5.29(0.87)	5.48(0.65)	5.31(1.64)	8.30(1.95)	5.52(1.48)	5.65(0.31)
Aq.E. %	9.3 (1.9 )	19.7(0.7 )	16.7(2.1 )	12.3(1.6 )	11.6(3.4 )	14.4(1.9 )	15.6(2.3 )	14.2(0.9 )
HOLO. %	50.7(1.2 )	51.5(1.2 )	51.3(1.0 )	50.4(2.7 )	50.1(2.3 )	46.2(1.0 )	50.8(1.6 )	50.0(1.8 )
R.LIG %	35.5(3.2 )	24.7(0.7 )	26.8(2.0 )	31.6(2.0 )	33.0(4.2 )	31.1(2.1 )	28.1(1.8 )	30.1(0.7 )
P, mg.g <sup>-1</sup>	1.03(0.14)	1.30(0.12)	1.08(0.38)	0.91(0.14)	1.13(0.16)	2.03(0.95)	1.14(0.14)	1.06(0.31)
K, mg.g <sup>-1</sup>	2.74(1.22)	5.37(0.82)	3.61(1.68)	2.60(0.25)	3.13(0.65)	4.56(2.14)	3.80(0.47)	2.82(0.56)
Mg.mg.g <sup>-1</sup>	1.53(0.29)	1.59(0.25)	1.39(0.23)	1.47(0.09)	1.53(0.07)	1.76(0.38)	1.49(0.16)	1.33(0.38)
Ca.mg.g <sup>-1</sup>	9.71(1.39)	8.08(2.59)	10.57(1.26)	9.43(0.60)	8.85(1.59)	6.71(3.05)	10.28(0.86)	10.36(3.42)

TABLE B.14 Mean chemical composition of annual branch and pollen cone litter-fall in the forest stands at Granville, Hanmer and Nelson

CONSTITUENTS	GRANVILLE		HANMER		NELSON		
	P/CONE	BRANCH	P/CONE	P/CONE	P/CONE <sub>reg.</sub>	BRANCH	BRANCH <sub>reg.</sub>
N, mg.g <sup>-1</sup>	6.30(0.39)	1.70(0.17)	6.31(0.36)	7.07(0.40)	6.91(0.28)	4.44(0.68)	2.26(0.63)
C, %	52.1(1.3)	46.7(1.8)	51.7(1.8)	49.8(2.7)	50.6(2.6)	46.8(0.7)	51.3(2.0 )
WSC,mg.g <sup>-1</sup>	49.2(0.9)	8.1 (3.7)	50.1(2.5)	26.7(10.4)	27.2(10.8)	17.2(8.9)	30.4(3.5 )
WSP,mg.g <sup>-1</sup>	72 (3)	14 (7)	73 (3)	38 (2)	38 (2)	11 (3)	28 (9)
WSF,mg.g <sup>-1</sup>	239 (72)	76 (45)	221 (15)	92 (5)	94 (6)	83 (50)	136 (4)
E.E. %	3.43(0.27)	0.63(0.26)	4.10(0.38)	3.81(0.57)	4.19(0.49)	0.50(0.42)	4.14(1.61)
Aq. E %	8.5 (1.8)	6.3 (1.9)	11.7(1.0)	8.6 (0.2)	8.2 (1.6)	5.3 (2.4)	9.7 (1.5 )
HOLO. %	50.3(0.4)	71.8(5.0)	47.1(1.8)	50.1(1.5)	50.7(1.8)	76.4(1.5)	65.1(3.5 )
R.LIG %	37.8(1.3)	21.2(4.7)	37.0(1.0)	37.5(1.5)	36.9(0.6)	17.0(1.7)	19.9(3.5 )
P, mg.g <sup>-1</sup>	0.75(0.20)	0.10(0.04)	0.58(0.09)	0.68(0.11)	0.71(0.13)	0.34(0.62)	0.61(0.29)
K, mg.g <sup>-1</sup>	2.68(0.44)	0.45(0.40)	3.10(0.22)	2.81(0.27)	2.56(0.62)	0.87(1.39)	n.d.
Mg,mg.g <sup>-1</sup>	1.28(0.05)	0.77(0.50)	1.05(0.09)	1.20(0.02)	1.14(0.15)	0.80(0.77)	n.d.
Ca,mg.g <sup>-1</sup>	3.69(3.28)	6.43(1.13)	2.06(0.18)	2.10(0.20)	2.17(0.18)	8.15(1.67)	n.d.

TABLE C.1

GRANVILLE: MEAN QUARTERLY NITROGEN BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	4.21(1.37)	2.42(0.95)	3.41(0.43)	10.04(0.85)
2	4.58(1.80)	3.19(2.21)	4.75(4.00)	12.52(5.61)
3	1.79(0.42)	0.33(0.23)	1.55(0.57)	3.67(0.65)
4	6.35(1.69)	2.79(1.58)	3.56(0.52)	12.70(2.88)
Annual	16.93(0.81)	8.73(4.36)	13.27(4.00)	38.93(6.46)
5	3.72(0.90)	1.53(0.75)	3.00(0.59)	8.25(1.22)
6	3.16(0.75)	0.80(0.47)	2.16(0.68)	6.12(0.73)
7	3.15(0.33)	1.02(0.16)	3.09(2.67)	7.26(2.76)
8	4.13(0.45)	0.91(0.19)	7.85(2.25)	12.89(2.34)
Annual	14.16(1.86)	4.26(1.31)	16.10(4.81)	34.52(3.70)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	7.25(2.18)	0.49(0.20)		7.74(2.32)
2	12.40(2.90)			12.40(2.90)
3	2.59(0.62)			2.59(0.62)
4	10.62(2.65)	1.94(0.60)		12.56(2.79)
Annual	32.86(5.66)	2.43(0.36)		35.29(5.53)
5	6.35(0.98)			6.35(0.98)
6	5.28(0.77)			5.28(0.77)
7	3.93(1.10)			3.93(1.10)
8	9.47(2.23)	1.93(0.37)		11.40(2.05)
Annual	25.03(2.22)	1.93(0.37)		26.96(2.00)

TABLE C.2

GRANVILLE: MEAN QUARTERLY CARBON BUDGET (kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	351(88)	254(106)	165(42)	770(47)
2	461(60)	460(341)	167(259)	1088(381)
3	170(16)	54(59)	59(24)	283(88)
4	454(62)	365(302)	160(4)	979(323)
Annual	1436(53)	1133(800)	551(317)	3120(775)
5	319(132)	153(102)	123(55)	595(207)
6	335(33)	103(103)	118(132)	555(170)
7	254(57)	110(35)	155(253)	520(220)
8	400(31)	86(25)	334(68)	820(88)
Annual	1308(185)	452(135)	730(450)	2490(266)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	450(126)	32(11)		482(134)
2	1024(123)			1024(123)
3	191(66)			191(66)
4	587(103)	190(7)		777(106)
Annual	2252(262)	222(5)		2474(259)
5	370(57)			370(57)
6	376(123)			376(123)
7	359(186)			359(186)
8	587(97)	166(11)		753(99)
Annual	1692(323)	166(11)		1858(329)

TABLE C.3

GRANVILLE: MEAN QUARTERLY PHOSPHORUS BUDGET (g/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	293(169)	156(37)	316(104)	765(71)
2	222(47)	221(152)	266(33)	709(419)
3	125(72)	26(26)	122(44)	273(127)
4	463(159)	192(231)	334(55)	989(856)
Annual	1103(391)	595(430)	1038(388)	2736(970)
5	219(140)	97(99)	256(71)	572(250)
6	176(35)	53(57)	170(121)	399(123)
7	146(66)	63(26)	248(385)	457(349)
8	228(39)	53(26)	584(119)	865(133)
Annual	769(209)	266(187)	1258(507)	2293(248)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	500(78)	46(17)		546(64)
2	874(199)			874(199)
3	161(50)			161(50)
4	794(372)	273(64)		1067(411)
Annual	2329(234)	319(72)		2648(288)
5	489(86)			489(86)
6	317(60)			317(60)
7	261(83)			261(83)
8	552(288)	238(72)		790(358)
Annual	1619(354)	238(72)		1857(426)

TABLE C.4

GRANVILLE: MEAN QUARTERLY POTASSIUM BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	1.08 (0.33)	0.61 (0.31)	0.58 (0.43)	2.27 (0.44)
2	1.05 (0.21)	1.28 (0.86)	0.65 (0.75)	2.98 (1.54)
3	0.43 (0.12)	0.15 (0.14)	0.41 (0.10)	0.99 (0.11)
4	2.02 (1.15)	0.93 (0.88)	0.65 (0.24)	3.60 (2.24)
Annual	4.58 (0.76)	2.97 (2.07)	2.29 (0.97)	9.84 (3.16)
5	1.51 (0.34)	0.58 (0.37)	0.56 (0.42)	2.65 (0.85)
6	1.08 (0.30)	0.33 (0.49)	0.54 (0.50)	1.95 (0.80)
7	0.98 (0.23)	0.39 (0.16)	1.62 (3.43)	2.99 (0.52)
8	1.06 (0.09)	0.24 (0.23)	1.32 (0.68)	2.62 (0.52)
Annual	4.63 (0.75)	1.54 (1.11)	4.04 (3.57)	10.21 (2.55)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1.75 (0.89)	0.17 (0.08)		1.92 (0.97)
2	3.41 (0.95)			3.41 (0.95)
3	0.64 (0.18)			0.64 (0.18)
4	2.79 (0.60)	0.98 (0.10)		3.77 (0.55)
Annual	8.59 (1.46)	1.15 (0.17)		9.74 (1.54)
5	1.96 (0.32)			1.96 (0.32)
6	2.13 (0.31)			2.13 (0.31)
7	1.04 (0.52)			1.04 (0.52)
8	1.78 (0.99)	0.86 (0.17)		2.64 (1.11)
Annual	6.91 (1.38)	0.86 (0.17)		7.77 (1.51)

TABLE C.5

GRANVILLE: MEAN QUARTERLY MAGNESIUM BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	1.16(0.24)	0.86(0.53)	0.52(0.31)	2.54(0.53)
2	1.36(0.24)	1.45(1.01)	0.41(0.50)	3.22(0.98)
3	0.44(0.02)	0.20(0.28)	0.18(0.08)	0.82(0.31)
4	1.41(0.56)	1.24(0.96)	0.45(0.04)	3.10(1.53)
Annual	4.37(0.34)	3.75(2.73)	1.56(0.83)	9.68(3.11)
5	1.42(0.88)	0.58(0.26)	0.36(0.14)	2.36(0.98)
6	1.33(0.54)	0.37(0.44)	0.30(0.27)	2.00(1.09)
7	0.71(0.14)	0.41(0.16)	0.42(0.73)	1.54(0.77)
8	1.00(0.07)	0.27(0.31)	0.82(0.14)	2.09(0.30)
Annual	4.46(0.36)	1.63(1.00)	1.90(1.14)	7.99(1.08)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1.08(0.50)	0.08(0.02)		1.16(0.52)
2	2.13(0.56)			2.13(0.56)
3	0.39(0.08)			0.39(0.08)
4	1.36(0.40)	0.47(0.05)		1.83(0.37)
Annual	4.96(0.92)	0.55(0.03)		5.51(0.90)
5	0.99(0.22)			0.99(0.22)
6	0.91(0.34)			0.91(0.34)
7	0.74(0.58)			0.74(0.58)
8	1.10(0.30)	0.41(0.02)		1.51(0.30)
Annual	3.74(0.88)	0.41(0.02)		4.15(0.89)



TABLE C.6

GRANVILLE: MEAN QUARTERLY CALCIUM BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	5.38(1.13)	5.97(3.72)	2.64(2.54)	13.99(5.46)
2	8.63(0.46)	10.77(12.88)	2.29(2.56)	21.69(11.60)
3	2.37(1.26)	1.31(2.04)	0.87(0.94)	4.55(3.21)
4	7.28(2.03)	9.15(3.11)	1.98(0.50)	18.41(0.74)
Annual	23.66(4.31)	27.20(2.10)	7.78(6.38)	58.65(18.47)
5	5.54(3.31)	3.49(1.63)	1.57(0.76)	10.60(4.26)
6	5.33(2.47)	2.14(2.51)	2.45(3.46)	9.92(6.68)
7	3.78(1.11)	2.86(1.61)	2.52(4.89)	9.16(5.87)
8	5.47(2.10)	1.93(2.02)	4.81(0.94)	12.21(3.09)
Annual	20.12(2.91)	10.42(5.35)	11.35(9.89)	41.89(7.20)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	3.76(0.89)	0.21(0.11)		3.97(0.80)
2	8.38(1.37)			8.38(1.37)
3	1.77(0.73)			1.77(0.73)
4	5.04(1.89)	1.36(1.30)		6.40(1.45)
Annual	18.95(2.04)	1.57(1.40)		20.52(1.42)
5	3.44(0.93)			3.44(0.93)
6	3.35(1.56)			3.35(1.56)
7	3.04(2.71)			3.04(2.71)
8	4.53(1.80)	1.17(1.01)		5.70(2.50)
Annual	14.36(4.53)	1.17(1.01)		15.53(5.49)

TABLE C.7

GRANVILLE: MEAN QUARTERLY WSC BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	40.4(14.3)	19.4(8.3)	16.4(6.7)	76.2(15.5)
2	56.7(15.1)	38.5(26.8)	14.0(23.2)	109.2(34.4)
3	23.3(4.3)	5.5(4.6)	5.7(4.4)	34.5(8.3)
4	63.5(11.0)	25.5(16.7)	13.1(3.5)	102.1(30.1)
Annual	183.9(25.4)	88.9(55.9)	49.2(34.6)	322.0(61.7)
5	51.0(24.8)	16.4(13.6)	12.8(9.4)	80.2(36.6)
6	38.5(6.0)	9.1(9.7)	10.8(9.9)	58.4(11.3)
7	34.0(10.4)	10.3(12.2)	16.5(28.5)	60.8(19.8)
8	58.1(10.0)	6.6(4.1)	31.6(13.7)	96.3(14.3)
Annual	181.6(37.6)	42.4(26.0)	71.7(51.2)	295.7(5.1)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	31.5(10.5)	3.0(1.1)		34.5(11.5)
2	79.1(15.6)			79.1(15.6)
3	14.3(5.6)			14.3(5.6)
4	41.5(7.7)	18.0(1.2)		59.5(7.2)
Annual	166.4(15.3)	21.0(1.1)		187.4(14.3)
5	29.5(2.6)			29.5(2.6)
6	28.1(13.8)			28.1(13.8)
7	23.4(12.3)			23.4(12.3)
8	44.1(11.6)	15.7(0.6)		59.8(11.5)
Annual	125.1(28.8)	15.7(0.6)		140.8(28.8)

TABLE C.8

GRANVILLE: MEAN QUARTERLY WSP BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	76.0(18.4)	28.9(4.6)	19.0(16.5)	123.9(13.1)
2	118.4(26.8)	59.8(44.9)	12.6(18.0)	190.8(39.8)
3	44.8(9.5)	8.6(7.9)	4.9(3.4)	58.3(15.4)
4	129.5(12.8)	38.0(18.9)	11.6(3.8)	179.1(25.9)
Annual	368.7(25.5)	135.3(75.7)	48.1(40.3)	552.1(59.9)
5	116.8(54.0)	34.0(21.3)	17.7(5.1)	168.5(62.2)
6	90.6(6.1)	20.2(14.6)	11.4(11.9)	122.2(23.2)
7	80.3(30.5)	18.0(3.4)	19.7(23.6)	118.0(8.1)
8	138.2(21.4)	8.9(8.9)	40.4(4.6)	187.5(33.7)
Annual	425.9(89.7)	81.1(42.4)	89.2(35.8)	596.2(74.8)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	32.5(8.9)	4.6(1.8)		37.1(10.3)
2	80.4(22.3)			80.4(22.3)
3	12.9(5.3)			12.9(5.3)
4	48.4(20.7)	27.3(3.6)		75.7(20.4)
Annual	174.2(28.4)	31.9(4.3)		206.1(26.8)
5	35.2(5.3)			35.2(5.3)
6	30.6(7.1)			30.6(7.1)
7	24.7(14.0)			24.7(14.0)
8	48.0(14.3)	23.8(1.6)		71.8(12.7)
Annual	138.5(29.3)	23.8(1.6)		162.3(27.7)

TABLE C.9

GRANVILLE: MEAN QUARTERLY WSF BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	190.2(50.9)	83.1(15.4)	59.8(42.8)	333.1(65.8)
2	268.5(38.4)	153.8(113.7)	50.2(75.5)	472.5(119.0)
3	93.6(18.4)	20.1(18.7)	16.2(8.5)	129.9(30.7)
4	269.0(37.5)	101.4(58.2)	43.3(6.6)	413.7(89.5)
Annual	821.3(65.4)	358.4(217.3)	169.5(130.0)	1349.2(210.9)
5	245.1(98.3)	73.5(46.5)	51.0(21.3)	369.6(124.9)
6	202.3(36.9)	42.8(35.5)	41.4(39.3)	286.5(48.5)
7	165.1(60.3)	42.6(7.2)	63.4(97.0)	271.1(45.2)
8	281.9(45.7)	25.0(20.0)	121.8(25.9)	428.7(59.0)
Annual	894.4(177.1)	183.9(95.9)	277.6(166.4)	1355.9(60.4)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	145.4(31.4)	15.0(9.4)		160.4(40.6)
2	358.0(105.8)			358.0(105.8)
3	50.0(18.7)			50.0(18.7)
4	184.7(50.3)	87.3(25.2)		272.0(24.1)
Annual	738.1(60.1)	102.3(33.9)		840.4(93.1)
5	140.0(21.1)			140.0(21.1)
6	116.0(15.4)			116.0(15.4)
7	107.6(60.4)			107.6(60.4)
8	199.0(54.9)	76.1(22.2)		275.1(33.4)
Annual	562.6(109.6)	76.1(22.2)		638.7(89.5)

TABLE C.10

GRANVILLE: MEAN QUARTERLY EE BUDGET ( kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	35.5(11.3)	13.1(6.0)		48.6(8.9)
2	45.5(3.8)	17.9(10.0)		63.4(6.2)
3	15.1(2.7)	2.3(1.6)		17.4(4.3)
4	37.7(2.3)	14.9(14.6)		52.6(16.8)
Annual	133.8(11.3)	48.2(30.3)		182.0(20.8)
5	29.0(16.8)	6.4(4.0)		35.4(19.2)
6	35.3(2.5)	4.7(5.7)		40.0(4.7)
7	26.1(7.5)	5.3(2.5)		31.4(5.6)
8	40.5(3.2)	4.0(2.5)		44.5(6.0)
Annual	130.9(21.9)	20.4(12.2)		151.3(22.3)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	29.2(3.8)	2.1(0.5)		31.3(4.3)
2	91.7(26.1)			91.7(26.1)
3	16.3(6.2)			16.3(6.2)
4	44.4(5.6)	12.5(1.2)		56.9(6.4)
Annual	181.6(17.7)	14.6(0.7)		196.2(18.4)
5	30.1(6.7)			30.1(6.7)
6	36.2(20.3)			36.2(20.3)
7	34.5(24.7)			34.5(24.7)
8	55.0(14.2)	10.9(1.0)		65.9(14.2)
Annual	155.8(43.0)	10.9(1.0)		166.7(43.5)

TABLE C.11

GRANVILLE: MEAN QUARTERLY AE BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	130.4(57.2)	48.2(31.8)		178.6(27.4)
2	191.8(32.0)	92.1(68.2)		283.9(38.9)
3	67.2(12.4)	11.3(10.9)		78.5(22.6)
4	202.3(58.3)	58.6(54.5)		260.9(108.7)
Annual	591.7(60.5)	210.2(150.2)		801.9(138.8)
5	190.0(81.9)	43.2(18.6)		233.2(90.0)
6	121.9(12.2)	16.0(13.9)		137.9(25.9)
7	131.8(25.9)	24.9(8.2)		156.7(17.9)
8	207.4(85.4)	17.7(6.0)		225.1(80.7)
Annual	651.1(158.4)	101.8(28.7)		752.9(150.0)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	82.8(5.4)	5.3(2.9)		88.1(7.8)
2	228.1(51.2)			228.1(51.2)
3	44.1(16.6)			44.1(16.6)
4	125.9(14.4)	31.0(5.8)		156.9(17.2)
Annual	480.9(31.6)	36.3(8.4)		517.2(24.5)
5	105.9(17.5)			105.9(17.5)
6	74.6(38.0)			74.6(38.0)
7	70.8(46.4)			70.8(46.4)
8	135.8(40.0)	27.1(5.6)		162.9(34.5)
Annual	387.1(108.5)	27.1(5.6)		414.2(103.2)

TABLE C.12

GRANVILLE: MEAN QUARTERLY HOLOCELLULOSE BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	273.7(95.1)	229.0(104.8)		502.7(20.6)
2	427.3(64.9)	445.8(343.6)		873.1(297.7)
3	150.5(19.0)	51.6(68.2)		202.1(71.7)
4	411.0(48.1)	360.6(277.0)		771.6(325.0)
Annual	1262.5(108.8)	1087.0(782.5)		2349.5(682.7)
5	271.5(120.5)	154.1(108.1)		425.6(194.3)
6	295.9(64.9)	98.8(88.2)		394.7(68.0)
7	231.6(49.9)	105.5(20.6)		337.1(42.3)
8	368.6(44.4)	98.0(30.7)		466.6(58.7)
Annual	1167.6(140.5)	456.4(208.2)		1624.0(253.0)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	411.8(98.8)	30.9(10.6)		442.7(105.9)
2	942.0(96.8)			942.0(96.8)
3	171.2(51.9)			171.2(51.9)
4	531.1(95.5)	183.8(12.8)		714.9(94.2)
Annual	2056.1(150.4)	214.7(8.0)		2270.8(142.5)
5	354.8(35.6)			354.8(35.6)
6	363.5(136.3)			363.5(136.3)
7	354.9(191.2)			354.9(191.2)
8	600.3(82.7)	160.1(6.5)		760.4(87.1)
Annual	1673.5(287.1)	160.1(6.5)		1833.6(290.9)

TABLE C.13

GRANVILLE: MEAN QUARTERLY R.LIGNIN BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	214.5(45.5)	198.4(87.8)		412.9(42.2)
2	245.2(35.6)	342.3(232.9)		587.5(230.2)
3	90.2(4.0)	44.1(41.3)		134.3(39.7)
4	256.7(49.5)	300.9(272.6)		557.6(321.5)
Annual	806.6(80.5)	885.7(626.2)		1692.3(628.6)
5	151.5(80.5)	107.3(73.3)		258.8(143.8)
6	185.2(12.6)	76.8(79.2)		262.0(74.6)
7	118.2(28.3)	81.9(27.6)		200.1(24.1)
8	173.8(53.2)	61.2(23.2)		235.0(47.9)
Annual	628.7(66.9)	327.2(180.6)		955.9(207.3)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	340.1(119.6)	23.2(7.5)		363.3(124.8)
2	649.9(111.4)			649.9(111.4)
3	128.4(58.7)			128.4(58.7)
4	429.9(139.6)	138.2(10.7)		568.1(147.4)
Annual	1548.3(324.2)	161.4(3.8)		1709.7(322.4)
5	234.8(50.3)			234.8(50.3)
6	228.7(23.7)			228.7(23.7)
7	214.1(86.5)			214.1(86.5)
8	253.5(95.1)	120.4(7.6)		473.9(102.4)
Annual	1031.1(205.6)	120.4(7.6)		1151.5(212.8)



TABLE C.14

HANMER: MEAN QUARTERLY NITROGEN BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	5.17(0.98)	1.61(0.63)	3.38(2.10)	10.16(1.75)
2	4.25(1.37)	0.94(0.43)	0.81(0.41)	6.00(2.01)
3	1.95(0.64)	0.33(0.15)	0.37(0.20)	2.65(0.53)
4	0.83(0.26)	0.75(0.13)	0.74(0.73)	2.32(0.80)
Annual	12.20(1.43)	3.63(0.87)	5.30(2.42)	21.13(2.88)
5	6.46(0.82)	0.91(0.35)	2.11(0.55)	9.48(1.37)
6	2.68(0.34)	1.31(0.43)	0.89(0.23)	4.88(0.74)
7	0.91(0.37)	0.55(0.22)	0.55(0.46)	2.01(0.93)
8	2.54(0.92)	0.68(0.28)	0.67(0.29)	3.89(1.12)
Annual	12.59(1.58)	3.45(0.75)	4.22(0.66)	20.26(2.26)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1.31(0.53)	0.42(0.25)		1.73(0.76)
2	2.76(0.80)			2.76(0.80)
3	2.16(0.65)			2.16(0.65)
4	1.35(0.81)			1.35(0.81)
Annual	7.78(2.21)	0.42(0.25)		8.00(2.31)
5	1.45(0.87)			1.45(0.87)
6	6.28(3.39)			6.28(3.39)
7	1.14(0.52)			1.14(0.52)
8	0.89(0.87)	0.38(0.10)		1.27(0.82)
Annual	9.76(3.52)	0.38(0.10)		10.14(3.59)

TABLE C.15

HANMER:		MEAN QUARTERLY		CARBON BUDGET	(kg/ha)
BEECH					
Q	LEAF	TWIG/STEM	OTHER	TOTAL	
1	538(144)	148(32)	291(164)	977(201)	
2	481(219)	92(98)	51(53)	624(344)	
3	199(111)	44(18)	20(1)	263(93)	
4	70(45)	76(1)	49(71)	195(106)	
Annual	1288(270)	360(87)	411(212)	2059(301)	
5	665(129)	95(62)	145(60)	905(217)	
6	322(89)	159(82)	55(29)	535(84)	
7	92(51)	52(45)	18(10)	162(104)	
8	193(115)	56(47)	55(36)	304(166)	
Annual	1272(221)	361(129)	273(40)	1906(316)	
RADIATA					
Q	NEEDLE	POL./CONE	OTHER	TOTAL	
1	119(21)	37(18)		156(42)	
2	262(84)			262(84)	
3	210(98)			210(98)	
4	95(71)			95(71)	
Annual	686(232)	37(18)		723(248)	
5	106(12)			106(12)	
6	474(345)			474(345)	
7	128(78)			128(78)	
8	45(32)	34(10)		79(38)	
Annual	753(450)	34(10)		787(459)	

TABLE C.16

HANMER: MEAN QUARTERLY PHOSPHORUS BUDGET (g/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	1090( 382)	252(106)	471(219)	1813( 400)
2	1048(1041)	141( 73)	97 ( 65)	1286(1050)
3	426 ( 256)	66 ( 49)	61 ( 20)	553 ( 232)
4	96 ( 58)	97 ( 21)	128(144)	321 ( 175)
Annual	2660(1054)	556( 53)	757(340)	3973(1310)
5	1241( 411)	145( 93)	264( 95)	1650( 523)
6	820 ( 177)	287(151)	119( 42)	1226( 210)
7	186 ( 118)	82 ( 69)	47 ( 51)	315 ( 232)
8	248 ( 164)	65 ( 47)	90 ( 42)	403 ( 221)
Annual	2495( 539)	579(226)	520( 45)	3594( 697)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	245 ( 18)	42(21)		287 ( 27)
2	810 ( 439)			810 ( 439)
3	475 ( 256)			475 ( 256)
4	174 ( 104)			174 ( 104)
Annual	1704( 755)	42(21)		1746( 763)
5	226 ( 53)			226 ( 53)
6	1276(1090)			1276(1090)
7	296 ( 188)			296 ( 188)
8	88 ( 67)	38(47)		126 ( 69)
Annual	1886(1381)	38(47)		1924(1387)

TABLE C.17

HANMER: MEAN QUARTERLY POTASSIUM BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	2.58(1.20)	0.71(0.44)	1.20(1.50)	4.49(2.19)
2	4.11(1.85)	0.46(0.30)	0.23(0.12)	4.80(2.18)
3	1.18(0.79)	0.16(0.05)	0.11(0.01)	1.45(0.78)
4	0.27(0.16)	0.27(0.02)	0.32(0.49)	0.86(0.59)
Annual	8.14(2.05)	1.60(0.46)	1.86(1.44)	11.60(2.56)
5	3.38(2.03)	0.39(0.15)	0.64(0.21)	4.41(1.94)
6	2.87(0.62)	0.84(0.22)	0.33(0.09)	4.04(0.32)
7	0.55(0.30)	0.21(0.16)	0.10(0.06)	0.86(0.50)
8	0.64(0.25)	0.16(0.10)	0.23(0.08)	1.03(0.29)
Annual	7.44(2.30)	1.60(0.42)	1.30(0.24)	10.34(2.44)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1.15(0.21)	0.22(0.12)		1.37(0.30)
2	3.29(1.31)			3.29(1.31)
3	1.77(0.78)			1.77(0.78)
4	0.57(0.39)			0.57(0.39)
Annual	6.78(2.36)	0.22(0.12)		7.00(2.43)
5	0.90(0.07)			0.90(0.07)
6	5.39(3.62)			5.39(3.62)
7	1.12(0.81)			1.12(0.81)
8	0.24(0.20)	0.20(0.05)		0.44(0.20)
Annual	7.65(4.49)	0.20(0.05)		7.85(4.53)

TABLE C.18

HANMER: MEAN QUARTERLY MAGNESIUM BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	1.41(0.15)	0.61(0.20)	0.64(0.50)	2.66(0.44)
2	1.44(0.73)	0.39(0.38)	0.14(0.08)	1.97(1.17)
3	0.50(0.34)	0.17(0.08)	0.06(0.02)	0.73(0.83)
4	0.17(0.11)	0.29(0.02)	0.19(0.28)	0.65(0.36)
Annual	3.62(0.55)	1.46(0.23)	1.03(0.61)	6.01(0.83)
5	1.76(0.42)	0.39(0.28)	0.37(0.15)	2.52(0.63)
6	0.89(0.21)	0.64(0.27)	0.18(0.05)	1.71(0.23)
7	0.23(0.14)	0.21(0.19)	0.06(0.03)	0.50(0.33)
8	0.43(0.20)	0.21(0.17)	0.14(0.05)	0.78(0.35)
Annual	3.31(0.67)	1.45(0.51)	0.75(0.12)	5.51(0.10)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	0.21(0.07)	0.08(0.04)		0.29(0.11)
2	0.65(0.27)			0.65(0.27)
3	0.52(0.36)			0.52(0.36)
4	0.16(0.09)			0.16(0.09)
Annual	1.54(0.64)	0.08(0.04)		1.62(0.65)
5	0.21(0.07)			0.21(0.07)
6	1.21(1.13)			1.21(1.13)
7	0.28(0.14)			0.28(0.14)
8	0.09(0.05)	0.07(0.02)		0.16(0.06)
Annual	1.79(1.33)	0.07(0.02)		1.86(1.34)

TABLE C.19

HANMER: MEAN QUARTERLY CALCIUM BUDGET ( kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	9.64(1.58)	2.95(1.04)	4.20(0.24)	16.79( 1.48)
2	11.92(6.75)	3.40(4.00)	0.86(0.86)	16.18(11.53)
3	4.07(2.49)	1.01(0.51)	0.30(0.13)	5.38( 2.21)
4	1.41(1.01)	2.01(0.62)	0.80(1.06)	4.22( 2.26)
Annual	27.04(5.06)	9.37(2.99)	6.16(2.80)	42.57( 6.24)
5	13.12(3.84)	2.12(1.07)	2.44(0.63)	17.68( 4.70)
6	7.51(3.58)	3.93(1.90)	0.88(0.44)	12.32( 3.68)
7	1.96(1.04)	1.37(1.04)	0.29(0.16)	3.62( 2.15)
8	4.09(2.41)	1.53(1.17)	0.92(0.67)	6.54( 3.64)
Annual	26.68(5.61)	8.95(2.12)	4.53(0.37)	40.16( 6.09)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1.19(0.40)	0.15(0.08)		1.34(0.46)
2	3.08(1.09)			3.08(1.09)
3	3.14(1.58)			3.14(1.58)
4	1.21(0.82)			1.21(0.82)
Annual	8.61(2.51)	0.15(0.08)		8.76(2.58)
5	1.23(0.43)			1.23(0.43)
6	5.92(0.60)			5.92(0.60)
7	1.75(1.11)			1.75(1.11)
8	0.63(0.45)	0.13(0.03)		0.76(0.47)
Annual	9.53(7.13)	0.13(0.03)		9.66(7.17)

TABLE C.20

HANMER: MEAN QUARTERLY WSC BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	65.4(20.0)	10.3(2.9)	18.6(9.5)	94.3(19.9)
2	61.7(33.3)	7.3(10.5)	4.6(5.4)	73.6(48.7)
3	25.3(13.2)	2.6(1.6)	1.4(0.8)	29.3(10.8)
4	9.8(6.7)	4.4(0.4)	6.2(10.0)	20.4(14.5)
Annual	162.2(33.8)	24.6(9.2)	30.8(17.1)	217.6(45.3)
5	102.0(24.9)	7.9(6.8)	15.2(3.6)	125.1(30.5)
6	48.3(14.4)	12.9(7.0)	5.3(2.4)	66.5(13.4)
7	11.7(6.1)	3.2(2.5)	1.3(0.7)	16.2(9.1)
8	20.4(13.7)	3.6(2.5)	3.9(2.6)	27.9(16.1)
Annual	182.4(26.0)	27.6(12.1)	25.7(4.5)	235.7(33.3)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	13.0(2.3)	3.6(1.9)		16.6(4.2)
2	32.1(10.9)			32.1(10.9)
3	27.2(13.9)			27.2(13.9)
4	11.9(8.5)			11.9(8.5)
Annual	84.2(27.7)	3.6(1.9)		87.8(28.9)
5	18.4(1.9)			18.4(1.9)
6	63.9(37.1)			63.9(37.1)
7	16.4(11.5)			16.4(11.5)
8	3.6(2.0)	3.3(1.0)		6.9(2.5)
Annual	102.3(28.4)	3.3(1.0)		105.6(52.8)

TABLE C.21

HANMER: MEAN QUARTERLY WSP BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	153.3(41.0)	18.3(7.4)	42.3(16.4)	214.9(34.8)
2	117.5(59.2)	12.2(15.5)	6.3(6.6)	136.0(80.3)
3	49.0(28.6)	5.5(3.9)	3.2(0.5)	57.7(25.1)
4	20.9(15.8)	8.8(1.4)	8.0(11.5)	37.7(24.5)
Annual	340.7(61.5)	45.8(11.5)	59.8(24.4)	446.3(65.8)
5	224.5(60.3)	13.4(13.2)	32.8(18.3)	270.7(82.3)
6	108.2(25.4)	26.4(15.0)	9.1(5.2)	143.7(21.1)
7	23.2(13.2)	6.6(5.6)	2.6(1.6)	32.4(19.4)
8	42.2(25.8)	6.4(5.1)	5.1(2.6)	52.7(31.0)
Annual	398.1(73.2)	52.8(22.8)	49.6(18.5)	500.5(94.0)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	17.2(3.4)	5.2(2.8)		22.4(6.2)
2	33.3(26.9)			33.3(26.9)
3	36.1(18.6)			36.1(18.6)
4	15.5(11.1)			15.5(11.1)
Annual	102.0(57.4)	5.2(2.8)		107.3(59.4)
5	18.1(3.8)			18.1(3.8)
6	82.9(55.7)			82.0(55.7)
7	17.5(8.7)			17.5(8.7)
8	4.1(2.1)	4.7(1.7)		8.8(3.1)
Annual	122.6(68.1)	4.7(1.7)		127.3(69.5)



TABLE C.22

HANMER: MEAN QUARTERLY WSF BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	327.2(88.2)	41.7(14.0)	84.8(43.5)	453.7(105.2)
2	256.1(125.3)	29.3(36.6)	18.7(19.9)	304.1(175.6)
3	107.7(58.9)	12.7(7.8)	9.4(2.0)	129.8(52.3)
4	48.5(35.3)	21.7(3.1)	24.5(35.8)	94.7(62.4)
Annual	739.5(150.6)	105.4(36.6)	137.4(41.5)	982.3(169.0)
5	508.3(151.1)	34.0(22.6)	71.2(34.5)	613.5(180.4)
6	251.9(108.1)	57.3(24.7)	24.0(12.4)	333.2(88.7)
7	52.4(31.4)	15.4(13.1)	7.3(5.6)	75.1(48.4)
8	95.5(60.5)	15.0(12.4)	16.3(11.1)	126.8(73.2)
Annual	908.1(145.8)	121.7(48.1)	118.8(31.1)	1148.6(169.4)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	59.9(13.3)	16.0(9.1)		75.9(22.1)
2	136.0(70.8)			136.0(70.8)
3	129.4(68.0)			129.4(68.0)
4	53.6(38.9)			53.6(38.9)
Annual	378.9(159.5)	16.0(9.1)		394.9(166.5)
5	69.6(9.3)			69.6(9.3)
6	287.0(183.1)			287.0(183.1)
7	66.2(47.2)			66.2(47.2)
8	17.0(10.2)	14.5(5.8)		31.5(13.1)
Annual	439.8(245.9)	14.5(5.8)		454.3(251.2)

TABLE C.23

HANMER: MEAN QUARTERLY EE BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	72.9(26.1)	8.6(0.7)		81.5(26.5)
2	45.2(24.1)	7.2(8.9)		52.4(30.7)
3	20.2(14.6)	3.1(1.8)		23.3(12.8)
4	7.1( 4.3)	5.4(1.0)		12.5( 5.4)
Annual	145.4(16.6)	24.3(10.0)		169.7( 6.7)
5	69.1(15.3)	6.4(4.7)		75.5(19.9)
6	27.3( 4.9)	10.3(5.4)		37.6( 1.2)
7	9.2( 5.4)	3.7(3.4)		12.9( 4.8)
8	18.5(12.6)	4.6(3.8)		23.1( 9.0)
Annual	124.1(25.0)	25.0(10.0)		149.1(34.2)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	11.3( 2.0)	2.9(1.4)		14.2( 1.6)
2	27.3(10.6)			27.3(10.6)
3	22.9(14.0)			22.9(14.0)
4	9.4( 6.7)			9.4( 6.7)
Annual	70.9(30.3)	2.9(1.4)		73.8(32.3)
5	10.5( 1.4)			10.5( 1.4)
6	48.4(33.3)			48.4(33.3)
7	13.3( 8.7)			13.3( 8.7)
8	4.3( 3.6)	2.7(1.0)		7.0( 3.6)
Annual	76.5(44.1)	2.7(1.0)		79.2(44.8)

TABLE C.24

HANMER: MEAN QUARTERLY AE BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	264.0( 86.3)	38.3( 9.6)		302.3( 77.2)
2	288.5(164.7)	28.9(25.8)		317.4(189.5)
3	95.5( 38.2)	10.8( 6.4)		106.3( 32.2)
4	28.1( 20.6)	17.6(11.3)		45.7( 21.7)
Annual	676.1(194.8)	95.6(22.8)		771.7(214.4)
5	300.0( 26.1)	25.4(18.1)		325.4( 20.1)
6	201.7( 52.7)	54.8(41.5)		256.5( 66.0)
7	47.1( 22.1)	12.8(11.8)		59.9( 32.0)
8	71.6( 36.6)	12.9(10.2)		84.5( 46.6)
Annual	620.4( 24.1)	105.9(39.5)		726.3( 23.9)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	43.1( 12.8)	8.4( 4.3)		51.5( 16.8)
2	126.1( 52.1)			126.1( 52.1)
3	92.9( 44.4)			92.9( 44.4)
4	40.2( 29.6)			40.2( 29.6)
Annual	302.3(113.6)	8.4( 4.3)		310.7(116.9)
5	38.9( 7.3)			38.9( 7.3)
6	224.5(175.3)			224.5(175.3)
7	54.9( 31.4)			54.9( 31.4)
8	12.1( 6.7)	7.7( 2.9)		19.8( 7.6)
Annual	330.4(208.9)	7.7( 2.9)		338.1(211.5)

TABLE C.25

HANMER: MEAN QUARTERLY HOLO BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	568.4(169.0)	146.7(43.1)		715.1(127.3)
2	551.6(290.4)	91.6(99.9)		643.2(381.1)
3	211.6(114.0)	43.2(16.6)		254.8( 97.9)
4	82.1( 62.9)	74.9( 2.7)		157.0( 65.5)
Annual	1413.7(329.2)	356.4(71.9)		1770.1(381.0)
5	720.1(204.4)	95.4(68.4)		815.5(271.5)
6	361.7(103.2)	154.6(80.3)		516.3( 72.1)
7	98.1( 53.2)	51.1(45.2)		149.2( 93.6)
8	207.8(139.0)	54.7(44.1)		262.5(183.0)
Annual	1387.7(318.7)	355.8(130.8)		1743.5(426.0)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	117.8( 19.3)	34.1(19.2)		151.9( 38.6)
2	244.9( 78.1)			244.9( 78.1)
3	199.9(107.6)			199.9(107.6)
4	91.3( 69.7)			91.3( 69.7)
Annual	653.9(250.3)	34.1(19.2)		688.0(265.8)
5	103.4( 10.2)			103.4( 10.2)
6	414.6(272.4)			414.6(272.4)
7	118.7( 73.9)			118.7( 73.9)
8	42.4( 30.1)	30.7(10.4)		73.1( 36.2)
Annual	679.1(372.4)	30.7(10.4)		709.8(382.1)

TABLE C.26

HANMER: MEAN QUARTERLY R. LIGNIN BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	180.5( 39.8)	86.7(13.9)		267.2( 28.5)
2	145.9( 67.3)	59.4(75.7)		205.3(125.5)
3	73.4( 53.9)	28.0(11.5)		101.4( 42.8)
4	33.2( 14.8)	52.4( 1.0)		85.6( 15.9)
Annual	433.0( 96.8)	226.5(72.8)		659.5(118.5)
5	230.8( 50.3)	57.6(36.9)		288.4( 87.1)
6	95.8( 31.2)	91.3(45.5)		187.1( 19.3)
7	33.0( 24.8)	35.7(30.3)		68.7( 51.2)
8	81.1( 60.5)	39.1(33.1)		120.2( 93.5)
Annual	440.7(109.6)	223.7(87.8)		664.4(189.5)

RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	53.8( 10.0)	26.6(13.7)		80.4( 23.2)
2	116.1( 41.5)			116.1( 41.5)
3	83.3( 43.0)			83.3( 43.0)
4	41.6( 30.7)			41.6( 30.7)
Annual	294.8(105.9)	26.6(13.7)		321.4(118.0)
5	47.9( 10.6)			47.9( 10.6)
6	221.0(178.4)			221.0(178.4)
7	57.7( 41.5)			57.7( 41.5)
8	25.0( 20.3)	24.1( 7.5)		49.1( 22.8)
Annual	351.6(233.6)	24.1( 7.5)		375.7(240.6)

TABLE C.27

NELSON: MEAN QUARTERLY NITROGEN BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	7.04(2.11)	2.10(0.97)	2.41(0.47)	11.55(3.29)
2	2.84(0.50)	0.82(0.37)	2.24(0.62)	5.90(0.78)
3	2.13(0.37)	0.72(0.32)	1.02(0.47)	3.87(0.46)
4	14.57(1.12)	3.72(1.58)	2.59(0.35)	20.88(1.46)
Annual	26.58(3.14)	7.36(1.91)	8.26(0.89)	42.20(4.82)
5	5.71(1.48)	4.42(3.66)	3.80(1.88)	13.93(6.52)
6	4.96(2.39)	0.80(0.56)	2.45(1.98)	8.21(3.77)
7	0.98(0.35)	0.74(0.31)	2.28(1.03)	4.00(1.25)
8	10.03(1.85)	2.52(1.86)	4.48(0.83)	17.03(3.88)
Annual	21.68(4.64)	8.48(4.43)	13.01(3.00)	43.17(9.58)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	9.44(2.96)	0.61(0.09)		10.05(2.96)
2	10.34(2.30)			10.34(2.30)
3	5.08(1.15)			5.08(1.15)
4	5.79(0.90)	5.33(1.20)		11.12(2.08)
Annual	30.65(5.22)	5.94(1.22)		36.59(6.36)
5	11.88(2.34)			11.88(2.34)
6	14.76(4.02)			14.76(4.02)
7	5.56(1.30)			5.56(1.30)
8	4.40(1.27)	1.48(0.18)		5.88(1.37)
Annual	36.60(4.66)	1.48(0.18)		38.08(4.66)
RADIATA reg.				
1	7.72(2.18)	0.90(0.44)		8.62(2.33)
2	6.31(1.94)			6.31(1.94)
3	5.67(1.35)			5.67(1.35)
4	6.46(3.41)	3.41(2.16)		9.87(0.97)
Annual	26.16(5.03)	4.31(0.86)		30.47(5.39)
5	8.51(2.19)			8.51(2.19)
6	12.31(3.26)			12.31(3.26)
7	4.57(1.68)			4.57(1.68)
8	3.82(1.69)	2.56(0.50)		6.38(1.21)
Annual	29.21(4.62)	2.56(0.50)		31.77(4.35)

TABLE c.28

NELSON: MEAN QUARTERLY CARBON BUDGET ( kg/ha )

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	547(327)	153(129)	140( 42)	840(483)
2	198( 78)	72( 10)	141( 49)	411( 96)
3	134( 21)	56( 51)	69( 38)	259( 65)
4	912(104)	334(289)	166( 33)	1412(212)
Annual	1791(400)	615(406)	516( 68)	2922(818)
5	422(164)	282(247)	151( 79)	855(247)
6	265(122)	55( 86)	76( 46)	396(214)
7	77( 42)	92( 34)	136( 93)	305( 45)
8	603(226)	154(208)	262( 66)	1019(486)
Annual	1367(534)	583(261)	625(187)	2575(777)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	609(100)	44( 16)		653( 89)
2	693(285)			693(285)
3	445(190)			445(190)
4	436(140)	415( 62)		851(150)
Annual	2183(316)	459( 58)		2642(349)
5	847(129)			847(129)
6	737(320)			737(320)
7	368( 23)			368( 23)
8	427(131)	106( 18)		533(133)
Annual	2379(175)	106( 18)		2485(161)
RADIATA reg.				
1	494( 82)	48( 36)		542(109)
2	390(120)			390(120)
3	357( 34)			357( 34)
4	573(166)	279(122)		852( 67)
Annual	1814(173)	327(109)		2141(144)
5	613(234)			613(234)
6	416( 62)			416( 62)
7	330(245)			330(245)
8	415( 25)	172( 34)		587(221)
Annual	1774(684)	172( 34)		1946(664)

TABLE C.29

NELSON MEAN QUARTERLY PHOSPHORUS BUDGET ( g/ha )

## BEECH

Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	1030(486)	237(232)	287( 84)	1554( 781)
2	478(259)	113( 23)	281( 98)	872( 290)
3	227( 43)	79( 64)	159( 98)	465( 164)
4	1543(150)	444(387)	394( 80)	2381( 362)
Annual	3278(818)	873(545)	1121(206)	5272(1464)
5	825(290)	428(320)	333(212)	1586( 466)
6	578(347)	92(179)	163( 49)	833( 563)
7	143( 56)	142( 69)	309(219)	594( 126)
8	985(248)	230(294)	532(155)	1747( 298)
Annual	2531(845)	892(419)	1337(367)	4760(1101)

## RADIATA

Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1048(106)	60( 21)		1108( 111)
2	1739(1151)			1739(1151)
3	941(344)			941( 344)
4	861(181)	567( 47)		1428( 208)
Annual	4589(1081)	627( 25)		5216(1105)
5	1703(538)			1703( 538)
6	1930(591)			1930( 591)
7	802( 36)			802( 36)
8	824(472)	146( 38)		970( 468)
Annual	5259(170)	146( 38)		5405( 131)

## RADIATA reg.

1	995(188)	66( 45)		1061( 234)
2	1009(393)			1009( 393)
3	791(265)			791( 265)
4	1011(151)	395(210)		1406( 190)
Annual	3806(682)	461(184)		4267( 558)
5	1331(452)			1331( 452)
6	1635(722)			1635( 722)
7	722(473)			722( 473)
8	834(353)	239( 18)		1073( 333)
Annual	4523(973)	239( 18)		4762( 975)



TABLE C.30

NELSON: MEAN QUARTERLY POTASSIUM BUDGET ( kg/ha)

## BEECH

Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	3.41(2.06)	0.94(1.09)	0.91(0.32)	5.26(3.24)
2	2.41(0.74)	0.36(0.14)	0.79(0.31)	3.56(0.91)
3	0.91(0.18)	0.30(0.26)	0.52(0.42)	1.73(0.69)
4	5.28(0.44)	2.23(2.49)	1.74(0.59)	0.25(2.75)
Annual	12.01(2.85)	3.83(3.48)	3.96(1.06)	19.80(6.88)
5	2.71(1.04)	1.65(1.49)	1.03(0.62)	5.39(1.82)
6	3.05(1.94)	0.34(0.66)	0.49(0.25)	3.88(2.83)
7	0.50(0.27)	0.52(0.24)	1.00(0.75)	2.02(0.53)
8	3.65(1.39)	0.64(0.76)	1.90(0.55)	6.19(1.68)
Annual	9.91(4.29)	3.15(1.59)	4.42(1.40)	17.48(5.29)

## RADIATA

Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	3.33(0.39)	0.25(0.09)		3.58(0.39)
2	7.93(5.52)			7.93(5.52)
3	3.33(0.88)			3.33(0.88)
4	2.54(1.02)	2.34(0.25)		4.88(1.11)
Annual	17.13(6.05)	2.59(0.22)		19.72(6.24)
5	5.32(1.47)			5.32(1.47)
6	6.61(1.93)			6.61(1.93)
7	2.88(0.37)			2.88(0.37)
8	2.59(1.35)	0.60(0.12)		3.19(1.36)
Annual	17.40(3.18)	0.60(0.12)		18.00(0.36)

## RADIATA reg.

1	2.62(0.98)	0.26(0.25)		2.88(1.10)
2	4.18(1.77)			4.18(1.77)
3	2.98(1.87)			2.98(1.87)
4	2.90(0.80)	1.41(0.66)		4.31(0.16)
Annual	12.68(4.03)	1.67(0.78)		14.35(4.34)
5	3.68(1.00)			3.68(1.00)
6	3.71(2.10)			3.71(2.10)
7	2.39(1.60)			2.39(1.60)
8	2.28(1.46)	0.88(0.40)		3.16(1.11)
Annual	12.06(4.10)	0.88(0.40)		12.94(4.14)

TABLE C.31

NELSON: MEAN QUARTERLY MAGNESIUM BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	1.33(0.75)	0.54(0.44)	0.32(0.16)	2.19(1.24)
2	0.54(0.24)	0.30(0.10)	0.34(0.21)	1.18(0.35)
3	0.34(0.03)	0.20(0.18)	0.18(0.09)	0.72(0.27)
4	2.07(0.58)	1.31(1.14)	0.38(0.10)	3.76(0.53)
Annual	4.28(0.57)	2.35(1.58)	1.22(0.22)	7.85(2.33)
5	1.04(0.34)	1.05(0.87)	0.37(0.24)	2.46(0.80)
6	0.70(0.43)	0.21(0.41)	0.21(0.13)	1.12(0.86)
7	0.19(0.11)	0.35(0.15)	0.34(0.28)	0.88(0.19)
8	1.49(0.82)	0.62(0.87)	0.57(0.09)	2.68(1.59)
Annual	3.42(1.63)	2.23(1.12)	1.49(0.55)	7.14(2.53)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	1.50(0.15)	0.11(0.04)		1.61(0.15)
2	2.05(0.62)			2.05(0.62)
3	1.33(0.56)			1.33(0.56)
4	1.19(0.18)	1.00(0.19)		2.19(0.24)
Annual	6.07(0.31)	1.11(0.19)		7.18(0.46)
5	2.28(0.26)			2.28(0.26)
6	2.05(0.89)			2.05(0.89)
7	1.05(0.14)			1.05(0.14)
8	1.16(0.49)	0.26(0.05)		1.42(0.49)
Annual	6.54(0.72)	0.26(0.05)		6.80(0.68)
RADIATA reg.				
1	1.48(0.51)	0.11(0.10)		1.59(0.58)
2	1.24(0.63)			1.24(0.63)
3	1.03(0.25)			1.03(0.25)
4	1.65(0.51)	0.62(0.31)		2.27(0.21)
Annual	5.40(1.17)	0.73(0.33)		6.13(1.36)
5	1.81(0.59)			1.81(0.59)
6	1.41(0.10)			1.41(0.10)
7	0.93(0.58)			0.93(0.58)
8	1.10(0.82)	0.38(0.13)		1.48(0.77)
Annual	5.25(1.75)	0.38(0.13)		5.63(1.75)

TABLE C.32

NELSON: MEAN QUARTERLY CALCIUM BUDGET (kg/ha)

## BEECH

Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	13.95(7.55)	3.96(4.00)	3.75(0.93)	21.66(12.17)
2	5.40(3.87)	2.46(0.87)	3.88(1.84)	11.74( 4.61)
3	3.58(0.49)	1.58(1.33)	2.10(1.23)	7.26( 2.21)
4	24.06(2.11)	9.45(8.99)	2.47(0.50)	35.98( 6.82)
Annual	46.99(9.72)	17.45(13.68)	12.20(1.08)	76.64(23.78)
5	10.95(4.18)	7.55(6.43)	4.22(2.06)	22.72( 6.64)
6	6.66(3.12)	1.44(2.30)	2.13(1.82)	10.23( 5.64)
7	2.03(1.18)	2.70(1.31)	4.06(3.04)	8.79( 1.42)
8	15.79(2.09)	5.04(6.01)	8.01(5.51)	28.84(18.49)
Annual	35.43(14.87)	16.73(6.19)	18.42(6.44)	70.58(24.37)

## RADIATA

Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	8.52(1.05)	0.19(0.07)		8.71(1.01)
2	9.13(2.60)			9.13(2.60)
3	7.57(3.55)			7.57(3.55)
4	8.04(3.03)	1.76(0.53)		9.80(3.06)
Annual	33.26(2.61)	1.95(0.56)		35.21(2.09)
5	12.32(1.82)			12.32(1.82)
6	8.72(4.49)			8.72(4.49)
7	5.71(1.02)			5.71(1.02)
8	7.06(4.40)	0.45(0.08)		7.51(4.44)
Annual	33.81(4.36)	0.45(0.08)		34.26(4.34)

## RADIATA reg.

1	9.36(2.14)	0.21(0.16)		9.57(2.30)
2	6.26(2.83)			6.26(2.83)
3	7.72(0.84)			7.72(0.84)
4	10.51(2.63)	1.21(0.59)		11.72(2.12)
Annual	33.85(6.36)	1.42(0.54)		35.27(6.01)
5	10.51(4.48)			10.51(4.48)
6	5.46(2.85)			5.46(2.85)
7	6.47(4.12)			6.47(4.12)
8	8.05(1.93)	0.74(0.14)		8.79(1.84)
Annual	30.49(11.11)	0.74(0.14)		31.23(11.10)

TABLE C.33

NELSON: MEAN QUARTERLY WSC BUDGET (kg/ha)

## BEECH

Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	60.9(40.5)	9.1(7.0)	11.5(3.6)	81.5(50.8)
2	24.1(11.3)	5.6(1.5)	11.4(1.8)	41.1( 9.3)
3	15.0(4.9)	3.6(3.1)	6.2(4.5)	24.8( 5.6)
4	119.1(8.1)	25.5(22.4)	26.0(7.2)	170.6(21.2)
Annual	219.1(57.8)	43.8(27.6)	55.1(10.2)	318.0(83.6)
5	59.5(25.2)	22.0(12.9)	17.0(8.8)	98.5(33.6)
6	42.3(21.0)	4.3(6.4)	10.0(7.2)	56.6(22.3)
7	9.2(4.2)	6.8(2.2)	11.3(7.2)	27.3( 2.4)
8	64.8(24.5)	11.4(12.8)	35.7(10.9)	111.9(35.6)
Annual	175.8(71.2)	44.5(19.5)	74.0(28.4)	294.3(86.2)

## RADIATA

Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	39.0(9.1)	2.4(1.6)		41.4( 7.7)
2	56.3(31.3)			56.3(31.3)
3	43.6(17.1)			43.6(17.1)
4	35.4(9.3)	22.0(4.8)		57.4( 6.4)
Annual	174.3(31.1)	24.4(6.4)		198.7(24.8)
5	96.2(9.4)			96.2( 9.4)
6	78.0(37.1)			78.0(37.1)
7	34.3(3.1)			34.3( 3.1)
8	32.6(11.6)	5.6(1.6)		38.2(10.1)
Annual	241.1(33.9)	5.6(1.6)		246.7(33.9)

## RADIATA reg.

1	29.9(5.4)	2.7(2.6)		32.6( 7.4)
2	24.7(2.7)			24.7( 2.7)
3	38.0(7.7)			38.0( 7.7)
4	43.8(14.9)	14.5(2.4)		58.3(13.2)
Annual	136.4(19.0)	17.2(4.0)		153.6(21.9)
5	86.1(33.6)			86.1(33.6)
6	32.8(10.7)			32.8(10.7)
7	30.6(23.5)			30.6(23.6)
8	31.6(16.8)	9.4(5.4)		41.0(11.3)
Annual	181.1(76.4)	9.4(5.4)		190.5(73.0)

TABLE C.34

NELSON:		MEAN QUARTERLY	WSP	BUDGET	( kg/ha )
BEECH					
Q	LEAF	TWIG/STEM	OTHER	TOTAL	
1	133.0(71.2)	20.1(13.1)	19.1(12,8)	172.2(95.3)	
2	53.8(29.3)	14.5( 3.6)	12.8( 4.3)	81.1(34.2)	
3	37.7(23.8)	7.5( 8.0)	5.5( 3.8)	50.7(32.6)	
4	212.5(25.6)	51.9(39.0)	11.5( 6.2)	275.9(34.3)	
Annual	437.0(97.3)	94.0(50.2)	48.9(22.9)	579.9(157.9)	
5	132.6(54.7)	51.3(42.4)	37.5(20.5)	221.4(81.4)	
6	88.5(42.4)	7.8(10.8)	7.9( 6.7)	104.2(56.7)	
7	18.5( 6.3)	14.1( 6.5)	10.8( 8.1)	43.4( 5.4)	
8	131.9(53.1)	21.2(26.1)	13.5( 6.2)	166.6(83.1)	
Annual	371.5(150.3)	94.4(47.0)	69.7(19.4)	535.6(197.8)	
RADIATA					
Q	NEEDLE	POL./CONE	OTHER	TOTAL	
1	35.3(12.4)	3.3( 1.3)		38.6(11.9)	
2	69.8(26.3)			69.8(26.3)	
3	55.1(19.5)			55.1(19.5)	
4	36.3(20.2)	31.4( 7.7)		67.7(19.3)	
Annual	196.5(33.7)	34.7( 8.0)		231.2(38.2)	
5	80.8(15.0)			80.8(15.0)	
6	80.9(36.5)			80.9(36.5)	
7	43.5( 7.0)			43.5( 7.0)	
8	34.0( 8.7)	8.0( 1.3)		42.0( 9.4)	
Annual	239.2(34.6)	8.0( 1.3)		247.2(33.9)	
RADIATA reg.					
1	27.6( 7.5)	3.7( 2.8)		31.3(10.3)	
2	27.7( 6.5)			27.7( 6.5)	
3	41.4( 8.4)			41.4( 8.4)	
4	44.7(14.6)	21.2( 9.4)		65.9(10.3)	
Annual	141.4(25.4)	24.9( 8.3)		166.3(17.8)	
5	66.5(27.8)			66.5(27.8)	
6	29.8(10.0)			29.8(10.0)	
7	35.7(26.9)			35.7(26.9)	
8	36.1(21.7)	13.0( 2.6)		49.1(19.4)	
Annual	168.1(74.3)	13.0( 2.6)		181.1(73.6)	

TABLE C.35

NELSON MEAN QUARTERLY WSF BUDGET ( kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	296.6(187.3)	40.4( 30.3)	41.9( 18.6)	378.9(232.0)
2	113.4( 52.8)	27.3( 8.7)	38.0( 6.0)	178.7( 60.7)
3	69.2( 17.5)	17.5( 17.5)	20.3( 13.5)	107.0( 31.2)
4	518.3( 77.5)	111.5( 87.2)	51.9( 15.0)	681.7( 81.6)
Annual	997.5(265.5)	196.7(102.8)	152.1( 38.4)	1346.3(377.8)
5	275.9( 93.5)	102.2( 70.0)	80.3( 46.2)	458.4(155.9)
6	206.0(116.3)	19.3( 29.2)	30.6( 17.3)	255.9(142.3)
7	42.3( 27.4)	31.0( 10.4)	40.5( 27.9)	113.8( 17.3)
8	341.5(138.3)	57.2( 69.9)	97.3( 26.5)	496.0(212.2)
Annual	865.7(340.5)	209.7( 92.7)	248.7( 10.4)	1324.1(434.8)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	148.0( 58.0)	8.1( 2.5)		156.1( 59.1)
2	281.3(131.2)			281.3(131.2)
3	193.2( 56.1)			193.2( 56.1)
4	166.1( 57.8)	77.0( 16.8)		243.1( 63.3)
Annual	788.6(148.5)	85.1( 15.9)		873.7(162.5)
5	343.4( 68.8)			343.4( 68.8)
6	350.6(156.8)			350.6(156.8)
7	161.1( 47.3)			161.1( 47.3)
8	162.7( 45.2)	19.7( 4.5)		182.4( 45.2)
Annual	1017.8(175.3)	19.7( 4.5)		1037.5(172.5)
RADIATA reg.				
1	98.2( 15.9)	9.0( 7.3)		107.2( 22.1)
2	131.9( 37.1)			131.9( 37.1)
3	178.3( 49.2)			178.3( 49.2)
4	181.9( 54.9)	52.1( 24.7)		234.0( 37.5)
Annual	590.3( 79.9)	61.1( 23.9)		651.4( 77.5)
5	296.0(119.6)			296.0(119.6)
6	144.8( 29.0)			144.8( 29.0)
7	138.8(136.1)			138.8(136.1)
8	156.0( 92.0)	32.0( 7.5)		188.0( 87.2)
Annual	735.6(327.2)	32.0( 7.5)		767.6(327.7)

TABLE C.36

NELSON	MEAN QUARTERLY		EE	BUDGET	(kg/ha)
BEECH					
Q	LEAF	TWIG/STEM	OTHER		TOTAL
1	49.6(24.7)	9.0( 6.8)			58.6(30.9)
2	14.3( 6.6)	3.9( 0.5)			18.2( 7.0)
3	10.7( 1.1)	3.0( 2.9)			13.7( 2.9)
4	71.8(13.5)	21.0(17.0)			92.8(12.4)
Annual	146.4(32.0)	36.9(25.1)			183.3(51.6)
5	37.9(16.6)	16.2(11.3)			54.1(13.3)
6	20.5( 9.3)	2.5( 3.1)			23.0(12.3)
7	6.1( 3.8)	5.2( 2.4)			11.3( 5.8)
8	53.7(22.0)	9.1(12.1)			62.8(32.9)
Annual	118.2(49.6)	33.0(14.6)			151.2(56.4)
RADIATA					
Q	NEEDLE	POL./CONE	OTHER		TOTAL
1	55.8(13.0)	3.3( 1.3)			59.1(12.4)
2	63.2(13.3)				63.2(13.3)
3	47.9(24.5)				47.9(24.5)
4	48.5(14.3)	31.6( 2.2)			80.1(14.4)
Annual	215.4( 9.3)	34.9( 1.1)			250.3( 8.4)
5	86.6(22.5)				86.6(22.5)
6	90.9(49.9)				90.9(49.9)
7	39.4( 7.5)				39.4( 7.5)
8	45.0(12.3)	8.1( 1.8)			53.1(11.9)
Annual	261.9(45.9)	8.1( 1.8)			270.0(45.6)
RADIATA reg.					
1	43.3( 2.7)	3.9( 2.9)			47.2( 4.0)
2	31.3( 2.6)				31.3( 2.6)
3	38.6( 3.8)				38.6( 3.8)
4	61.5(24.5)	23.3(11.9)			84.8(13.7)
Annual	174.7(24.3)	27.2(10.9)			201.9(13.3)
5	63.2(34.0)				63.2(34.0)
6	67.1(19.4)				67.1(19.4)
7	33.9(16.7)				33.9(16.7)
8	45.3(22.5)	14.1( 2.0)			59.4(21.4)
Annual	209.5(72.8)	14.1( 2.0)			223.6(73.0)

TABLE C.37

NELSON MEAN QUARTERLY AE BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	216.8(134.1)	34.2(26.4)		251.0(160.5)
2	115.6( 47.0)	20.6( 5.5)		136.2( 45.0)
3	44.4( 9.0)	11.7( 9.7)		56.1( 18.3)
4	353.7(132.6)	78.3(63.1)		432.0(120.6)
Annual	730.5(254.5)	144.8(83.6)		875.3(310.0)
5	170.6( 63.7)	67.1(58.6)		237.7( 60.9)
6	165.9(101.4)	14.3(19.8)		180.2(110.2)
7	28.1( 10.6)	22.3( 7.3)		50.4( 17.8)
8	235.8( 99.6)	35.1(42.5)		270.9(138.2)
Annual	600.4(267.7)	138.8(67.2)		739.2(302.7)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	120.0( 22.9)	7.6( 1.5)		127.6( 23.4)
2	274.3( 90.4)			274.3( 90.4)
3	136.4( 57.1)			136.4( 57.1)
4	104.7( 39.0)	72.0(16.3)		176.7( 37.9)
Annual	635.4( 69.4)	79.6(16.5)		715.0( 82.2)
5	210.3( 92.4)			210.3( 92.4)
6	280.5(139.0)			280.5(139.0)
7	117.5( 3.5)			117.5( 3.5)
8	111.4( 27.6)	18.4( 3.1)		129.8( 29.1)
Annual	719.7(176.6)	18.4( 3.1)		738.1(174.0)
RADIATA reg.				
1	89.5( 11.7)	7.8( 5.9)		97.3( 17.0)
2	152.5( 56.4)			152.5( 56.4)
3	121.8( 7.7)			121.8( 7.7)
4	137.6( 56.7)	45.0(17.2)		182.6( 43.9)
Annual	501.4( 79.2)	52.8(11.9)		554.2( 68.1)
5	137.1( 58.2)			137.1( 58.2)
6	115.9( 12.8)			115.9( 12.8)
7	101.0( 86.2)			101.0( 86.2)
8	113.9( 57.3)	27.9( 7.3)		141.8( 27.6)
Annual	467.9(159.0)	27.9( 7.3)		495.8(151.9)



TABLE C.38

NELSON MEAN QUARTERLY HOLO. BUDGET (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	567.4(350.4)	144.5(125.3)		711.9(471.0)
2	207.4( 94.2)	73.8( 15.0)		281.2(108.3)
3	147.0( 22.5)	54.9( 46.5)		201.9( 49.6)
4	1006.7( 60.2)	336.2(298.5)		1342.3(243.9)
Annual	1927.9(429.9)	609.4(389.6)		2537.3(795.9)
5	441.6(170.7)	278.0(206.2)		719.6(174.9)
6	272.4(149.7)	61.7( 94.4)		334.1(243.9)
7	81.6( 43.4)	95.1( 44.8)		176.7( 87.1)
8	636.8(216.9)	159.0(201.7)		795.8(404.4)
Annual	1432.4(301.9)	593.8(260.8)		2026.2(729.6)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	629.2(101.0)	44.1( 14.4)		673.3( 98.8)
2	703.0(287.8)			703.0(287.8)
3	464.7(185.9)			464.7(185.9)
4	454.5(184.6)	418.1( 85.8)		872.6(219.9)
Annual	2251.4(361.9)	462.2( 83.4)		2713.6(430.8)
5	856.8( 79.4)			856.8( 79.4)
6	685.2(322.4)			685.2(322.4)
7	374.5( 44.3)			374.5( 44.3)
8	420.9(159.4)	106.8( 22.0)		527.7(162.3)
Annual	2337.4(275.8)	106.8( 22.0)		2444.2(254.9)
RADIATA reg.				
1	487.5( 65.1)	48.9( 40.8)		536.4(100.5)
2	398.7(137.8)			398.7(137.8)
3	374.6( 34.4)			374.6( 34.4)
4	560.5(123.9)	279.7(119.5)		840.2( 18.8)
Annual	1821.3(209.4)	328.6(115.6)		2149.9(252.9)
5	593.0(200.2)			593.0(200.2)
6	373.7( 56.0)			373.7( 56.0)
7	323.4(237.7)			323.4(237.7)
8	404.2(228.2)	172.7( 46.3)		576.9(193.8)
Annual	1694.3(635.2)	172.7( 46.3)		1867.0(619.8)

TABLE C.39

NELSON                      MEAN QUARTERLY R. LIG. BUDGET                      (kg/ha)

BEECH				
Q	LEAF	TWIG/STEM	OTHER	TOTAL
1	279.1(158.8)	101.7( 84.5)		380.8(241.9)
2	82.9( 29.4)	50.7( 10.1)		133.6( 38.9)
3	79.6( 17.2)	39.8( 36.1)		119.4( 38.6)
4	465.7( 42.8)	239.7(203.3)		705.4(191.6)
Annual	907.3(148.4)	431.9(291.7)		1339.2(439.2)
5	221.0( 95.3)	199.4(154.8)		420.4(117.1)
6	105.9( 57.3)	38.4( 60.0)		144.3(116.7)
7	44.1( 32.4)	67.7( 32.6)		111.8( 64.2)
8	301.6( 94.1)	120.2(147.1)		421.8(232.2)
Annual	672.6(256.4)	425.7(167.8)		1098.3(354.5)
RADIATA				
Q	NEEDLE	POL./CONE	OTHER	TOTAL
1	377.0( 90.9)	33.1( 12.6)		410.1( 78.3)
2	320.5(139.8)			320.5(139.8)
3	215.0( 77.2)			215.0( 77.2)
4	257.1( 54.7)	312.9( 71.4)		570.0( 45.6)
Annual	1169.6(185.7)	346.0( 73.9)		1515.6(203.7)
5	507.4(114.2)			507.4(114.2)
6	408.1(139.6)			408.1(139.6)
7	240.2( 96.4)			240.2( 96.4)
8	247.9( 75.4)	77.9( 3.9)		325.8( 81.2)
Annual	1403.6(120.9)	77.9( 3.9)		1481.5(127.5)
RADIATA reg.				
1	342.6( 79.8)	35.4( 28.5)		388.0( 97.4)
2	191.0( 63.7)			191.0( 63.7)
3	195.6( 28.9)			195.6( 28.9)
4	352.3(107.0)	203.7( 89.1)		556.0( 18.1)
Annual	1081.5(162.9)	239.1( 45.3)		1320.6(186.7)
5	393.6(175.1)			393.6(175.1)
6	251.7( 49.8)			251.7( 49.8)
7	178.0(120.2)			178.0(120.2)
8	241.7(124.6)	125.4( 29.3)		367.1(102.1)
Annual	1065.0(426.4)	125.4( 29.3)		1190.4(419.1)

## APPENDIX III

LITTER DECOMPOSITION DATA  
FOR FOREST STANDS AT  
GRANVILLE, HANMER AND NELSON

## TABLE.

- D. Mean litter dry weight remaining in litter-bags after various periods of decomposition.
- E. Concentration of carbon, macro-nutrients and water-soluble and organic constituents in litter enclosed in litter-bags after various periods of decomposition.
- F. Total content of carbon, macro-nutrients and water-soluble and organic constituents in litter remaining in litter-bags after various of decomposition

Data given in parenthesis refer to 95 percent confidence intervals

TABLE D.1 Percentage of the original litter dry weight remaining in litterbag after various periods of decomposition. Values are means with 95 percent confidence intervals

GRANVILLE

	Oct 1976 (0 mth)	Jan 1977 (3rd mth)	Mar 1977 (5th mth)	Jun 1977 (8th mth)	Aug 1977 (10th mth)		Jan 1978 (15th mth)	Jul 1978 (21st mth)	Dec 1978 (26th mth)
Beech	100.0	81.0(1.8)	71.5(1.9)	70.2(1.5)	66.1(2.2)		62.0(2.8)	55.2(3.7)	53.2(4.1)
Radiata	100.0	83.7(1.1)	75.6(2.2)	73.5(4.6)	75.1(3.1)		62.1(2.5)	57.3(6.7)	59.8(4.7)

HANMER

	Oct 1976 (0 mth)	Feb 1977 (4th mth)		Jun 1977 (8th mth)	Aug 1977 (10th mth)		Jan 1978 (15th mth)	Jul 1978 (21st mth)	Dec 1978 (26th mth)
Beech	100.0	76.7(2.8)		68.5(3.5)	64.1(3.0)		60.4(3.1)	54.3(2.2)	51.8(2.0)
Radiata	100.0	79.2(4.6)		68.9(2.6)	67.1(2.0)		60.9(1.7)	58.1(2.3)	53.9(3.8)

NELSON

	Nov 1976 (0 mth)	Jan 1977 (2nd mth)	Mar 1977 (4th mth)	Jun 1977 (7th mth)	Aug 1977 (9th mth)	Oct 1977 (11th mth)	Jan 1978 (14th mth)	Jul 1978 (20th mth)	Dec 1978 (25th mth)
Beech	100.0	81.6(1.3)	76.0(1.9)	70.8(1.9)	67.2(4.6)	66.5(3.3)	53.0(3.3)	52.3(4.3)	46.4(2.7)
Radiata	100.0	81.4(1.6)	73.1(1.1)	68.0(1.8)	66.6(1.6)	63.2(3.3)	56.2(2.0)	48.1(3.9)	45.7(5.3)
Radiata (reg.)	100.0	84.0(1.4)	78.3(2.4)	74.2(5.5)	74.0(1.9)	73.9(3.6)	62.5(3.3)	64.1(4.1)	63.2(3.0)

TABLE E.1 GRANVILLE LEAF LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	OCTOBER 1976 (0 month)	MARCH 1977 (5th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N, mg.g <sup>-1</sup>	6.46 (0.62)	9.20 (0.57)	10.64(1.15)	11.16(0.83)	12.64(1.13)	13.27(0.40)
C, %	51.2 (1.0)	53.2 (2.4)	51.8 (1.5)	51.9 (2.5)	49.9 (1.7)	51.0 (2.5)
WSC,mg.g <sup>-1</sup>	59.2 (2.3)	29.7 (1.2)	30.9 (1.7)	32.3 (3.7)	27.6 (1.6)	28.3 (1.7)
WSP,mg.g <sup>-1</sup>	136.8(12.3)	38.8 (2.9)	32.9 (7.1)	29.9 (0.6)	23.8 (2.6)	24.9 (3.6)
WSF,mg.g <sup>-1</sup>	321.7(24.9)	170.5(17.1)	155.1(19.0)	150.2(20.2)	135.2(7.7)	125.6(18.7)
E.E., %	4.55 (0.07)	4.09 (0.15)	3.85 (0.29)	3.59 (0.06)	3.27 (0.22)	3.07 (0.42)
Aq.E, %	21.13(1.91)	8.46 (0.74)	6.97 (0.77)	7.21 (0.68)	6.15 (1.08)	6.20 (0.91)
HOLO. %	46.8 (1.0)	46.4 (1.4)	45.4 (1.4)	42.7 (1.4)	42.3 (12.0)	39.4 (1.4)
R. LIG. %	27.5 (2.3)	41.0 (1.2)	43.8 (1.6)	46.5 (1.9)	48.3 (1.4)	51.4 (2.1)
P, µg.g <sup>-1</sup>	496 (14)	664 (43)	708 (118)	706 (55)	760 (89)	800 (53)
K, mg.g <sup>-1</sup>	1.73 (0.17)	1.09 (0.09)	1.11 (0.15)	1.18 (0.14)	1.10 (0.09)	1.15 (0.11)
Mg. mg.g <sup>-1</sup>	1.67 (0.05)	1.93 (0.19)	1.48 (0.16)	1.48 (0.32)	1.45 (0.19)	1.21 (0.27)
Ca. mg.g <sup>-1</sup>	11.01(0.21)	13.29(0.58)	14.29(1.03)	10.48(1.75)	9.62 (1.8)	7.34 (2.0)

TABLE E.2

## GRANVILLE TWIG/STEM LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	OCTOBER 1976 (0 month)	MARCH 1977 (5th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N, mg.g <sup>-1</sup>	4.19 (0.52)	5.34 (0.40)	5.69 (0.50)	5.58 (0.65)	6.49 (0.78)	8.04 (0.40)
C, %	51.0 (2.0)	50.5 (1.2)	50.3 (1.2)	50.9 (1.0)	49.7 (0.60)	50.9 (1.2)
WSC,mg.g <sup>-1</sup>	31.5 (4.0)	20.5 (3.4)	24.4 (2.2)	26.8 (1.9)	24.0 (2.5)	24.0 (2.0)
WSP,mg.g <sup>-1</sup>	72.8 (22.1)	24.2 (8.4)	31.4 (3.7)	27.3 (5.5)	24.0 (3.4)	23.2 (3.6)
WSF,mg.g <sup>-1</sup>	154.9(27.3)	115.0(14.6)	136.3(4.0)	129.4(6.7)	121.6(16.6)	115.0(9.6)
E.E., %	1.59 (0.17)	1.48 (0.10)	1.49 (0.14)	1.44 (0.07)	1.57 (0.14)	1.94 (0.23)
Aq.E, %	8.56 (0.31)	5.80 (0.82)	5.09 (0.92)	5.60 (1.01)	5.31 (0.76)	5.40 (0.61)
HOLO. %	52.5 (2.2)	52.4 (1.6)	51.6 (2.5)	52.9 (3.0)	52.6 (4.0)	44.1 (3.4)
R. LIG. %	37.4 (1.7)	40.3 (1.6)	41.8 (2.0)	40.0 (3.0)	40.6 (4.1)	48.6 (3.7)
P, ug.g <sup>-1</sup>	360 (72)	520 (47)	392 (60)	298 (49)	348 (36)	432 (63)
K, mg.g <sup>-1</sup>	1.03 (0.20)	0.75 (0.17)	0.70 (0.15)	0.79 (0.12)	0.69 (0.06)	0.77 (0.11)
Mg. mg.g <sup>-1</sup>	1.34 (0.34)	1.57 (0.29)	1.33 (0.16)	1.21 (0.24)	1.22 (0.20)	1.03 (0.21)
Ca. mg.g <sup>-1</sup>	13.34(0.47)	17.11(0.91)	18.92(0.86)	13.69(1.92)	14.71(4.22)	10.65(2.48)

TABLE E.3

## GRANVILLE NEEDLE LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	OCTOBER 1976 (0 month)	MARCH 1977 (5th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N, mg.g <sup>-1</sup>	12.10(0.58)	14.09(0.83)	15.34(1.14)	16.26(1.19)	17.20(1.01)	17.41(1.1)
C, %	53.8 (1.2)	52.5 (3.0)	51.0 (2.9)	53.0 (1.6)	50.7 (3.2)	49.4 (2.6)
WSC,mg.g <sup>-1</sup>	23.7 (1.0)	18.2 (2.6)	16.4 (1.7)	18.6 (3.1)	19.8 (4.3)	16.2 (2.6)
WSP,mg.g <sup>-1</sup>	32.5 (5.8)	12.4 (1.6)	10.2 (0.5)	11.1 (1.0)	11.2 (3.3)	9.5 (1.9)
WSF,mg.g <sup>-1</sup>	132.5(6.1)	84.8 (11.4)	87.5 (2.5)	77.5 (25.7)	85.6 (31.8)	71.1 (5.6)
E.E., %	2.78 (0.17)	2.01 (0.16)	1.38 (0.11)	1.11 (0.14)	0.93 (0.27)	0.82 (0.16)
Aq.E, %	7.42 (0.29)	6.18 (0.45)	5.26 (0.38)	5.46 (0.19)	5.51 (1.28)	4.22 (0.51)
HOLO. %	54.2 (1.2)	43.2 (1.2)	42.6 (1.4)	37.3 (0.6)	36.8 (1.7)	33.6 (3.4)
R. LIG. %	35.7 (1.2)	48.6 (1.1)	51.5 (0.7)	56.1 (0.6)	56.7 (1.6)	61.2 (3.0)
P, ug.g <sup>-1</sup>	940 (113)	958 (136)	908 (77)	866 (42)	904 (53)	834 (117)
K, mg.g <sup>-1</sup>	4.34 (0.34)	2.31 (0.70)	0.96 (0.06)	0.80 (0.07)	0.83 (0.15)	0.77 (0.31)
Mg. mg.g <sup>-1</sup>	1.63 (0.20)	1.86 (0.25)	1.92 (0.27)	1.78 (0.34)	1.58 (0.36)	1.47 (0.38)
Ca. mg.g <sup>-1</sup>	6.32 (0.72)	6.69 (0.47)	7.92 (1.06)	5.67 (0.40)	5.22 (0.68)	4.83 (1.44)

TABLE E.4

## HANMER LEAF LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	OCTOBER 1976 (0 month)	FEBRUARY 1977 (4th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N, mg.g <sup>-1</sup>	11.19(0.50)	13.37(1.25)	14.50(1.79)	14.39(0.88)	15.95(1.04)	15.67(0.55)
C, %	50.0 (0.6)	49.1 (1.4)	n.d.	49.8 (0.5)	n.d.	48.5 (0.2)
WSC,mg.g <sup>-1</sup>	32.8 (2.7)	28.2 (2.5)	26.0 (1.5)	28.5 (2.5)	25.1 (0.6)	26.1 (2.2)
WSP,mg.g <sup>-1</sup>	46.4 (4.6)	26.4 (4.0)	21.9 (2.7)	21.3 (2.5)	16.7 (0.9)	16.9 (0.9)
WSF,mg.g <sup>-1</sup>	163.2(19.2)	151.2(18.0)	145.2(9.4)	147.6(20.5)	142.0(17.1)	136.6(9.9)
E.E., %	3.13 (0.31)	3.47 (0.16)	3.39 (0.21)	3.33 (0.16)	2.93 (0.17)	3.22 (0.10)
Aq.E. %	10.69(0.69)	8.02 (0.42)	7.03 (0.32)	6.97 (0.36)	6.35 (0.63)	5.84 (0.51)
HOLO. %	54.4 (1.7)	49.5 (0.9)	45.4 (1.4)	44.8 (2.2)	43.8 (1.5)	42.9 (0.9)
R. LIG. %	31.8 (1.5)	39.0 (0.6)	44.2 (1.6)	44.9 (2.5)	46.9 (2.1)	48.0 (1.1)
P, ug.g <sup>-1</sup>	1042 (22)	1113 (16)	1124 (78)	1254 (76)	1222 (151)	1155 (22)
K, mg.g <sup>-1</sup>	1.62 (0.22)	1.48 (0.05)	1.40 (0.07)	1.64 (0.22)	1.62 (0.23)	1.65 (0.07)
Mg. mg.g <sup>-1</sup>	1.56 (0.27)	1.55 (0.10)	1.38 (0.10)	1.37 (0.28)	1.30 (0.25)	1.05 (0.35)
Ca. mg.g <sup>-1</sup>	15.71(0.59)	19.04(1.02)	16.57(0.42)	16.64(2.32)	14.07(4.72)	12.17(3.21)



TABLE E.5 HANMER TWIG/STEM LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	OCTOBER 1976 (0 month)	FEBRUARY 1977 (4th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N, mg.g <sup>-1</sup>	7.30 (0.62)	9.81 (0.68)	10.69(1.02)	10.00(0.55)	12.35(0.92)	12.50(0.33)
C, %	51.2 (0.5)	50.7 (1.7)	n.d.	50.9 (1.4)	n.d.	50.0 (0.9 )
WSC,mg.g <sup>-1</sup>	24.6 (2.7)	24.0 (1.4)	25.5 (1.9)	29.0 (2.7)	25.2 (0.6)	24.2 (2.1 )
WSP,mg.g <sup>-1</sup>	27.3 (3.1)	27.8 (1.1)	23.1 (3.0)	22.6 (1.5)	16.8 (0.9)	19.1 (1.6 )
WSF,mg.g <sup>-1</sup>	114.9(10.7)	131.9(11.4)	133.4(13.9)	137.4(17.3)	142.6(17.2)	120.9(10.8)
E.E., %	2.53 (0.14)	3.39 (0.27)	2.94 (0.15)	2.27 (0.25)	2.43 (0.32)	2.71 (0.38)
Aq.E. %	7.84 (0.37)	7.77 (0.21)	6.89 (0.30)	6.65 (0.55)	5.96 (0.81)	5.65 (0.43)
HOLO. %	53.5 (0.6)	47.9 (2.1)	48.5 (1.5)	49.3 (2.2)	46.1 (3.6)	43.9 (0.9 )
R. LIG. %	36.2 (0.4)	40.9 (1.9)	41.7 (1.9)	41.8 (2.7)	44.6 (2.6)	47.6 (1.2 )
P, ug.g <sup>-1</sup>	817 (61)	882 (52)	953 (20)	908 (107)	926 (55)	964 (38 )
K, mg.g <sup>-1</sup>	1.30 (0.27)	1.08 (0.04)	1.31 (0.07)	1.19 (0.15)	1.23 (0.17)	1.29 (0.07)
Mg. mg.g <sup>-1</sup>	1.41 (0.11)	1.53 (0.11)	1.38 (0.11)	1.27 (0.23)	1.14 (0.32)	1.07 (0.33)
Ca. mg.g <sup>-1</sup>	18.01(2.24)	19.78(0.93)	20.03(2.21)	20.60(1.67)	21.17(1.97)	19.59(1.86)

TABLE E.6

## HANMER NEEDLE LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	OCTOBER 1976 (0 month)	FEBRUARY 1977 (4th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N, mg.g <sup>-1</sup>	11.58(0.69)	13.85(0.82)	15.21(0.86)	17.19(1.70)	17.61(0.64)	17.58(1.40)
C, %	53.0 (0.9)	52.6 (2.0)	n.d.	53.1 (0.7)	n.d.	51.0 (3.2 )
WSC,mg.g <sup>-1</sup>	46.0 (5.0)	28.1 (1.9)	24.6 (2.6)	24.0 (2.5)	21.3 (0.9)	19.7 (5.2 )
WSP,mg.g <sup>-1</sup>	52.0 (2.7)	22.7 (4.2)	16.7 (1.5)	14.9 (1.5)	12.7 (0.9)	11.6 (1.6 )
WSF,mg.g <sup>-1</sup>	244.9(9.1)	130.0(22.1)	115.2(12.5)	99.5 (27.2)	86.7 (4.1)	79.0 (13.1)
E.E., %	2.96 (0.11)	2.74 (0.23)	2.36 (0.36)	1.78 (0.16)	1.61 (0.25)	1.15 (0.16)
Aq.E. %	17.40(0.72)	9.12 (0.63)	7.49 (0.74)	6.77 (0.43)	6.09 (0.12)	5.39 (0.81)
HOLO. %	50.3 (1.5)	45.5 (1.7)	39.6 (0.7)	37.1 (1.2)	35.2 (1.1)	33.9 (2.2 )
R. LIG. %	29.4 (2.1)	42.6 (2.3)	50.6 (1.4)	54.4 (1.1)	57.1 (0.7)	59.5 (3.1 )
P,ug.g <sup>-1</sup>	1576 (98)	1395 (207)	1358 (135)	1226 (62)	1132 (42)	1032 (119 )
K,mg.g <sup>-1</sup>	6.26 (0.26)	4.35 (0.21)	1.71 (0.32)	1.25 (0.17)	1.04 (0.09)	0.99 (0.37)
Mg. mg.g <sup>-1</sup>	1.28 (0.07)	1.77 (0.19)	1.93 (0.21)	1.70 (0.09)	1.44 (0.10)	1.31 (0.36)
Ca. mg.g <sup>-1</sup>	8.01 (0.38)	9.89 (1.03)	11.77(0.47)	8.12 (0.37)	8.36 (0.37)	8.12 (0.89)

TABLE E.7

## NELSON LEAF LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N, mg.g <sup>-1</sup>	15.68(0.58)	18.44(1.05)	19.06(1.31)	18.50(1.41)	20.20(1.90)	19.15(3.09)
C, %	52.0 (1.0)	50.4 (1.9)	n.d.	50.0 (0.7)	n.d.	46.7 (1.6 )
WSC,mg.g <sup>-1</sup>	35.4 (6.1)	21.3 (2.7)	17.6 (2.0)	22.0 (0.7)	20.4 (1.1)	20.1 (4.5 )
WSP,mg.g <sup>-1</sup>	55.8 (10.5)	26.4 (3.5)	20.9 (5.8)	24.4 (2.3)	19.0 (2.5)	16.8 (2.8 )
WSF,mg.g <sup>-1</sup>	199.6(37.2)	157.0(13.3)	156.1(8.1)	154.7(25.8)	131 (15.3)	121.7(17.6)
E.E., %	2.67 (0.15)	2.42 (0.17)	2.21 (0.16)	1.93 (0.15)	1.83 (0.16)	1.84 (0.17)
Aq.E. %	12.96(0.22)	7.06 (0.32)	6.16 (0.67)	5.80 (0.57)	5.20 (0.22)	4.41 (0.66)
HOLO. %	52.8 (1.2)	47.4 (2.1)	45.1 (2.0)	40.3 (1.0)	40.4 (2.5)	39.9 (3.8 )
R. LIG. %	31.5 (1.4)	43.2 (2.0)	46.5 (2.1)	52.0 (1.5)	52.6 (2.2)	53.9 (3.3 )
P, mg.g <sup>-1</sup>	1.19 (0.09)	1.14 (0.50)	1.34 (0.15)	1.23 (0.12)	n.d.	1.25 (0.19)
K, mg.g <sup>-1</sup>	2.62 (0.11)	1.83 (0.22)	1.29 (0.11)	1.31 (0.11)	n.d.	1.68 (0.20)
Mg. mg.g <sup>-1</sup>	1.68 (0.11)	1.81 (0.10)	1.69 (0.11)	1.64 (0.16)	n.d.	1.63 (0.15)
Ca. mg.g <sup>-1</sup>	16.25(1.39)	16.07(1.14)	19.29(1.20)	19.61(1.56)	n.d.	17.61(0.36)

TABLE E.8 NELSON TWIG/STEM LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N, mg.g <sup>-1</sup>	8.44 (0.58)	10.08(0.41)	11.79(0.61)	11.29(0.58)	13.40(0.82)	14.87(1.65)
C, %	50.2 (2.4)	50.9 (1.9)	n.d.	50.2 (0.7)	n.d.	48.1 (0.7 )
WSC,mg.g <sup>-1</sup>	39.7 (4.5)	20.5 (3.5)	20.9 (2.0)	24.1 (2.7)	21.4 (0.9)	19.7 (4.3 )
WSP,mg.g <sup>-1</sup>	93.0 (20.8)	42.8 (8.3)	41.4 (12.9)	50.5 (2.4)	42.5 (4.5)	31.4 (13.6)
WSF,mg.g <sup>-1</sup>	219.5(44.1)	138.0(18.8)	160.3(16.4)	155.1(22.2)	148.8(11.5)	132.1(25.7)
E.E., %	4.35 (0.42)	4.07 (0.35)	4.12 (0.35)	2.93 (0.17)	2.72 (0.35)	2.86 (0.82)
Aq.E. %	15.45(1.22)	8.24 (0.78)	9.25 (0.55)	7.01 (0.43)	6.30 (0.50)	5.58 (1.13)
HOL. %	44.0 (2.5)	39.3 (1.4)	41.5 (1.2)	44.1 (1.2)	41.9 (2.6)	37.3 (0.1 )
R. LIG. %	36.2 (2.4)	48.4 (2.2)	44.5 (2.1)	45.8 (1.4)	49.1 (2.5)	54.2 (2.1 )
P, mg.g <sup>-1</sup>	0.92 (0.07)	0.74 (0.05)	0.88 (0.11)	0.80 (0.05)	n.d.	0.95 (0.15)
K, mg.g <sup>-1</sup>	3.12 (0.09)	1.53 (0.36)	1.20 (0.12)	1.13 (0.17)	n.d.	1.37 (0.33)
Mg. mg.g <sup>-1</sup>	1.84 (0.16)	1.89 (0.12)	1.56 (0.07)	1.56 (0.10)	n.d.	1.46 (0.15)
Ca. mg.g <sup>-1</sup>	16.90(0.97)	17.54(0.69)	19.36(1.71)	19.65(0.40)	n.d.	21.49(2.59)

TABLE E.9 NELSON NEEDLE (RADIATA 1956) LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N, mg.g <sup>-1</sup>	12.62(1.26)	15.76(1.72)	15.92(1.00)	16.50(0.67)	18.14(1.44)	17.56(1.17)
C, %	51.0 (0.9)	54.0 (0.6)	n.d.	53.5 (0.9)	n.d.	50.2 (1.7 )
WSC,mg.g <sup>-1</sup>	36.1 (5.2)	21.5 (2.6)	19.1 (2.7)	20.2 (1.2)	20.9 (2.9)	22.1 (5.6 )
WSP,mg.g <sup>-1</sup>	41.2 (4.3)	15.2 (2.9)	13.0 (1.1)	13.5 (1.0)	12.8 (1.2)	12.9 (1.5 )
WSF,mg.g <sup>-1</sup>	209.5(12.0)	116.2(7.2)	102.6(23.2)	94.5 (21.5)	103.1(28.8)	110.1(24.4)
E.E., %	3.72 (0.25)	2.39 (0.12)	2.01 (0.20)	1.58 (0.12)	1.82 (0.30)	1.50 (0.11)
Aq.E. %	16.28(0.68)	8.44 (0.15)	7.16 (0.53)	6.58 (0.50)	5.96 (0.68)	6.13 (1.05)
HOLO. %	51.8 (1.3 )	44.9 (0.7)	39.2 (1.1)	36.0 (0.7)	34.9 (1.2)	33.2 (1.1 )
R. LIG. %	28.2 (0.9)	44.3 (0.9)	51.6 (1.6)	55.8 (0.9)	57.3 (2.0)	59.0 (1.0 )
P, mg.g <sup>-1</sup>	1.47 (0.14)	1.40 (0.07)	1.36 (0.06)	1.16 (0.06)	n.d.	1.22 (0.12)
K, mg.g <sup>-1</sup>	5.18 (0.41)	4.03 (0.40)	1.97 (0.63)	1.30 (0.14)	n.d.	1.27 (0.19)
Mg. mg.g <sup>-1</sup>	1.23 (0.10)	1.45 (0.15)	1.84 (0.10)	1.79 (0.27)	n.d.	1.67 (0.15)
Ca. mg.g <sup>-1</sup>	8.59 (1.11)	9.79 (0.53)	9.59 (0.42)	9.15 (0.40)	n.d.	9.59 (1.08)

TABLE E.10 NELSON NEEDLE (RADIATA reg.) LITTER DECOMPOSITION, CONCENTRATION CHANGES

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N, mg.g <sup>-1</sup>	11.68(0.97)	13.37(1.41)	14.63(0.61)	15.12(0.64)	16.46(0.56)	16.15(0.63)
C, %	50.4 (0.6)	53.6 (0.7)	n.d.	52.2 (1.0)	n.d.	51.6 (1.2 )
WSC,mg.g <sup>-1</sup>	38.8 (6.6)	19.2 (3.5)	16.7 (0.6)	19.5 (3.5)	18.7 (2.4)	17.6 (2.5 )
WSP,mg.g <sup>-1</sup>	34.6 (8.1)	12.9 (1.5)	11.4 (1.6)	12.5 (3.1)	10.2 (1.2)	10.8 (0.2 )
WSF,mg.g <sup>-1</sup>	186.4(26.0)	105.3(7.2)	97.4 (12.8)	95.4 (31.0)	84.2 (15.5)	73.3 (7.3 )
E.E., %	3.28 (0.46)	1.93 (0.20)	1.77 (0.20)	1.65 (0.17)	1.58 (0.01)	1.18 (0.11)
Aq.E. %	13.62(1.74)	7.24 (0.62)	6.28 (0.07)	5.82 (0.71)	5.69 (0.30)	5.26 (0.27)
HOLO. %	49.1 (2.4)	42.7 (1.0)	39.9 (1.7)	36.7 (1.6)	35.2 (1.5)	35.0 (1.9 )
R. LIG. %	34.1 (4.6)	48.1 (1.6)	52.0 (1.6)	55.8 (1.2)	57.6 (1.6)	58.5 (1.7 )
P, mg.g <sup>-1</sup>	1.41 (0.19)	1.47 (0.15)	1.19 (0.10)	1.09 (0.50)	n.d.	1.02 (0.09)
K, mg.g <sup>-1</sup>	4.95 (0.39)	3.69 (0.88)	1.38 (0.22)	1.21 (0.35)	n.d.	1.24 (0.57)
Mg. mg.g <sup>-1</sup>	1.60 (0.17)	1.93 (0.22)	2.13 (0.31)	2.17 (0.41)	n.d.	2.13 (0.21)
Ca. mg.g <sup>-1</sup>	9.22 (0.48)	9.61 (0.30)	9.28 (0.60)	9.35 (1.15)	n.d.	8.88 (0.25)

TABLE F.1 GRANVILLE BEECH LITTER CONTENT  
(percent weight remaining)

CONSTITUENTS	OCTOBER 1976 (0 month)	MARCH 1977 (5th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N	100.0	100.3(11.5)	105.6(10.3)	104.5(15.4)	107.8(15.5)	112.1(21.9)
C	100.0	73.1( 2.2)	66.2( 3.9)	62.4( 4.2)	53.7( 5.8)	54.8( 8.5)
WSC	100.0	37.0( 5.3)	36.6( 5.0)	36.3( 3.6)	28.0( 3.2)	28.6( 7.1)
WSP	100.0	20.6( 4.0)	17.7( 3.7)	14.9( 1.4)	10.8( 2.1)	11.2( 3.6)
WSF	100.0	39.5( 7.1)	35.2( 6.5)	32.3( 2.9)	25.8( 4.6)	23.9( 5.8)
E.E.	100.0	63.8( 6.2)	56.4(10.0)	49.8( 3.7)	42.0( 4.2)	40.1( 6.8)
Aq. E.	100.0	30.8( 5.1)	23.7( 5.3)	23.3( 2.6)	18.1( 4.0)	19.1( 5.4)
HOLO	100.0	71.4( 3.9)	64.6( 3.3)	58.0( 1.4)	50.8( 5.3)	46.3( 7.6)
R. LIG.	100.0	98.7( 9.2)	96.9(13.4)	94.7(11.1)	87.7(11.8)	94.5(13.3)
P	100.0	111.2( 6.4)	89.1(14.6)	82.0( 4.9)	81.3(14.4)	85.1(11.4)
K	100.0	53.7( 8.7)	43.3(10.1)	43.2( 5.4)	36.1( 6.7)	37.4( 4.7)
Mg.	100.0	95.5( 8.2)	60.6( 9.6)	55.6(12.5)	48.9( 7.2)	40.7( 9.9)
Ca.	100.0	97.2( 5.7)	88.2(13.7)	61.1(10.1)	49.8(10.7)	37.9( 8.6)

TABLE F.2 GRANVILLE RADIATA LITTER CONTENT  
(percent weight remaining)

CONSTITUENTS	OCTOBER 1976 (0 month)	MARCH 1977 (5th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N	100.0	88.1( 6.2)	95.4( 5.7)	83.5( 8.8)	81.5(12.2)	86.0( 8.6)
C	100.0	73.8( 4.5)	71.2( 5.2)	61.2( 5.2)	53.7( 5.8)	54.8( 4.6)
WSC	100.0	58.1( 7.3)	51.8( 5.6)	48.9(11.9)	47.2( 6.1)	41.2(11.2)
WSP	100.0	29.0( 5.7)	23.7( 2.7)	21.4( 4.1)	20.9( 6.6)	17.7( 6.0)
WSF	100.0	48.6( 9.2)	49.6( 2.5)	36.1(10.7)	36.3( 9.8)	32.1( 4.3)
E.E.	100.0	54.8( 4.8)	37.5( 5.2)	24.8( 4.3)	19.1( 5.0)	17.8( 5.6)
Aq. E.	100.0	63.0( 5.3)	53.4( 6.1)	45.8( 5.5)	42.1( 6.7)	34.2( 8.2)
HOLO	100.0	60.4( 4.3)	58.1( 2.9)	42.8( 2.6)	39.0( 5.6)	36.9( 3.1)
R. LIG.	100.0	103.0( 4.5)	108.6( 7.6)	97.7( 7.1)	91.2(12.0)	103.2(18.1)
P	100.0	86.1(18.5)	73.1(11.4)	57.5( 6.3)	55.9(13.4)	54.0(14.6)
K	100.0	44.3(11.9)	16.7( 1.2)	11.6( 1.9)	11.0( 2.6)	10.6( 3.6)
Mg.	100.0	97.1(23.3)	89.0(15.4)	68.5(14.5)	57.0(20.1)	54.4(17.9)
Ca.	100.0	89.2(11.5)	94.2(13.3)	56.1( 9.1)	47.2( 6.1)	46.2(16.9)



TABLE F.3

## HANMER BEECH LITTER CONTENT

(percent weight remaining)

CONSTITUENTS	OCTOBER 1976 (0 month)	FEBRUARY 1977 (4th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N	100.0	94.6(10.6)	86.2(12.4)	82.3( 9.2)	82.0(10.4)	77.0( 5.0)
C	100.0	75.4( 5.7)	n.d.	59.9( 5.1)	n.d.	50.8( 3.0)
WSC	100.0	69.1( 7.6)	56.0( 7.8)	58.2( 6.4)	46.2( 6.2)	45.0( 2.5)
WSP	100.0	52.3( 7.7)	36.3( 4.5)	33.1( 5.6)	23.3( 3.4)	23.4( 1.7)
WSF	100.0	76.5( 9.5)	62.5( 5.5)	60.7( 9.8)	53.6( 9.9)	47.6( 5.8)
E.E.	100.0	90.5( 4.8)	71.8( 7.0)	64.9(11.5)	48.2( 9.9)	55.2(10.2)
Aq. E.	100.0	63.1( 5.5)	46.5( 4.8)	43.2( 5.2)	35.3( 7.2)	31.3( 3.8)
HOLO	100.0	69.8( 4.9)	55.1( 0.9)	51.2( 4.2)	44.7( 3.8)	41.8( 2.4)
R. LIG.	100.0	90.7( 5.8)	83.1( 2.6)	79.7( 8.2)	75.1( 5.1)	74.8( 4.5)
P	100.0	81.3( 6.8)	71.4( 9.4)	73.2(10.0)	63.0( 5.7)	58.5( 5.7)
K	100.0	69.3( 8.9)	59.0( 9.7)	63.1(15.9)	54.1( 2.9)	53.6( 9.4)
Mg.	100.0	78.8(12.7)	58.8( 7.9)	55.0(20.2)	45.1(12.2)	37.0(16.0)
Ca.	100.0	89.7( 8.7)	71.2( 5.7)	64.0(11.4)	53.3(14.2)	46.7(11.0)

TABLE F.4

## HANMER RADIATA LITTER CONTENT

(percent weight remaining)

CONSTITUENTS	OCTOBER 1976 (0 month)	FEBRUARY 1977 (4th month)	AUGUST 1977 (10th month)	JANUARY 1978 (15th month)	JULY 1978 (21st month)	DECEMBER 1978 (26th month)
N	100.0	95.2(13.7)	88.2( 8.4)	90.7(13.0)	88.4( 8.2)	82.0( 9.9)
C	100.0	78.8( 7.6)	n.d.	61.1( 2.2)	n.d.	51.9( 3.5)
WSC	100.0	48.6( 4.5)	36.1( 4.6)	31.8( 2.7)	26.9( 2.1)	23.1( 6.2)
WSP	100.0	34.6( 6.6)	21.6( 2.4)	17.5( 2.4)	14.2( 1.4)	12.0( 1.4)
WSF	100.0	42.0( 6.8)	31.7( 5.0)	24.8( 7.3)	20.6( 2.2)	17.4( 3.5)
E.E.	100.0	73.5( 8.9)	53.5( 8.3)	36.8( 4.8)	31.5( 5.2)	20.9( 3.4)
Aq. E.	100.0	41.5( 3.7)	29.0( 4.3)	23.7( 2.2)	20.3( 1.1)	16.7( 2.9)
HOLO	100.0	71.7( 3.6)	52.8( 3.0)	44.9( 0.9)	40.6( 3.0)	36.4( 3.3)
R. LIG.	100.0	115.3(14.6)	115.8( 8.7)	113.1( 8.6)	113.3(10.9)	109.5(11.2)
P	100.0	70.0( 8.7)	57.8( 5.5)	47.6( 5.8)	41.8( 5.1)	35.4( 5.7)
K	100.0	57.6( 7.6)	18.5( 4.0)	12.2( 2.0)	9.7( 1.2)	8.5( 3.4)
Mg.	100.0	109.6(17.3)	100.8( 9.9)	80.9( 8.7)	65.4( 9.9)	55.3(16.0)
Ca.	100.0	97.9(10.7)	98.7( 7.9)	61.9( 4.7)	60.6( 3.4)	54.8( 8.4)

TABLE F.5

## NELSON BEECH LITTER CONTENT

(percent weight remaining)

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N	100.0	89.0( 7.9)	80.5( 9.0)	64.1(10.2)	70.9( 8.6)	62.5(16.8)
C	100.0	74.2( 2.9)	n.d.	51.3( 4.6)	n.d.	42.3( 3.6)
WSC	100.0	45.2(10.2)	34.6( 6.5)	32.9( 6.5)	30.5( 5.3)	29.7(18.5)
WSP	100.0	39.2(11.5)	28.8(11.2)	24.1( 5.8)	19.3( 5.6)	14.4( 3.5)
WSF	100.0	57.5( 9.0)	52.2( 5.8)	40.3( 3.8)	37.0( 3.2)	27.9( 7.2)
E.E.	100.0	69.2( 7.3)	60.4( 4.5)	36.4( 2.7)	34.8( 5.7)	31.4( 5.3)
Aq. E.	100.0	41.3( 1.4)	34.8( 3.7)	23.6( 3.1)	21.3( 2.7)	16.0( 3.3)
HOLO	100.0	68.0( 3.0)	58.1( 2.9)	42.3( 4.2)	42.5( 8.9)	35.6( 2.0)
R. LIG.	100.0	103.2( 3.6)	95.1( 3.2)	83.3( 4.6)	85.5(13.0)	77.7(10.3)
P	100.0	76.6( 9.6)	72.0( 8.8)	54.8( 9.1)	n.d.	49.4(11.8)
K	100.0	53.6( 7.2)	31.4( 2.7)	25.2( 2.1)	n.d.	27.9( 5.8)
Mg.	100.0	87.4( 7.7)	65.0( 5.3)	50.3( 6.7)	n.d.	43.5( 6.2)
Ca.	100.0	81.5( 1.6)	79.5(10.4)	63.1( 3.8)	n.d.	52.7( 7.2)

TABLE F.6

## NELSON RADIATA LITTER CONTENT

(percent weight remaining)

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N	100.0	92.9(17.2)	84.3( 7.2)	73.9( 9.1)	67.8( 8.7)	62.6( 9.4)
C	100.0	77.5( 0.7)	n.d.	59.0( 3.2)	n.d.	44.2( 5.3)
WSC	100.0	44.3(10.3)	35.7( 8.6)	31.2( 5.3)	27.8( 6.8)	26.9( 7.8)
WSP	100.0	26.7( 7.2)	21.0( 2.8)	18.5( 2.0)	14.8( 1.7)	14.1( 2.6)
WSF	100.0	40.6( 3.5)	32.9( 9.3)	25.5( 6.5)	23.0( 5.1)	23.6( 5.9)
E.E.	100.0	47.0( 1.9)	36.3( 6.3)	24.0( 1.7)	23.1( 3.6)	18.2( 3.4)
Aq. E.	100.0	38.0( 2.1)	29.4( 3.8)	22.8( 2.7)	17.4( 3.7)	17.4( 3.2)
HOLO	100.0	63.4( 2.6)	50.4( 1.7)	39.1( 1.9)	32.0( 5.1)	28.8( 4.0)
R. LIG.	100.0	114.9( 4.8)	121.8( 5.5)	111.4( 8.4)	96.4(15.8)	94.0(14.0)
P	100.0	77.9( 9.6)	61.9( 8.6)	44.4( 5.3)	n.d.	37.3( 7.9)
K	100.0	63.6( 9.9)	25.8(10.4)	14.1( 1.7)	n.d.	11.1( 2.7)
Mg.	100.0	95.7(13.3)	99.6( 8.2)	82.0(16.1)	n.d.	61.0(10.2)
Ca.	100.0	93.3( 8.9)	75.0(11.0)	60.6(10.2)	n.d.	50.0( 3.4)

TABLE F.7 NELSON RADIATA reg. LITTER CONTENT  
(percent weight remaining)

CONSTITUENTS	NOVEMBER 1976 (0 month)	MARCH 1977 (4th month)	AUGUST 1977 (9th month)	JANUARY 1978 (14th month)	JULY 1978 (20th month)	DECEMBER 1978 (25th month)
N	100.0	89.7( 9.7)	92.8( 4.8)	81.3(10.9)	90.4( 8.3)	87.6( 8.7)
C	100.0	83.3( 4.8)	n.d.	64.0( 4.2)	n.d.	64.6( 2.5)
WSC	100.0	39.3( 9.2)	32.1( 4.6)	31.7( 5.8)	31.8( 9.8)	29.0( 6.1)
WSP	100.0	29.9( 8.1)	25.3( 7.7)	22.9( 5.7)	19.3( 4.8)	20.3( 5.5)
WSF	100.0	44.5( 4.3)	37.8( 4.1)	32.2(10.2)	29.2( 7.6)	25.2( 5.0)
E.E.	100.0	46.7(10.8)	40.4( 8.3)	31.7( 5.5)	31.3( 6.6)	23.0( 4.1)
Aq. E.	100.0	42.0( 7.1)	34.4( 4.8)	26.7( 1.4)	27.2( 6.7)	24.6( 4.0)
HOLO	100.0	68.2( 4.3)	60.2( 2.6)	46.9( 6.0)	46.3( 9.4)	45.3( 6.3)
R. LIG.	100.0	111.4(11.0)	113.9(14.0)	103.3(15.3)	108.8( 9.4)	109.5(15.3)
P	100.0	86.5(10.1)	63.0( 9.8)	48.2( 4.2)	n.d.	45.7( 3.2)
K	100.0	62.8(16.4)	20.6( 2.2)	15.5( 5.9)	n.d.	16.2( 8.7)
Mg.	100.0	101.6(10.4)	98.7( 8.1)	86.9(30.5)	n.d.	85.4(19.1)
Ca.	100.0	87.7( 6.1)	74.6( 7.3)	63.2( 5.7)	n.d.	60.9( 3.6)

APPENDIX IV

CARBON AND NITROGEN MINERALIZATION DATA  
FOR BEECH AND RADIIATA PINE STAND AT  
GRANVILLE

Data given parenthesis refer to 95 percent  
confidence intervals

TABLE G.1 Forest floor carbon dioxide evolution rates  
(mg CO<sub>2</sub> per m<sup>2</sup> per day)

GRANVILLE		
DATE	BEECH SITE	RADIATA SITE
18 AUG 76	914(316)	774( 260)
17 SEP 76	1157(291)	850( 235)
16 OCT 76	1148(278)	809( 274)
28 DEC 76	2694(515)	1965( 501)
5 FEB 77	2779(562)	1711( 578)
3 MAR 77	2738(631)	1975( 598)
2 APR 77	2797(606)	1906( 680)
4 JUN 77	1628(303)	1080( 293)
5 AUG 77	993(208)	641( 226)
6 OCT 77	2024(500)	1525( 498)
5 JAN 78	2855(637)	2596(1141)
6 APR 78	2231(607)	2018( 677)
6 JUL 78	1344(258)	963( 283)
5 OCT 78	1706(483)	1169( 410)

TABLE G.2 Mean forest floor temperatures for the stands at Granville, together with the air temperature recorded for a corresponding period. ( $^{\circ}\text{C}$ )

PERIOD				BEECH SITE	RADIATA SITE	WEATHER STATION
15 JUL 76	to	17 AUG 76		6.87(1.43)	7.48(1.21)	6.7
18 SEP 76	to	18 OCT 76		8.08(0.15)	8.43(0.38)	10.2
19 OCT 76	to	29 DEC 76		11.87(0.13)	12.79(0.45)	13.5
30 DEC 76	to	4 DEC 77		17.15(0.47)	17.87(0.19)	15.6
3 FEB 77	to	6 MAR 77		16.84(0.16)	17.21(0.16)	17.8
7 MAR 77	to	4 JUN 77		10.96(0.67)	10.56(0.26)	12.6
3 APR 77	to	4 JUN 77		9.17(0.24)	8.97(0.25)	10.9
5 JUN 77	to	6 AUG 77		7.02(0.26)	6.53(0.24)	7.6
7 AUG 77	to	6 OCT 77		5.92(0.32)	5.31(0.32)	9.1
7 OCT 77	to	7 JAN 78		11.21(0.24)	11.90(0.56)	14.9
8 JAN 78	to	8 APR 78		15.76(0.22)	16.19(0.26)	19.6
9 APR 78	to	8 JUL 78		13.53(0.20)	13.46(0.37)	n.d.
9 JUN 78	to	7 OCT 78		10.53(0.26)	10.09(0.33)	n.d.



TABLE G.3 Regressions of forest floor carbon dioxide evolution rate and forest floor temperature and moisture content (no. of samples = 9)

	REGRESSION MODEL	CORRELATION COEFFICIENT
BEECH	$R = 3019.07 - 18.64(\text{SMC})$	0.185 ns
	$R = 2309.58 - 0.981(\text{HMC})$	-0.087 ns
	$R = 590.77 + 124.99(\text{T})$	0.896 ***
	$R = 3128.08 - 17.60(\text{SMC}) - 0.59(\text{HMC})$	0.192 ns
	$R = -1599.43 + 23.25(\text{SMC}) + 2.46(\text{HMC}) + 148.78(\text{T})$	0.945 **
RADIATA	$R = 3011.82 - 37.17(\text{SMC})$	0.220 ns
	$R = 2997.86 - 5.37(\text{HMC})$	0.295 ns
	$R = 236.57 + 110.69(\text{T})$	0.906 ***
	$R = 4051.55 - 30.10(\text{SMC}) - 4.86(\text{HMC})$	0.344 ns
	$R = 971.14 - 21.17(\text{SMC}) + 0.41(\text{HMC}) + 109.94(\text{T})$	0.914 *

Carbon Mineralization (R)

Soil (0-20 cm) Moisture Content (SMC)

Humus Moisture Content (HMC)

Forest Floor (8 cm depth) Temperature (T)

\* denotes  $p < 0.05$  ; \*\* denotes  $p < 0.01$  ; \*\*\* denotes  $p < 0.001$

TABLE G.4 Regressions of forest floor carbon dioxide evolution rate and forest floor and air temperature

1. CARBON MINERALIZATION AND AIR TEMPERATURE

SITES	REGRESSION MODEL	NO. OF SAMPLES	CORRELATION COEFFICIENT
BEECH	$R = 150.43 + 139.97 T_a$	14	0.864***
RADIATA	$R = -71.39 + 117.95 T_a$	14	0.897***

2. MEAN AIR TEMPERATURE AND MEAN FOREST FLOOR TEMPERATURE

SITES	REGRESSION MODEL	NO. OF SAMPLES	CORRELATION COEFFICIENT
BEECH	$T_f = -0.407 + 0.906 T_a$	11	0.921***
RADIATA	$T_f = -0.938 + 0.965 T_a$	11	0.911***

3. CARBON MINERALIZATION AND FOREST FLOOR TEMPERATURE

SITES	REGRESSION MODEL	NO. OF SAMPLES	CORRELATION COEFFICIENT
BEECH	$R = 209.34 + 154.63 T_f$	14	0.865***
RADIATA	$R = 55.97 + 120.75 T_f$	14	0.893***

\*\*\* denotes  $p < 0.001$

Carbon Mineralization Rates,  $R$

Air Temperature,  $T_a$

Forest Floor Temperature,  $T_f$  (determined by sucrose inversion method)

TABLE G.5 Forest floor carbon dioxide evolution rates recorded at Larry's Creek  
(mg CO<sub>2</sub> per m<sup>2</sup> per day)

DATE	FORESTED SITE	CLEARCUT SITE	BURNED SITE
4 MAR 77	3481(931)	4835(1590)	4684(1114)
1 APR 77	1892(575)	3471(1115)	2327( 553)
3 JUN 77	1364(364)	1322( 384)	846( 234)
4 AUG 77	960(301)	997( 237)	743( 157)
6 OCT 77	1305(377)	1810( 641)	1525( 289)
5 JAN 78	1951(312)	3197(1663)	2342( 421)
6 APR 78	1625(390)	1946( 685)	1605( 220)
6 JUL 78	909(179)	601( 212)	743( 127)
5 OCT 78	1154(256)	1071( 486)	1134( 299)

TABLE G.6 Mean forest floor temperatures recorded at Larry's Creek ( $^{\circ}\text{C}$ )

PERIOD		FORESTED SITE	CLEARCUT SITE	BURNED SITE
15 JUL 76	to 17 AUG 76	6.93(0.53)	7.54(0.57)	-
18 SEP 76	to 18 OCT 76	8.53(0.38)	9.75(0.54)	-
19 OCT 76	to 29 DEC 76	13.12(0.80)	15.10(0.60)	-
3 MAR 77	to 3 APR 77	13.32(0.10)	14.57(0.48)	15.58(0.44)
4 APR 77	to 4 JUN 77	9.25(0.23)	9.36(0.41)	9.22(0.37)
5 JUN 77	to 6 AUG 77	6.34(0.22)	5.67(1.02)	6.26(0.72)
7 AUG 77	to 6 OCT 77	5.47(0.14)	5.86(0.24)	5.30(0.36)
7 OCT 77	to 7 JAN 78	12.73(1.08)	15.47(0.39)	14.76(1.04)
8 JAN 78	to 8 APR 78	15.74(0.05)	21.12(0.61)	19.62(1.24)
9 APR 78	to 8 JUL 78	13.84(0.44)	13.80(0.36)	13.86(0.41)
9 JUL 78	to 7 OCT 78	10.08(0.13)	11.11(0.43)	10.42(0.41)

TABLE G.7 Ammonium-N concentrations ( $\mu\text{g/g}$ ) in humus samples of beech and radiata pine stand at Granville

BEECH	CONTROL SAMPLES (FRESH)	INCUBATED SAMPLES (CORE)	NETT CHANGE IN MEAN CONC. (CORE-FRESH)
1 JAN 77	-	-	
5 MAR 77	63.1( 6.1)	-	
2 APR 77	60.3(13.1)	106.2(21.6)	+ 43.1
4 JUN 77	27.8( 7.8)	20.8( 6.4)	- 39.5
5 AUG 77	19.3( 5.0)	38.8(23.4)	+ 11.0
6 OCT 77	25.3( 2.4)	129.9(21.5)	+ 110.6
6 JAN 78	11.0( 1.9)	17.7( 8.7)	- 7.6
6 APR 78	22.6( 6.4)	17.3(12.8)	+ 6.3
6 JUL 78	13.3( 2.5)	15.7( 2.7)	- 6.9
5 OCT 78	28.0( 9.1)	22.6( 4.6)	+ 9.3
1 DEC 78	27.7(15.7)	25.8( 9.9)	- 2.2

#### RADIATA

1 JAN 77	-	-	
5 MAR 77	85.4(27.9)	-	
2 APR 77	82.7(11.6)	124.3(33.3)	+ 38.9
4 JUN 77	31.9(14.2)	36.5( 6.1)	- 46.2
5 AUG 77	22.6( 3.8)	36.2(11.1)	+ 4.3
6 OCT 77	46.9(16.4)	164.2(22.6)	+ 141.6
6 JAN 78	36.1(12.3)	62.7(56.6)	+ 15.8
6 APR 78	29.9(15.6)	25.4( 8.2)	- 10.7
6 JUL 78	35.5(29.1)	27.0(10.5)	- 2.9
5 OCT 78	27.8( 5.0)	31.8( 7.6)	- 3.7
1 DEC 78	34.4(15.4)	34.1(13.8)	+ 6.3

TABLE G.8 Ammonium-N concentrations ( $\mu\text{g/g}$ ) in top-soil samples of beech and radiata pine stand at Granville

BEECH	CONTROL SAMPLES (FRESH)	INCUBATED SAMPLES (CORE)	NETT CHANGE IN MEAN CONC. (CORE-FRESH)
1 JAN 77	11.0(3.8)		
5 MAR 77	1.5(0.4)	7.2(10.3)	- 3.8
2 APR 77	13.3(5.0)	8.5( 1.7)	+ 7.0
4 JUN 77	8.3(0.7)	7.9( 0.4)	- 5.4
5 AUG 77	10.0(1.1)	10.2( 1.9)	+ 1.9
6 OCT 77	9.4(1.3)	21.9( 3.8)	+ 11.9
6 JAN 78	4.2(1.0)	8.0( 5.8)	- 1.4
6 APR 78	5.3(0.7)	3.3( 1.6)	- 0.9
6 JUL 78	3.2(0.7)	5.5( 0.7)	- 0.2
5 OCT 78	4.6(0.9)	6.9( 2.8)	+ 3.7
1 DEC 78	10.2(2.6)	13.5( 1.6)	+ 8.9
RADIATA			
1 JAN 77	12.2(7.6)		
5 MAR 77	1.4(0.5)	4.2( 2.2)	- 8.0
2 APR 77	10.8(1.5)	8.2( 0.8)	+ 6.8
4 JUN 77	7.6(2.1)	6.8( 0.9)	- 4.0
5 AUG 77	8.7(0.4)	11.0( 3.5)	+ 3.4
6 OCT 77	11.3(2.0)	17.4( 2.3)	+ 8.7
6 JAN 78	6.3(2.0)	5.7( 1.3)	- 5.6
6 APR 78	6.7(3.8)	2.7( 0.9)	- 3.6
6 JUL 78	3.9(0.6)	3.4( 0.7)	- 3.3
5 OCT 78	7.0(1.6)	7.1( 3.3)	+ 3.2
1 DEC 78	9.2(1.9)	9.4( 1.5)	+ 2.4

TABLE G.9 Moisture contents (% D.W.) of humus samples  
of beech and radiata pine stand at Granville

BEECH	CONTROL SAMPLES (FRESH)	INCUBATED SAMPLES (CORE)	NETT CHANGE IN MEAN MC (CORE-FRESH)
1 JAN 77	-	-	
5 MAR 77	209(29)	-	
2 APR 77	248(48)	285(53)	+ 76
4 JUN 77	290(65)	304(83)	+ 56
5 AUG 77	241(42)	296(54)	+ 6
6 OCT 77	346(30)	300(53)	+ 59
6 JAN 78	359(39)	319(48)	- 27
6 APR 78	214(27)	323(34)	- 36
6 JUL 78	350(41)	337(35)	+123
5 OCT 78	258(44)	327(15)	- 23
1 DEC 78	282(48)	283(38)	+ 25
<hr/> RADIATA <hr/>			
1 JAN 77	-	-	
5 MAR 77	210(40)	-	
2 APR 77	313(33)	285(62)	+ 75
4 JUN 77	245(78)	330(21)	+ 17
5 AUG 77	281(25)	247(29)	+ 2
6 OCT 77	312(32)	319(25)	+ 38
6 JAN 78	248(30)	284(25)	- 28
6 APR 78	266(37)	264(39)	+ 16
6 JUL 78	303(44)	336(41)	+ 70
5 OCT 78	264(23)	265(35)	- 38
1 DEC 78	228(53)	252(16)	- 12

TABLE G.10 Moisture contents (% D.W.) of top-soil samples of beech and radiata pine stand at Granville

BEECH	CONTROL SAMPLES (FRESH)	INCUBATED SAMPLES (CORE)	NETT CHANGE IN MEAN MC (CORE-FRESH)
1 JAN 77	47( 7)	-	
5 MAR 77	52( 6)	59( 8)	+ 12
2 APR 77	59( 8)	59( 8)	+ 7
4 JUN 77	48( 6)	56( 5)	- 3
5 AUG 77	62( 5)	59( 5)	+ 11
6 OCT 77	51( 6)	65(10)	+ 3
6 JAN 78	55( 8)	59( 8)	+ 8
6 APR 78	39( 6)	65( 8)	+ 10
6 JUL 78	56( 7)	59( 8)	+ 20
5 OCT 78	53( 6)	64( 5)	+ 8
1 DEC 78	57( 4)	62( 8)	+ 9

#### RADIATA

1 JAN 77	37( 4)	-	
5 MAR 77	43( 8)	38( 4)	+ 1
2 APR 77	46( 6)	46( 6)	+ 3
4 JUN 77	38( 8)	45( 4)	- 1
5 AUG 77	43( 8)	45( 8)	+ 7
6 OCT 77	37( 6)	48( 7)	+ 5
6 JAN 78	36( 9)	37( 7)	0
6 APR 78	35( 9)	40( 9)	+ 4
6 JUL 78	40( 7)	51( 7)	+ 16
5 OCT 78	38( 6)	42( 7)	+ 2
1 DEC 78	39( 9)	41( 6)	+ 3



TABLE G.11 Ammonium-N and nitrate-N concentration, and moisture content of soils incubated with water extracts of beech and radiata pine litter, and glucose and catechin solution

1. Ammonium-N Concentration ( $\mu\text{g/g}$ )

Solution	HOM Soil	LOM Soil
Control	156.1(3.2)	91.6(1.4)
RAD85	135.8(1.5)	78.8(2.6)
RAD260	128.8(2.4)	69.8(1.5)
B260	136.6(2.8)	67.4(1.8)
CAT260	139.2(2.1)	66.1(2.1)
GLU200	163.2(4.4)	88.5(2.3)
GLU200+CAT260	143.1(1.4)	60.6(1.1)

2. Nitrate-N Concentration ( $\mu\text{g/g}$ )

Solution	HOM Soil	LOM Soil
Control	0.9(0.6)	<0.1
RAD85	1.0(0.2)	<0.1
RAD260	1.5(0.3)	<0.1
B260	1.2(0.7)	<0.1
CAT260	1.2(0.4)	<0.1
GLU200	1.0(0.2)	<0.1
GLU200+CAT260	0.7(0.2)	<0.1

3. Moisture Content (percentage dry weight)

Solution	HOM Soil	LOM Soil
Control	42.4(5.0)	36.2(0.9)
RAD85	41.7(1.1)	34.0(0.4)
RAD260	40.4(0.4)	34.6(0.5)
B260	40.3(0.1)	34.6(0.4)
CAT260	40.7(0.4)	33.9(0.2)
GLU200	41.2(0.4)	34.7(0.7)
GLU200+CAT260	41.4(0.2)	35.3(0.6)

TABLE G.12 Carbon dioxide evolution rates ( $\mu\text{g CO}_2/\text{hour. g soil}$ ) for soils incubated with different solutions as a function of time

Soil	Period (hour)	Control	CAT260	RAD85	B260	RAD260
HOM	0 - 6	3.5	2.9	3.2	3.4	3.8
	6 - 24	27.2	25.3	30.4	28.2	30.9
	24 - 30	26.6	23.0	30.3	29.2	54.4
	30 - 36	24.4	20.8	24.1	21.6	32.1
	36 - 52	26.1	24.4	28.0	24.9	28.9
	52 - 79	14.0	12.8	14.9	14.4	18.2
	79 - 118	8.5	8.1	8.1	8.5	9.7
	118 - 148	6.8	6.5	6.9	7.0	7.5
	148 - 195	6.0	5.6	6.1	6.1	6.6
LOM	0 - 6	1.8	1.9	2.0	2.6	2.6
	6 - 24	4.7	4.4	6.5	5.7	7.4
	24 - 30	14.6	21.1	18.6	18.6	37.2
	30 - 36	12.7	9.3	19.0	11.8	30.5
	36 - 52	10.9	9.0	11.8	10.2	21.4
	52 - 79	6.5	5.6	6.6	6.5	9.3
	79 - 118	4.6	4.1	5.2	5.0	6.4
	118 - 148	3.8	3.8	4.2	3.9	5.3
	148 - 195	3.0	2.7	2.9	3.0	4.0