The Decomposition of *Nothofagus fusca* Floral and Bark Litter

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A thesis submitted in partial fulfilment
of the requirements for the degree of

Master of Science in Microbiology

in the
University of Canterbury

By

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University of Canterbury
2001

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ABSTRACT

Nutrient cycles and budgets have been calculated for various ecosystems, but the impact of floral and bark litter decomposition on nutrient cycling has been little investigated. In this study, the characteristics and decomposition of floral and bark litter produced by *Nothofagus fusca* in the Lewis Pass Reserve, New Zealand, was investigated, using both field and laboratory studies.

Nothofagus fusca floral litter production in 1999 was 734 ± 76 kg ha^{-1}. Floral production in 2000 was estimated to be approximately 1% of this mass, the considerable difference being due to mast flowering in 1999. The decay rate constant, *k*, for floral litter in the field was 0.94 ± 0.01, and mass loss after one year was estimated to be 61%. The input of nitrogen to the litter layer in *Nothofagus fusca* floral litter was 12 ± 1 kg ha^{-1}, and it was estimated that 65% of this nitrogen was released from the floral litter in the one year. Phosphorous input to the litter layer through *Nothofagus fusca* floral litter in 1999 was 0.8 ± 0.1 kg ha^{-1}, of which 69% was released in one year. It was estimated that in 1999 nitrogen and phosphorous inputs to the litter layer through *Nothofagus fusca* floral litter were 117% and 73% respectively of that through foliar litter.

Four types of *Nothofagus fusca* were identified and further differences between bark types were confirmed by chemical analysis. Inner bark contained less nitrogen than outer bark, and was slower to decompose in microcosms, contradicting the findings of other research. Annual nitrogen and phosphorous inputs through the production of all types of *Nothofagus fusca* bark litter was estimated to be 1.0 kg ha^{-1} and 0.2 kg ha^{-1} respectively, although confidence in these values was low. Significant proportions of the nitrogen and phosphorous content in bark were water soluble. Field and laboratory experiments indicated net nitrogen immobilisation occurred in all bark litter types after one year in the field, while net release of phosphorous occurred after one year.

CHAPTER ONE: INTRODUCTION

1.1 Plant Litter Production

The decomposition of plant litter is a process vital to the development and continued functioning of terrestrial ecosystems. Whittaker and Likens (1975) estimated global annual net plant production to be 117.5 x 10^{12} kg (equivalent to 7800 kg ha^{-1}) on a dry weight basis, and the majority of this falls as litter (Bowen, 1979; Swift *et al*., 1979; Barbour, 1987). The level of productivity and litterfall can vary significantly from ecosystem to ecosystem depending upon factors such as climate and the maturity of the ecosystem (Johnson and Risser, 1974), but the ratio between productivity and litterfall, remains relatively constant (Bray and Gorham, 1964; Jordan, 1971). Plant litter is a significant sink for both energy and nutrients within an ecosystem (Ovington, 1961), and consequently the layers of litter that accumulate as ecosystems develop and reach maturity are sites of intense biogeochemical activity, providing an energy source and habitat for innumerable species of invertebrates and microorganisms.

Communities of decomposer organisms obtain energy and nutrients by processing organic plant matter into simpler inorganic substances, releasing the nutrients as excrement, exudates or upon death. This process forms the basis of nutrient cycling, by which the nutrients contained in plant litter are made available through decomposition, to eventually support further plant growth (Swift *et al*., 1979). It should be noted that rapid nutrient release from plant litter can also take place via the leaching of water soluble substances. These leachates often contain high concentrations of nitrogen and other essential elements and may be quickly decomposed and assimilated by microbes, and can account for a significant fraction of the mass and total nutrient contents of the litter (Nykvist, 1959; Gosz *et al*., 1973; Berg and Staaf, 1981).

1.2 Nutrient Cycling

The rate at which nutrient cycling occurs can generally be considered the result of the metabolic activity of the decomposer community present, influenced by soil, climate, and litter composition (Coleman and Crossley, 1996). A number of studies focusing on these factors have been carried out, often with a view to developing improved predictive capability for nutrient cycling rates. Witkamp and van der Drift (1961) concluded that edaphic conditions (mull and mor) were the most important factor, but later work (Brinson, 1977; Meentemeyer, 1978) determined climatic conditions, such as evapotranspiration, were the best predictors for decay rates. The effect of the chemical composition of the litter, termed "litter quality", has also been the subject of many papers. Lignin and phosphorous content (Schlesinger and Hasey, 1981), initial lignin to initial nitrogen ratios (Melillo *et al*., 1982) and the content of water soluble and acid soluble or insoluble substances (McClaugherty *et al*., 1985) have been found to be significant factors in predicting decay rates, depending upon litter type.

In litter with high carbon to nutrient ratios (low quality), the scarce supply of nutrients can limit microbial growth, and hence the rate of microbially mediated decomposition, whereas in litter types with low C:nutrient ratios (high quality), decomposition is generally faster, as greater amounts of nutrients such as nitrogen and phosphorous are available to support microbial growth (Swift *et al*., 1979). As carbon in a low quality litter is mineralised, C:nutrient ratios decrease and litter quality improves (Heal *et al*., 1982). The decomposition of low quality litters often involves the import of nutrients into the litter, again decreasing C:nutrient ratios and improving litter quality (Berg and Staaf, 1981). Conversely, mineralised nutrients are released immediately during the decomposition of high quality litter, since microbial growth is not inhibited by nutrient supply (Gosz *et al*., 1973; Swift *et al*., 1979). The organic forms of nutrients may also be an important factor in determining nutrient availability in litter, greater, in some cases, than C:nutrient ratios (Wardle and Greenfield, 1991).

Another factor potentially capable of influencing litter decomposition is the presence or absence of other litter types (Blair *et al*., 1990; Williams and Alexander, 1991; Wardle *et al*., 1997; Finzi and Canham, 1998). Research into the effects of mixing litter types has tended to focus on combinations of high and low quality litters (Blair *et al*., 1990; Scowcroft, 1997; Finzi and Canham, 1998). Expectations of non-additive decomposition were based on nutrient release from high quality litter augmenting the nutrient content of low quality litters, increasing the overall decay rate, or the release of inhibitory compounds from low quality litter slowing overall decay rates. (Blair *et al*., 1990; Finzi and Canham, 1998). The results of such studies have been varied. Some investigations found mixing could result in significant synergistic effects in terms of weight loss and nutrient release rates (Willams and Alexander, 1991; Wardle *et al*., 1997). However, only subtle effects on nitrogen mineralisation rates were detected by Finzi and Canham (1998) and solely additive effects on weight loss rates have been determined in other studies (Blair *et al*., 1990; Scowcroft, 1997). The common denominator between these studies was the use of litter from different species – data on the results of mixing different litter types from the same species has not been produced.

Despite the lack of consensus regarding the factors that control plant litter decomposition, the importance of these phenomena to nutrient cycling is well understood. Global calculations of nitrogen reservoirs indicate $1.9 – 3.3 \times 10^3$ Tg of nitrogen is resident in plant litter (Söderlund and Svensson, 1976). Moreover, the flux of nitrogen between plant biomass, decomposer organisms and soil represents 95% of total global nitrogen cycling, overwhelming greater than atmospheric or water mediated inputs and outputs of nitrogen to the majority of ecosystems (Rosswall, 1976). Biogeochemical cycling also accounts for a significant proportion of terrestrial phosphorous transfers - approximately 133 Tg of phosphorus may be released globally from decomposing plant material on an annual basis, while the total inventory of phosphorous in plant biomass is estimated to be 1800 Tg (Pierrou, 1976). Although research has indicated that in

some ecosystems virtually all phosphorous cycling occurs through litter breakdown (Pare and Bernier, 1989), phosphorous cycling is generally considered open, as inputs and outputs to an ecosystem are often as important as internal cycling (Attiwill and Adams, 1993; Newman, 1995). Other phenomena, such as throughfall and stemflow (Parker, 1983), can provide alternate pathways for nutrients, particularly cations, to enter soil without the need for litter breakdown, and internal nutrient distribution strategies employed by various plant species can reduce nutrients flux through litter (Vitousek, 1981). Additionally, developing terrestrial ecosystems tend to display net exports of nutrients, but as successional changes lead to a mature "climax" ecosystem, nutrient loss generally decreases and a steady state of external input and output balancing is achieved (Odum, 1969; Reiners, 1981). Despite these factors, however, the breakdown of plant litter and the release of essential elements, mediated by a decomposer community, is a process vital to all terrestrial ecosystems (Swift *et al*., 1979).

1.3 Applications of Litter Production and Nutrient Cycling Studies

Understanding the dynamics of nutrient flux in an ecosystem is valuable for several reasons. Generating data on the levels of litter production and nutrient cycling in pristine ecosystems allows the natural patterns of nutrient transfers to be determined, enabling theories into the impact of nutrient constraints on ecosystem development to be formulated (Hedin *et al*., 1995). The data can also be used for biomonitoring – detecting changes to nutrient dynamics in an ecosystem in response to a disturbance, and quantifying the effects (Turner *et al*., 1976). Examples of biomonitoring include detailed studies into the effects of invasion by a foreign species on nitrogen cycling (Vitousek and Walker, 1989; Scowcroft, 1997), as well as anthropogenic influences including fertilisers, air pollution and urban spread (Pang and Kolenko, 1986; Findlay and Jones, 1990;

McDonnell and Pickett, 1990). It may also be possible to detect the effects of climate change and changes to biodiversity in an ecosystem in this way. Nutrient cycling studies have also been recognised as crucial for the development of sustainable land management practices, particularly in agriculture (Coleman, 1989) and forestry (Jorgensen *et al*., 1975). By calculating the effects of plant material removal upon both nutrient reservoirs and nutrient cycling in an ecosystem, the impacts of harvesting on the ecosystem functions of a site can be determined, and the viability of land management practices assessed (Miller, 1963; Weetman and Webber, 1972; Levett *et al*., 1985). The physical effects of plant material must also be considered, such as the role played by coarse woody debris as a habitat and nutrient sink in many forests (Harmon *et al*., 1986; Harmon and Hua, 1991; Zimmerman *et al*., 1995).

1.4 Inputs and Decomposition of Floral litter

Numerous studies on nutrient cycling in forests have been undertaken (Attiwill and Adams, 1993), examining litter production, litter decomposition and rates of nutrient mineralisation, as well as the factors that influence these processes, such as the studies on the Hubbard Brook ecosystem (Gosz *et al*., 1972; Gosz *et al*., 1973; Whittaker *et al*., 1974). However, it has been found that litter sampling can provide false representations of actual litter production due to the timing of litter collection and the seasonality of litter production, causing underestimates of the significance of certain litter types to nutrient cycling, such as floral material (Ovington, 1963; Stocker *et al*., 1995). Although the presence of flowers in litter may be noted, masses of floral material are rarely considered alone, instead they are usually combined with other litter types (Rochow, 1974; Kunkel-Westphal and Kunkel, 1979; Sweetapple and Fraser, 1992) or not reported at all (Johnson and Risser, 1974).

Consequently, comparatively little data on floral litter production, nutrient content and decomposition has been generated, despite the few studies that have

been performed concluding nutrient concentrations in floral litter can be markedly higher than in other litter types, with potentially significant implications for nutrient cycling and ecosystem function (Woodwell *et al*., 1975, Pregitzer and Burton, 1991; Walker, 1994). The importance of understanding nutrient flux through floral litter is complicated by mast seeding events, in which plants produce greater quantities of floral material than in other years. This phenomenon occurs in semi-regular cycles, the interval between mast events dependent upon species and environment, and undoubtedly increases the significance of floral litter decomposition to nutrient flux in the ecosystem (Webb and Kelly, 1993; Alley *et al*., 1998).

1.5 Inputs and Decomposition of Bark Litter

Another type of litter produced in forest ecosystems that has been the subject of little investigation is bark. Bark can be divided into inner and outer layers, based on differences in tissue characteristics and nutrient contents, and is often defined as all tissue exterior to the vascular cambium (Martin and Crist, 1970; Woodwell *et al*., 1975, Sandved, 1993), although vascular cambium falls with bark in some species (Zimmermann and Brown, 1971). Approximately 15% by volume of bole material is bark, and the same percentage is expected in the majority of coarse woody debris inputs (Käärik, 1974; Keays, 1975), although this proportion is influenced by both species and diameter of the coarse woody debris (Wardle, 1984; Brown *et al*., 1996).

Natural disturbances such as windthrow (Zimmerman *et al*., 1995; Allen *et al*., 1997) or pathogen activity (Hosking and Kershaw, 1985) can significantly augment production and forest floor volumes of coarse woody debris, increasing bark input. Bark can also fall from trees as a result of normal growth (Harmon *et al*., 1986; Zimmermann and Brown, 1971), but there are no clear data on rates of bark input to ecosystems by either means. Nutrient concentrations in bark have

been reported in several studies (Miller, 1963; Woodwell *et al*., 1975; Allen *et al*., 1997), indicating that bark litter can contain significant quantities of nutrients, but decay resistant suberose tissue and recalcitrant substances such as lignin and phenolic derivatives are also commonly found in bark (Zimmermann and Brown, 1971; Käärik, 1974; Olsson, 1978).

The general consensus is that bark decay is slow, taking years to decades for complete decomposition (Fogel and Cromack, 1977; Brown *et al*., 1996; Scowcroft, 1997), although inner bark decay rates have been found to be significantly more rapid than outer (Olsson, 1978; Scholwalter, 1992). Other studies have identified the retardation of decay rates of wood by bark, due to inhibition of microbial colonisation and prevention of water movement (Harmon *et al*., 1986; Rayner and Boddy, 1988; Krankina *et al*., 1999) although this has not always been found to be the case (Grier, 1978). Consequently, the presence and condition of bark on fallen logs and snags is often used to assess the likely extent of wood decomposition (Graham and Cromack, 1982; Bingham and Sawyer, 1988; Stewart and Burrows, 1994).

The importance of understanding bark decomposition has applied value when the accumulation of bark litter as a by-product of the logging industry is considered. In 1973 it was estimated over 200,000 metrics tons of bark litter was produced annually in New Zealand (Harris and Nash, 1973; Prince, 1973). The often localised accumulation of bark can have severe effects resulting from the leaching of water soluble substances, huge biological oxygen demand and the threat presented as a fire hazard (McKelvey, 1973; Olsson, 1978). Bark has been used as a source of energy and chemicals, or as a fertiliser with varying degrees of success (Bollen and Glennie, 1963; Finney and Sotter, 1975; Troncino, 1975), but the burning or accumulation of a pool of chemically leached bark can potentially increase environmental hazards further. It has been recommended that due to the variations in bark characteristics, both within and between species, this material should be the subject of detailed studies to find effective uses that are both commercially viable and ecologically beneficial (Harris, 1973; Porter, 1973).

1.6 *Nothofagus fusca* ecology

It was the aim of this thesis to investigate the issues of nutrient content and release from floral and bark litter so as to improve the knowledge base on ecosystem nutrient cycling. This has been achieved by examining the composition of *Nothofagus fusca* (Red Beech) litter, focusing on the physical, chemical and decomposition characteristics of the bark and floral material under various conditions. *Nothofagus fusca* (Fagaceae) is the tallest of the Southern Beech species found in New Zealand, and is distributed in lowland or montane forests between in the latitude range 37^{o} 30' to 46^{o} S. The species is monoecious, flowering from September to December, with infloresences approximately 4mm long. The bark of *Nothofagus fusca* is readily identifiable due to distinctive colouration in young trees and thickness and texture in older specimens (Cockayne and Turner, 1958; Wardle, 1984; Metcalf, 1987).

Litter collections and field decomposition studies were carried out within old-growth *Nothofagus fusca – Nothofagus menziesii* forested areas of the Lewis Pass Reserve (Stewart and Burrows, 1994). The findings of this study will contribute to the understanding of *Nothofagus fusca* ecology and nutrient cycling dynamics.

The objectives of this thesis were:

- Estimate the annual production of floral material by *Nothofagus fusca*, and calculate the nitrogen and phosphorous transfers involved in this production.

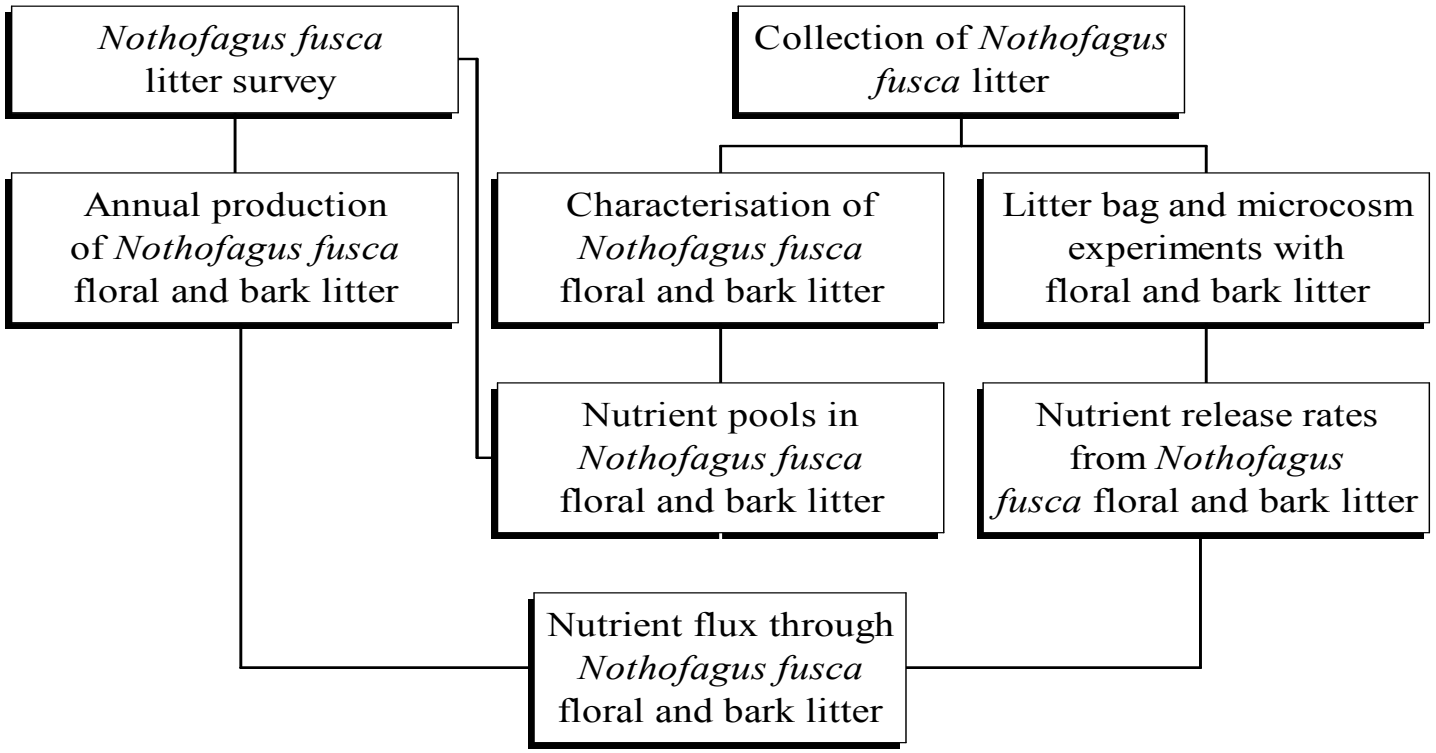
- Characterise the different types of bark produced by *Nothofagus fusca* in terms of nitrogen and phosphorous content and physical properties.

- Determine the rates of mass loss and mineralisation of nitrogen and phosphorous from *Nothofagus fusca* floral and bark material, using both microcosm and litterbag based experiments.

- Estimate the flux of nutrients through *Nothofagus fusca* floral and bark litter on an annual basis.

- Determine the effects of litter mixing upon decomposition rates of *Nothofagus fusca* bark and flowers using microcosm based experiments.

Figure 1.1: Basic experimental scheme



CHAPTER TWO: METHODS & MATERIALS

2.1 Surveys of *Nothofagus fusca* litter on the forest floor

2.1.1 Litter Fractions

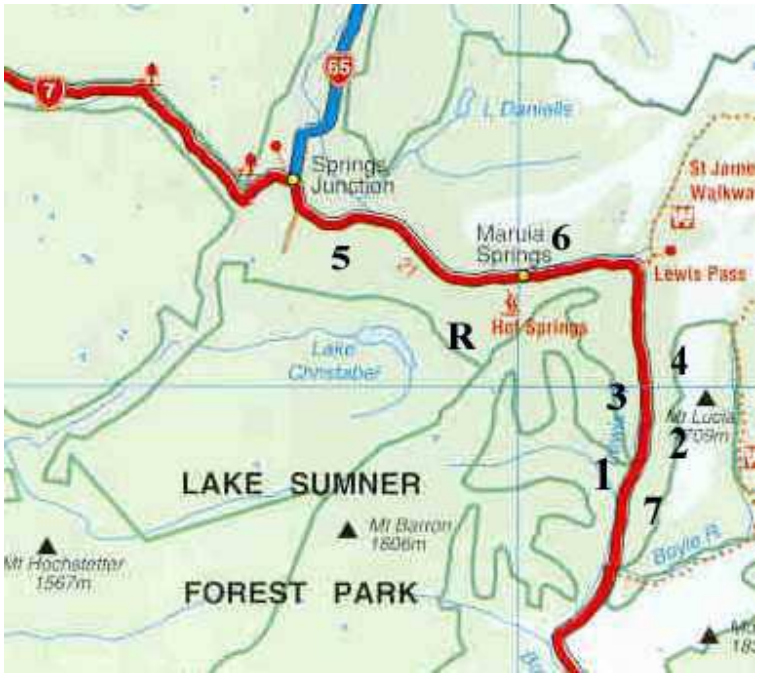
Floral production in *Nothofagus fusca* (Red Beech) during the 1999 flowering season was particularly high due to a mast seeding event. *Nothofagus fusca* litter, including floral material, was collected during November 1999 from seven sites in the Lewis Pass Reserve on State Highway 7, New Zealand (Figure 2.1). Sampling sites were chosen at random within the range of the *Nothofagus fusca*, although areas adjacent to frequently used locations, such as rest areas, were avoided. The elevation of the sites ranged approximately from 500 to 700m a.s.l., within the altitude range for *Nothofagus fusca* described by Wardle (1984). Four quadrats, 300mm × 300mm, were randomly placed on the forest floor at the chosen sites, and plant material from the upper litter layers was collected. This was repeated four times for each site. Quadrat placement was biased to some extent, as the sampling of litter on fallen logs and large pieces of coarse woody debris was avoided. This was due to the lack of uniformity in litter coverage and depth over these materials as compared to the forest floor. The litter samples were taken to a depth of 20-30mm into the litter, to the start of the fermentation layer. Below this depth the forms of litter became less recognisable and amorphous black-brown material became more common.

The collected material was air dried for two weeks, then sorted into flowers, leaves, twigs and fragments of coarse woody debris, including bark. Living material, such as moss, was discarded. No difficulty was encountered in distinguishing *Nothofagus fusca* flowers and leaves from those of other species, but accurately identifying the species of twigs and coarse woody debris fragments

proved more challenging. This problem was satisfactorily remedied by careful examination of the bark coloration of the twigs and the texture of the bark and wood fibres in coarse woody debris, although a small fraction of coarse woody debris fragments remained unidentifiable. The litter fractions from each site were oven dried and weighed, allowing each litter fraction to be expressed as a percentage of the total litter collected from individual samplings, entire sites and across all sites.

Further sampling at four of the original seven sites took place in May 2000, using the same procedure. The May sampling was performed to determine if any floral litter was still present in the litter layer, and to detect any differences in litter production that may have resulted from changes to resource allocation strategies of the *Nothofagus fusca* outside of the flowering season (Bazzaz *et al.*, 1987).

Figure 2.1: Map of Lewis Pass Reserve indicating where litter samples were collected and field work was performed.



Note: Numbers indicate approximate location and reference number of each site sampled, R indicates approximate location of Rough Creek.

2.1.2 Coarse Woody Debris Quantification

To estimate the volume of *Nothofagus fusca* coarse woody debris (CWD) in the form of fallen logs and branches on the forest floor, a line intersect method was used (van Wagner, 1968). Two $4m^2$ quadrats were laid out randomly on the forest floor at sites 2, 3, 4, 5 and 6 (refer Figure 2.1) and a 2.2m line placed diagonally across each quadrat so that both ends of the line rested exactly on the boundary lines of the quadrat. Each quadrat was sampled twice, with the second line transect placed at approximately 90^o to the first. This was done to account for any bias in the orientation of the CWD on the forest floor. The diameters of all sizeable (>50mm) pieces of CWD identifiable as *Nothofagus fusca* material intersected by the line were recorded, if eligible as determined by the selection criteria detailed by van Wagner (1968). These data were used to determine the volume of CWD on the forest floor as follows:

$$V = \frac{\pi^2 \Sigma d^2}{8L} \qquad (2.1)$$

where

V is the volume of wood per unit area in m^3

d is the diameter of each intersected piece of CWD in m

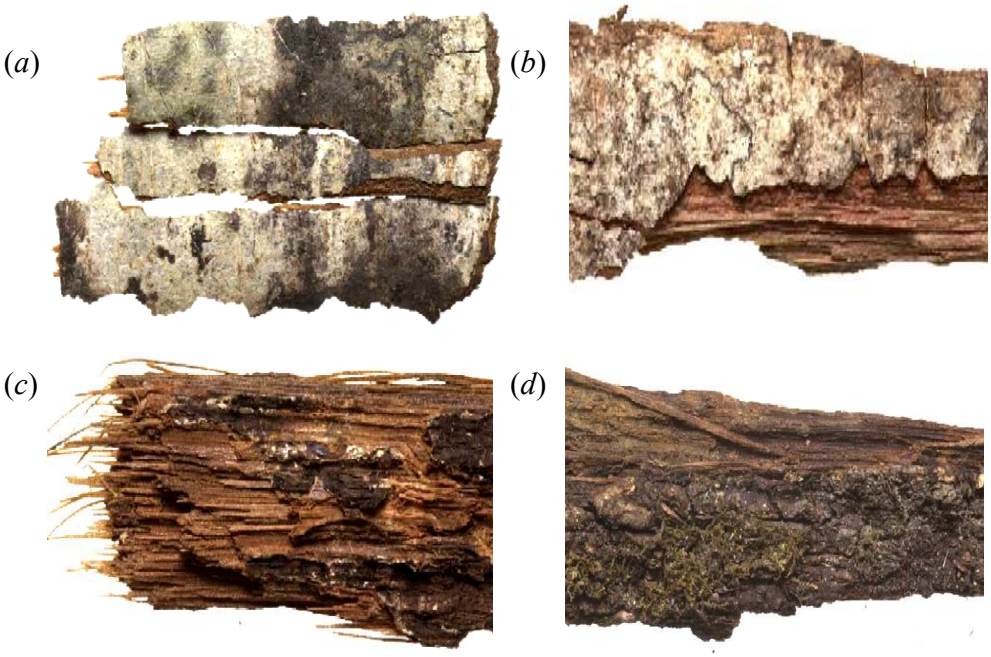
L is the length of the transect line in m

The figure for volume was then compared to that given by Stewart and Burrows (1994) for Rough Creek, located within the study area (refer Figure 2.2). Using the density values calculated for *Nothofagus fusca* CWD (Stewart and Burrows, 1994), the biomass of CWD on the forest floor was then estimated. The sites were monitored over time for changes to CWD volumes.

2.1.3 Physical Characterisation of Nothofagus fusca *bark types*

Field observations of *Nothofagus fusca* indicated that bark changes substantially depending upon the age of the tree and location of the bark on the tree. A literature search suggested this may also be reflected in nutrient concentrations (Miller, 1963; Martin and Crist, 1970; Zimmerman and Brown, 1971; Olsson, 1978; Attiwill, 1979; Sandved, 1993). Consequently, four distinct types of *Nothofagus fusca* bark were identified: branch bark (BrB), young stem bark (YSB), old stem inner bark (OSIB) and old stem outer bark (OSOB). These were dealt with as separate litter types for the purpose of the experiments described subsequently.

Figure 2.2: Bark types of identified from *Nothofagus fusca* (*a*) Branch Bark, (*b*) Young Stem Bark, (*c*) Old Stem Inner Bark and (*d*) Old Stem Outer Bark.



2.2 Characterisation of *Nothofagus fusca* litter

To increase confidence in results and minimise the chance of undetected experimental error, triplicates were used in all of the following experiments. All *Nothofagus fusca* litter was examined for leaching or decomposition prior to use to ensure the material used was fresh.

2.2.1 Oven dry and ash weights

Samples of *Nothofagus fusca* litter were air dried for four days, and sub-samples placed into pre-weighed crucibles and weighed on an analytical balance, giving an air dry (AD) weight. These were then heated to 105^{o}C for 24 hours, cooled to room temperature in a desiccator, then reweighed to produce moisture free, oven dry (OD) weights (Gardner, 1965). The ash fraction of the litter types was determined by heating the samples to 570^{o}C for 4 hours in a muffle furnace, incinerating the organic materials of the litter (Chapman and Pratt, 1961). The resulting ash was cooled in a desiccator, then weighed. The ash fraction resulting from incineration at 480^{o}C for 4 hours was also determined for several litter types, as this was required from later experimental work (refer section *2.2.3*).

2.2.2 Nitrogen Content

The total nitrogen content of the litter types was determined using the Kjeldahl method, adapted from Bremner (1965b), except for *Nothofagus fusca* CWD, as values given by Stewart and Burrows (1994) were used instead. Known amounts of ground (<2mm) AD samples were digested using mercury and copper titanium catalyst tablets, and concentrated H_2SO_4. Upon completion of digestion, approximately 2 hours later, the flasks were cooled. The flasks were then steam distilled with a solution of 10M NaOH and thiosulphate, and the liberated ammonium collected in boric acid indicator solution. Solutions were then titrated

against 0.025M H_2SO_4, of which 1ml was required to reach the end point of the titrate with 70μg of ammonium in solution, indicated by colour change from aqua to faint pink. Using the volume of 0.025M H_2SO_4 required to reach end point, the amount of ammonium in each distillate was calculated according to Equation *2.2*.

$$N = \frac{(T - B) \times 70}{1000} \qquad (2.2)$$

where

N is the mass of NH_3 liberated from the sample in mg

T is the volume of 0.025M H_2SO_4 required to reach end point

B is the volume of 0.025M H_2SO_4 required to reach end point for a blank

This allowed the calculation of the nitrogen concentration in the various *Nothofagus fusca* litter types, by relating the total nitrogen to the weight of sample used as shown:

$$\%N = \frac{N \times 100}{m} \qquad (2.3)$$

where

%N is the percentage of nitrogen in the sample type

m is the mass of oven dried sample digested in mg

The effect of oven drying on dried *Nothofagus fusca* litter nitrogen content was also determined, as Bremner (1965a) indicated nitrogen content may decrease. After the calculation of the nitrogen concentration of the *Nothofagus fusca* litter types, the distribution of the nitrogen was determined. Hydrolysates were prepared by refluxing known amounts of ground air dry litter, ranging from 1 to 4 grams, containing approximately 10μg of nitrogen, with 6N HCl for 24 hours (Bremner, 1965c). The flasks containing the sample and acid were immersed in oil baths, and heated to 110^0C. The hydrolysate, once recovered and neutralised, was analysed for the presence of ammoniacal nitrogen, hexosamine nitrogen and α-amino nitrogen, following the method described in Bremner (1965c). Total soluble nitrogen content of the hydrolysate was also determined.

The insoluble residue produced during the hydrolysis of the litter was collected, thoroughly washed with double deionised water (DDW), oven dried, weighed and analysed for nitrogen content.

2.2.3 Phosphorous Content

The preparation of *Nothofagus fusca* litter samples, including CWD at various decay stages, for determination of phosphorus content was adapted from a method used for the detection of several mineral constituents (Nicholson, 1984). A known quantity of litter was placed in a crucible and ashed for four hours at 480^0C. The resulting ash was slightly moistened with DDW, then treated with 5ml of a 1:1 solution of DDW and concentrated HCl. The crucible was placed on a boiling water bath for 5 minutes, catalysing ash digestion. The digest solution was then filtered through Whatman 41 filter paper into a 50ml volumetric flask, using DDW heated to approximately 75^oC to rinse the crucible and filter paper. After cooling, the flask was made up to volume with DDW. The phosphorous content of the digest solution was determined by the method described by Kitson and Mellon (1944). A stock phosphate solution (500 ppm phosphorous) was prepared, and used to produce several solutions of known phosphate concentration. These were treated with nitric-vanadomolybdate reagent and diluted with DDW, and the light absorbency (at a wavelength of 465nm) of the solutions was recorded, enabling the construction of a calibration curve. This was then used to calculate the phosphorous content of experimental litter solutions from absorbency readings, again at 465nm wavelength, using the following equation:

$$\%P = \frac{P^{PPM} \times 25 \times 50 \times 100}{10 \times m \times 1000000} \qquad (2.4)$$

where

$\%P$ is the percentage of phosphorous in the sample

P^{PPM} is the ppm of phosphorous in the vanadomolybdophosphate solution

m is the OD mass of the sample

2.2.4 Total Oxidisable Organic Carbon

To allow the calculation of C:N ratios and C:P ratios of the *Nothofagus fusca* litter types, values for the total oxidisable organic carbon content were determined using the Walkley-Black method as described by Hesse (1971), with the ammonium iron(II) sulphate solution made to a concentration of 0.5mol l^{-1}. Preliminary experiments using cellulose, with a known organic carbon content of 44.4% (Krässig *et al*., 1996), were performed to calculate a correction factor (*f*) to account for incomplete organic carbon recovery. *f* was determined to be 1.32 ± 0.01, very similar to the conventional factor of 1.33 (Hesse, 1971), and was consequently assumed to be accurate. Approximately 50mg of ground (<2mm) AD *Nothofagus fusca* litter was used, with triplicates performed for all litter types. The following equation was used to calculate oxidisable carbon content:

$$\%C = \frac{(B - T) \times 0.003 \times 100 \times M \times f}{m} \qquad (2.5)$$

where

%C is the corrected percentage of oxidisable organic carbon

B is the blank titre

T is the experimental titre

M is the molarity of the ammonium iron(II) sulphate solution

f is the correction factor of 1.32

m is the OD mass of the sample

Using these data, as well as the nitrogen and phosphorous content data, the C:N and C:P ratios of the different litter types was calculated.

2.2.5 Water Soluble Substances

Weighed amounts, between 500 and 750mg, of AD *Nothofagus fusca* floral and bark litter were placed into pre-weighed glass tubes, and to each, approximately 20ml of DDW was added. To prevent microbial growth in the tubes during leaching, 0.2ml of chloroform were also added to each tube. The tubes were then tightly sealed with rubber stoppers to prevent chloroform evaporation. After 48 hours, the leachates were removed from the tubes, filtered through GF/A paper, and set aside. Any solid material left on the filter paper was washed back into the tube, which was then refilled to the original volume with DDW and resealed after chloroform addition. Subsequently, after every 48 hours, the leachates were drawn off and the tubes refilled, until ten days had passed and five extractions from each tube had been taken. The litter sample was then oven dried, allowing mass loss due to leaching to be calculated. Changes to the nitrogen and phosphorous concentration of the leached material was determined using the methods described in sections *2.2.2* and *2.2.3* respectively. Concurrently, the potential for microbial growth in the leachates extracted from the first two days of leaching was examined. The pH values of the leachates produced from the initial two days of leaching were recorded using a Digi-Sense pH meter model #5985-20, which was used for all subsequent pH determinations in this study. The leachates then were placed in a 43^{o}C oven for 12 hours to evaporate any chloroform still present. The leachate was divided into two equal portions, which were both inoculated with two drops of a soil suspension, made from soil obtained from the Ilam campus grounds, produced using the method described in section *2.3.1*. From each pair, one flask was treated with the addition of 0.5ml chloroform to serve as a control, then both were sealed. The flasks were then put on a shaker, oscillating approximately 100 times per minute, for ten days and monitored for signs of microbial growth, indicated by changes to the turbidity, smell and pH of the leachate.

2.3 Studies of *Nothofagus fusca* floral litter decomposition

The decomposition and release of nutrients from *Nothofagus fusca* floral litter was studied under a range of conditions, using both laboratory microcosms and litterbags buried in the Maruia Springs region. All floral litter used in decomposition experiments was examined for "freshness", to ensure material that had already undergone leaching or decomposition prior to collection was not used.

2.3.1 Rates of mass loss at various temperatures

Microcosms were established to investigate the rates of weight loss of *Nothofagus fusca* floral litter due to microbial activity. To construct these microcosms, 500 ± 5mg of whole AD litter were placed in glass tubes, moistened with 1ml of DDW and inoculated with 2 drops (approximately 60µl) of a soil suspension. This soil suspension, and all others, was made by mixing 4g of soil in 80ml of tap water, then allowing it to settle after vigorous shaking for five minutes. Clear, particle free, liquid was drawn from the solution and subsequently used to inoculate the microcosms. Unless stated, the soil was obtained from the Ilam campus grounds of the University of Canterbury, and will be referred to as Ilam soil. The method was based on that described by Greenfield (1993).

Microcosms were set at four different temperatures: 3^{o}C, 10^{o}C, 17^{o}C and 25^{o}C. For each combination, 3 replicate microcosms were established to run simultaneously. Two control microcosms were also set up for each combination, the first lacking the 1ml of DDW, the second without DDW and soil inoculum. The microcosms were capped with polythene, to allow gas diffusion and minimise water loss. The sets of microcosms were left to run for 40, 100 or 200 days. At regular intervals the microcosms were opened and aerated to prevent CO_2 build

up. Moisture levels in the microcosms were monitored and maintained by regularly weighing the tubes, adding DDW as required. To ensure accurate maintenance of temperature in the various incubators used, temperature recordings were taken every three days, and thermostat adjustments made if necessary. After the appropriate time interval, the mass loss was determined for each microcosm by oven drying the tubes at 105°C for 24 hours, cooling the tubes in a desiccator, then re-weighing until a constant weight was achieved. These data were then used to calculate the percentage of mass loss as shown below and to generate decay rate constants, *k*, (Olson, 1963).

$$\%M^{Loss} = \left(\frac{M^{Initial} - M^{Actual}}{M^{Initial}} \right) \times 100 \qquad (2.6)$$

where

$\%M^{Loss}$ is the percentage mass loss on an OD, ash-free basis

M^{Actual} is the OD, ash free mass after incubation

$M^{Initial}$ is the expected initial OD, ash free mass

Figure 2.3: Microcosm containing *Nothofagus fusca* floral litter prior to inoculation and incubation.

2.3.2 Nitrogen mineralisation at various temperatures

The following protocol was based on the techniques described by Bremner (1965d) for determining mineral nitrogen availability in soils. Known amounts of ground (<2mm) AD litter, ranging from 495 to 505 mg, were weighed into flasks containing approximately five grams of ignited sand, used to form a matrix for the decomposition of the plant material. The contents of the flasks were mixed, moistened with a volume of DDW approximately equal to 500% of the litter mass, or 45% of the mass of both sand and litter. All flasks were inoculated with Ilam soil suspension, except for control flasks, which were not moistened or inoculated. As with the mass loss rate experiments, 3 replicate microcosms were established to run simultaneously for each combination, and duplicate control microcosms were also set up for each combination, as described in section *2.3.1*. To ensure that nitrogen mineralisation rates were not underestimated due to losses of ammonia via volatilisation, acid traps were prepared and placed in the flasks. Acid traps consisted of bijoux bottles containing 2M H_2SO_4, with nichrome wire wrapped around the necks of the bottles and bent into a small hook, then placed over the lip of the flask. The flasks were then incubated at 3^{o}C, 10^{o}C, 17^{o}C or 25^{o}C, for 40, 100 or 200 days. Preliminary experimental work determined nitrogen input to the microcosms through soil suspension addition was negligible, and was not considered a source of error. Following incubation, flasks were opened, and microbial growth in each flask was visually assessed and graded, indicating microbial biomass density as described in Table 2.1.

Table 2.1: Rankings of microbial growth in microcosms

Growth Ranking	Details of Growth
0	No visible growth.
+	Slight signs of growth – 1 or 2 visible colonies
++	Obvious growth – 3 – 10 colonies
+++	Dense growth – majority of substrate colonised
++++	Very dense growth – substrate completely colonised

Ten ml of DDW were added to each flask, and the contents stirred until the sand and litter aggregates were broken up and uniformly mixed. The pH values of the flasks were recorded, using exactly 10ml DDW to rinse any solution collected on the pH electrode back into the flasks. The flasks were treated with 30ml of 2M KCl solution, then left to stand for 24 hours. 20 ml aliquots were taken and steam distilled with MgO and Devarda's alloy as described by Bremner (1965c) to determine the content of NH_4-N and NO_3-N , if present. The ammonia absorbed by the acid traps was ascertained by washing the acid into Kjeldahl flasks, then distilling the contents with 10M NaOH. The total and net percentages of mineral nitrogen produced in the sample were calculated using the following formulas:

$$\%\, N^{Min} = \frac{(N^{Min} + N^{Nit}) \times 2.5 + N^{AT}}{N^{Total}} \times 100 \qquad (2.7)$$

and

$$\%\ net\ N^{Min} = \%N^{Min} - \%\ initial\ N^{Min} \qquad (2.8)$$

where

$\%\, N^{Min}$ is the final mineral nitrogen as a percentage of total nitrogen

N^{Min} is the mass of mineral nitrogen

N^{Nit} is the mass of nitrate

N^{AT} is the mass of ammonia in the acid traps

N^{Total} is the total mass of nitrogen present in the sample

$\%\ initial\ N^{Min}$ is the initial N^{Min} as a percentage of total nitrogen

$\%\ net\ N^{Min}$ is the net percentage of nitrogen mineralised from the sample

Since 20ml of the 50ml solution is used, a correction factor of 2.5 is also incorporated in equation *2.7*.

Figure 2.4: Microcosm containing ground *Nothofagus fusca* floral litter and ignited sand, prior to addition of acid trap.

2.3.3 Decomposition and release of nutrients from floral litter in the field

Litter bags were made from nylon mesh, which was used as the mesh size allowed unimpeded movement of moisture, but minimised import or export of solid particles bigger then 10 – 20μm. Known amounts of floral litter were weighed into bags, which were then sealed. The litter bags were buried approximately 15mm deep in litter at site 5 in the Lewis Pass Reserve (refer Figure 2.1). Seven collections were made over time, three litter bags taken in each case.

Upon retrieval, litter bags were air dried for 72 hours, and any debris attached to the outside of the bags removed. The litter bags were then opened, and the contents transferred carefully to pre-weighed crucibles. The material was oven dried at 105^{o}C for 24 hours, cooled in a desiccator, then weighed. The oven dried replicates were pooled, and approximately 400mg was removed and ground to

<2mm. Known weights of this material were then used to perform total nitrogen analyses as described in section *2.2.2*. The remaining oven dried material was transferred to pre-weighed crucibles and ashed at 480^{o}C, as required for accuracy in later phosphorous analyses. The ash was allowed to cool in a desiccator, then weighed and re-weighed to obtain a constant weight. Soil contamination of the sample was investigated by comparing ash weights to expected values, and this data was also used to calculate the percentage weight loss of the floral material on an OD, ash free basis. The ashed material was subsequently analysed for phosphorous content as described in section *2.2.3*.

Figure 2.5: Burial site of litter bags at site reference 5 in the Lewis Pass Reserve.

2.4 Studies of *Nothofagus fusca* bark litter decomposition

As with the studies of the characteristics of *Nothofagus fusca* bark, the four bark types were examined individually for rates of mass loss and nutrient release. It was not necessary to collect bark from living trees to perform experiments, as a fresh bark material of various types was available from a site where a number of *Nothofagus fusca* had been felled as a part of a track maintenance program. Inquiries revealed that the trees had been felled 3-4 days prior to bark collection, and little rain had fallen during this period, minimising leaching losses. The methods for the decomposition experiments carried out on bark litter are virtually identical to those for floral litter, and will not be described in great detail (refer sections *2.3.1 – 2.3.3*).

2.4.1 Rates of mass loss at various temperatures

Microcosms were established to investigate the rates of weight loss from *Nothofagus fusca* bark litter due to microbial activity, using 500 ± 5mg of whole AD litter in glass tubes, moistened with 1ml of DDW and soil suspension. Bark material in the microcosms was visibly moist, and were kept moist throughout incubation. Microcosms were incubated at four different temperatures: 3^{o}C, 10^{o}C, 17^{o}C and 25^{o}C. For each combination, 3 replicate microcosms were established to run simultaneously, and control microcosms were also set up for each combination. The sets of microcosms were left to run for 100 or 200 days. This data was then used to calculate the percentage of mass loss (Equation *2.6*) and to generate decay rate constants, *k*, (Olson, 1963). The size of the bark fragments placed in the tubes varied from approximately 5 – 200mg, and an even mix of fragment sizes was used in all tubes.

2.4.2 Nitrogen mineralisation at various temperatures

500 ± 5mg of ground (<2mm) AD bark litter were weighed into flasks containing approximately 5g ignited sand, and the contents of the flasks evenly mixed and moistened with a volume of DDW approximately equal to 500% of the AD litter mass. All flasks were inoculated with Ilam soil suspension, except for control flasks. Three replicate microcosms were established to run simultaneously for each combination, using acid traps to detect any volatilised nitrogen. The flasks were incubated at 3°C, 10°C, 17°C or 25°C, for 100 or 200 days. After the appropriate time interval, microbial growth levels in each flask were assessed (refer Table 2.1), the pH values of the flasks recorded, and the flasks treated with 30ml of 2M KCl solution. The flasks were left to stand for 24 hours, and 20 ml aliquots were steam distilled with MgO as described by Bremner (1965c) to determine the mineral nitrogen content. The ammonia absorbed by the acid traps was ascertained by washing the acid into Kjeldahl flasks, then distilling the contents with 10M NaOH. The total and net percentages of mineral were then calculated (Equations *2.7* and *2.8*).

2.4.3 Decomposition and release of nutrients from bark litter in the field

Known amounts (approximately 1 gram) of young stem bark litter were weighed into nylon mesh bags, which were then sealed. The litter bags were buried approximately 15mm deep in litter at site 5 in the Lewis Pass Reserve and at a site in the Ilam campus grounds, and left for a set period of time. Upon completion, the material from the litterbags was collected, oven dried at 105°C for 24 hours, cooled in a desiccator, then weighed. Samples were taken for nitrogen analysis, soil contamination determination and phosphorous analysis.

Figure 2.6: Burial site of litter bags in the Ilam Campus grounds.

2.5 Mass loss from *Nothofagus fusca* litter mixtures

Interactions between decomposing litter were studied by determining mass loss rates in microcosms containing up to four types of *Nothofagus fusca* litter. *Nothofagus fusca* flowers, young stem bark, leaves and twigs were mixed equally in microcosms in all possible combinations, with 3 replicates and controls prepared for each combination. The total weight of AD litter in each microcosm was 500 ± 5mg, and the mass of each litter type used was kept in proportion to the number of litter types present, i.e. if two litter types were present, 250 ± 2.5mg of each were weighed into the microcosm. The microcosms were moistened with a volume of DDW equal to 200% of the total AD litter mass, inoculated with Ilam soil suspension, incubated at 25°C for 200 days. The litter in microcosms was initially moist, although visible moisture levels varied somewhat depending upon the litter types in the microcosms, but all kept moist over the course of the incubation. After incubation, the tubes were processed to give OD, ash free weights as described earlier. These weights were then compared to expected weight losses, generated by summing the expected mass loss from each litter type in the microcosm (Equation *2.9*). The expected mass loss of each litter type was determined using microcosms containing only that type of litter, incubated under the identical conditions for 200 days.

$$EML^{Total} = \Sigma\,[(\%EML^{Litter\ Type} \times M^{Initial})/100] \qquad (2.9)$$

where

EML^{Total} is the total expected mass loss in a microcosm

$\%EML^{Litter\ Type}$ is the expected mass loss percentage for a litter type

$M^{Initial}$ is the calculated initial OD ash free mass of the sample.

CHAPTER THREE: RESULTS

3.1 Litter surveys

3.1.1 Litter Fractions

The oven dry masses of *Nothofagus fusca* floral, leaf, twig and CWD litter collected during the November 1999 sampling are shown in Table 3.1. The amount of CWD in the samples varied considerably, from 286.1 kg ha^{-1} to 1373.8 kg ha^{-1}, and this affected the relative percentages of the other litter types. Data from the May 2000 survey is shown in Table 3.2. Significant amounts of seed material were collected during this second survey, whereas in the November 1999 seed material was present at a negligible level (less than 0.01%). In both surveys only insignificant amounts of bark were found associated with the *Nothofagus fusca* CWD fragments, and even less bark material was found independent of wood.

Figure 3.1: Mixed *Nothofagus fusca* litter prior to sorting

Table 3.1: Mass and percentages of *Nothofagus fusca* litter collected from seven sites in the Lewis Pass area during November 1999

Site #	Flowers		Leaves		CWD		Twigs		Seed Material	
	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)
Site 1	558 ± 28	12.9 ± 1.0	1926 ± 61	44.4 ± 0.5	705 ± 35	16.3 ± 2.0	1149 ± 45	26.5 ± 0.5	0	0
Site 2	582 ± 26	13.8 ± 0.9	2040 ± 56	48.4 ± 0.4	350 ± 54	8.3 ± 2.1	1244 ± 29	29.5 ± 0.9	0	0
Site 3	814 ± 15	18.2 ± 0.7	2165 ± 68	48.4 ± 0.4	286 ± 41	6.4 ± 1.9	1207 ± 37	27.0 ± 0.4	0	0
Site 4	935 ± 34	13.3 ± 1.1	3084 ± 102	43.8 ± 0.8	940 ± 85	13.4 ± 1.4	2082 ± 51	29.6 ± 0.7	0	0
Site 5	593 ± 18	11.4 ± 0.7	2083 ± 44	40.1 ± 0.2	1374 ± 40	26.4 ± 5.1	1149 ± 34	22.1 ± 0.6	0	0
Site 6	1094 ± 27	21.8 ± 0.8	2391 ± 53	47.7 ± 0.4	484 ± 55	9.7 ± 1.3	1043 ± 68	20.8 ± 1.2	0	0
Site 7	559 ± 38	12.9 ± 1.3	1997 ± 72	45.9 ± 0.5	534 ± 28	12.3 ± 0.6	1259 ± 35	28.9 ± 0.4	0	0
Average	**734 ± 76**	**14.9 ± 1.3**	**2241 ± 140**	**45.5 ± 1.1**	**668 ± 133**	**13.3 ± 2.3**	**1305 ± 123**	**26.3 ± 1.2**	**0**	**0**

Note: Errors indicated are standard errors of the mean.

Table 3.2: Mass and percentages of *Nothofagus fusca* litter collected from four sites in the Lewis Pass area during May 2000

Site #	Flowers		Leaves		CWD		Twigs		Seed Material	
	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)	(kg ha^{-1})	(%)
Site 1	8 ± 1	0.1 ± 0.1	3273 ± 24	57.3 ± 1.1	605 ± 43	10.6 ± 2.1	1300 ± 21	22.8 ± 0.4	525 ± 16	9.2 ± 0.2
Site 2	1 ± 1	0 ± 0.1	3131 ± 16	53.1 ± 0.3	1180 ± 51	16.2 ± 1.9	1199 ± 26	20.3 ± 0.5	612 ± 13	10.4± 0.1
Site 5	3 ± 1	0.1 ± 0.1	3111 ± 42	53.3 ± 0.9	923 ± 29	15.8 ± 1.2	1265 ± 19	21.7 ± 0.2	531 ± 9	9.1 ± 0.1
Site 6	12 ± 1	0.2 ±0.1	3337 ± 37	57.8 ± 1.3	298 ± 64	9.0 ± 2.5	1364 ± 24	23.6 ± 0.2	542 ± 11	9.4 ± 0.2
Average	**6 ± 1**	**0.1 ± 0.1**	**3213 ± 48**	**55.5 ± 1.7**	**752 ± 166**	**12.8 ± 2.6**	**1282± 30**	**22.2 ± 0.9**	**553 ± 17**	**9.5 ± 0.2**

Note: Errors indicated are standard errors of the mean.

3.1.2 Coarse Woody Debris Quantification

The volume of *Nothofagus fusca* CWD on the forest floor was estimated to be 184 $m^3 ha^{-1}$. The average density of the *Nothofagus fusca* CWD was determined to be 0.39 g cm^{-3}, using the values given by Stewart and Burrows (1994), weighted according to the number of logs and branches counted in each decay class. The biomass of the *Nothofagus fusca* standing crop of CWD was therefore calculated to be 72 ± 5 Mg ha^{-1}. Estimated volumes in individual quadrats are shown Table 3.3. Variability within quadrats was often high, as was variability between different quadrats. Observations over six months indicated negligible inputs of *Nothofagus fusca* CWD occurred in the quadrat areas, and the only mass loss observed was the gradual fragmentation of bark associated with relatively fresh branches. The volume of *Nothofagus menziesii* CWD was not accurately determined, but was estimated to be 5% of the *Nothofagus fusca* CWD volume. Unidentifiable CWD was more common, approximately 20-25% of total *Nothofagus fusca* CWD volume.

Table 3.3: Volumes of *Nothofagus fusca* coarse woody debris in North-South and East-West orientations

Quadrat #	Volume N-S ($m^3 ha^{-1}$)	Volume E-W ($m^3 ha^{-1}$)	Quadrat Volume ($m^3 ha^{-1}$)
1	182.6	154.7	169 ± 10
2	200.8	177.7	189 ± 8
3	163.6	140.4	152 ± 8
4	157.6	236.3	197 ± 28
5	170.7	215	193 ± 16
6	195.5	184.2	190 ± 4
7	172.6	188.2	180 ± 6
8	136.2	192.7	164 ± 20
9	232.4	188	210 ± 16
10	204.6	183.7	194 ± 7
Average	**182 ± 8**	**186 ± 8**	**184 ± 14**

Note: Errors indicated are standard errors of the mean

3.2 Characterisation of *Nothofagus fusca* litter

3.2.1 Oven dry and ash weights

The OD mass and ash content of the major litter types of *Nothofagus fusca* are shown in Table 3.4. The moisture content ranged from 13.3% in YSB to 7.0% in OSIB, while ash content of the *Nothofagus fusca* litter varied from 5.36% in OSIB to 2.20% in flowers. Following the determination of these values, all results were calculated on an oven dry basis.

Table 3.4: Oven dry mass and ash mass of *Nothofagus fusca* litter expressed as a percentage of air dry and oven dry mass

Litter Type	OD Mass/AD Mass (%)	Ash Mass/OD Mass (%)
Flowers	86.7 ± 0.1	2.20
Branch Bark	92.4 ± 0.2	2.31
Young Stem Bark	92.4 ± 0.2	3.13
Old Stem Inner Bark	93.0 ± 0.1	5.36
Old Stem Outer Bark	91.1 ± 0.2	2.22
Twigs	91.4 ± 0.3	2.79
Fallen Leaves	91.8 ± 0.2	4.65

Note: Errors indicated are standard errors of the mean.

3.2.2 Nitrogen Content

The concentration and distribution of nitrogen in different types of *Nothofagus fusca* litter is shown in Table 3.5, as are the organic and inorganic forms in which this nitrogen was present within the litter. Total nitrogen concentration in the litter types varied from 0.25% for OSOB to 1.58% for floral material. Oven drying any of the litter types at 105^{o}C prior to analysis did not alter nitrogen content (Appendix E).

Branch bark had the highest concentration of hydrolysable mineral nitrogen of all litter types, but due to the higher overall concentration of nitrogen, floral litter contained the greatest absolute amount of hydrolysable mineral nitrogen. The amounts of identifiable organic and inorganic nitrogen present varied considerably between the different bark types.

Table 3.5: Total nitrogen content and forms of nitrogen in *Nothofagus fusca* litter following acid hydrolysis

Litter Type	Nitrogen (%)	NH_4-N (%)	Hexosamine-N (%)	α-amino-N (%)	Hydrolysable Unidentified Nitrogen (%)	Insoluble-N (%)
Flowers	1.58 ± 0.01	6.7 ± 0.1	0	61.3 ± 0.2	23.9 ± 0.2	8.1 ± 0.1
Branch Bark	0.65 ± 0.01	9.1 ± 0.2	0.5 ± 0.1	43.6 ± 0.1	31.4 ± 0.2	15.4 ± 0.1
Young Stem Bark	0.38 ± 0.01	4.8 ± 0.1	1.2 ± 0.1	29.4 ± 0.1	22.3 ± 0.2	42.4 ± 0.1
Old Stem Inner Bark	0.25 ± 0.01	6.1 ± 0.1	Trace	32.4 ± 0.1	26.9 ± 0.5	34.6 ± 0.5
Old Stem Outer Bark	0.34 ± 0.03	6.3 ± 0.1	0	36.5 ± 0.7	27.4 ± 0.7	30.7 ± 0.1
Twigs	0.45 ± 0.01	ND	ND	ND	ND	ND
Fallen Leaves	0.66 ± 0.01	ND	ND	ND	ND	ND

Note: Errors indicated are standard errors of the mean.

The distribution of nitrogen in twigs and fallen leaves was not determined.

3.2.3 Phosphorous Content

The calibration curve produced from the phosphorous solutions of known concentrations is shown in Appendix A. The phosphorous content of the litter types was found to vary considerably, from 0.118% in branch bark to 0.025% "fresh" *Nothofagus fusca* wood.

Table 3.6: Total phosphorous content in the litter of *Nothofagus fusca*

Litter Type	Phosphorous (%)
Flowers	0.110 ± 0.001
Branch Bark	0.118 ± 0.004
Young Stem Bark	0.073 ± 0.002
Old Stem Inner Bark	0.084 ± 0.001
Old Stem Outer Bark	0.027 ± 0.001
Twigs	0.032 ± 0.001
Fallen Leaves	0.070 ± 0.003
CWD – Fresh	0.025 ± 0.001
CWD – Moderate Decay	0.035 ± 0.001
CWD – Significant Decay	0.057 ± 0.002

Note: Errors indicated are standard errors of the mean

3.2.4 Total Oxidisable Organic Carbon

The content of oxidisable organic carbon in the litter of *Nothofagus fusca* ranged from 64.4% for floral litter to 55.1% for both fractions of old stem bark. Carbon : nitrogen ratios were lowest in floral litter, and all other litter types were over double this, varying from 86.1 for leaf litter to 220.4 for old stem inner bark. Branch bark possessed the lowest carbon : phosphorous ratio at 488, while old stem outer bark was the highest with a ratio of 2041.

Table 3.7: Total oxidisable organic carbon content, C:N ratios and C:P ratios of *Nothofagus fusca* litter.

Litter Type	Oxidisable Carbon (%)	C:N Ratio	C:P Ratio
Flowers	64.4 ± 0.02	40.8	585
Branch Bark	57.6 ± 0.77	88.6	488
Young Stem Bark	58.1 ± 0.35	152.9	796
Old Stem Inner Bark	55.1 ± 0.81	220.4	656
Old Stem Outer Bark	55.1 ± 0.43	141.3	2041
Twigs	55.9 ± 0.27	124.2	1747
Fallen Leaves	56.8 ± 0.07	86.1	811

Note: Errors indicated are standard errors of the mean

3.2.5 Water Soluble Substances

Mass losses due to the extraction of water soluble substances over ten days are shown in Table 3.8. This table also shows the nitrogen and phosphorous concentration of *Nothofagus fusca* floral and bark litter after ten days leaching, and the mass of nitrogen and phosphorous leached from the litter, expressed as a percentage of the initial nitrogen and phosphorous mass. Mass loss from leaching was highest in young stem bark, at 13.3%, and ranged down to 6.4% branch bark. Overall, floral litter lost the least mass of nitrogen and phosphorous, only 12.9% and 24.0% respectively. All bark litter types lost greater proportions of nitrogen than floral litter, and all lost so much phosphorous that the mass of phosphorous remaining in the litter was below the level of detection, equal to the blank value in all cases. Consequently, it was not possible to calculate the percentage of phosphorous mass loss, although it can be assumed to be high.

Table 3.8: Mass loss, nutrient concentration and nutrient mass loss in *Nothofagus fusca* floral and bark litter following leaching

Litter Type	Mass Loss (%)	Nitrogen (%)	Nitrogen mass loss (%)	Phosphorous (%)	Phosphorous mass loss (%)
Flowers	8.6 ± 0.05	1.51 ± 0.01	12.9 ± 0.3	0.08 ± 0.01	23.7 ± 0.6
Branch Bark	6.4 ± 0.14	0.39 ± 0.01	43.8 ± 0.1	UD	ND
Young Stem Bark	13.3 ± 0.31	0.26 ± 0.01	42.9 ± 0.6	UD	ND
Old Stem Inner Bark	8.2 ± 0.06	0.21 ± 0.01	24.8 ± 0.6	UD	ND
Old Stem Outer Bark	8.2 ± 0.04	0.28 ± 0.01	35.0 ± 0.2	UD	ND

Note: Errors indicated are standard errors of the mean.
UD indicates a value was undetectable.
ND indicates a value was not determined.

The characteristics and results of inoculation of the leachates drawn off after the first two days of leaching are shown in Table 3.9. All leachates were shown to support microbial growth, although growth in the old stem inner bark leachate took much longer to become apparent, and was generally much less dense than in the other leachates after ten days. No microbial growth was detected in the control flasks.

Table 3.9: pH of *Nothofagus fusca* floral and bark leachates, microbial growth density and pH of leachate after incubation

Litter Type	Initial Leachate pH	Microbial density following 10 days incubation	Leachate pH following 10 days incubation
Flowers	4.1	++++	5.3
Branch Bark	5.6	++++	6.8
Young Stem Bark	4.8	+++	5.5
Old Stem Inner Bark	5.2	+	5.1
Old Stem Outer Bark	4.1	+++	4.5

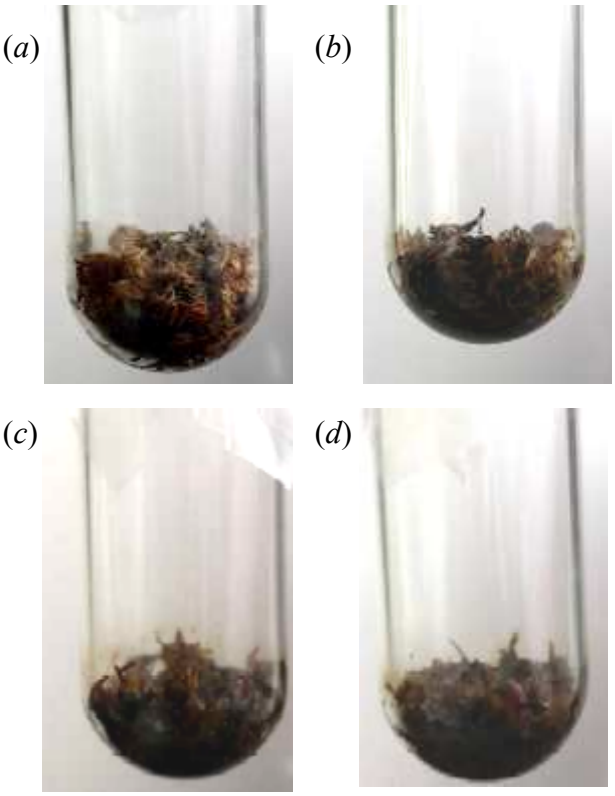
Note: Error values are not given for pH as all values were identical.

3.3 Studies of *Nothofagus fusca* floral litter decomposition

3.3.1 Mass loss at various temperatures

Percentage mass loss from floral litter in microcosms over 40, 100 and 200 days was calculated on an OD, ash free basis. Mass loss over time is shown in Figure 3.3, while numerical values are presented in Table 3.10. Overall, the rate of mass loss increased with temperature of incubation, although the differences in mass loss between microcosms incubated at 17°C and 25°C were often slight. Rates of mass loss differed significantly over time for the higher temperatures, but were more consistent for the two lower temperatures. Decay rate constants, *k*, were also calculated and are shown in Table 3.10. Several control microcosms displayed minor changes in weight, but these were slight, in the order of 0.01%, and were put down to differences in temperature and humidity affecting the accuracy of the balance. Precision of measurements, ignoring the source of error already mentioned, was ± 50µg.

Figure 3.2: Condition of *Nothofagus fusca* litter after 200 days decomposition in microcosms incubated at (*a*) 3°C, (*b*) 10°C, (*c*) 17°C and (*d*) 25°C



The physical appearance of the floral litter in the tubes incubated at the higher temperatures changed markedly over 200 days. The structure of individual flowers deteriorated into an amorphous mass, and the colouration of the litter changed from yellow to dark brown. Evidence of microbial growth in the tubes was indicated by dense microbial colonisation of the litter, although the types of colonies visible change gradually over time. Changes in the floral litter incubated at lower temperatures were less apparent. The structure of the floral material incubated at 3°C was virtually unchanged, while incubation at 10°C resulted in only slight visible deterioration. Colouration did not alter, and the extent of microbial growth visible on the litter was significantly less than at higher temperatures.

Figure 3.3: Mass loss from *Nothofagus fusca* floral litter after incubation at various temperatures

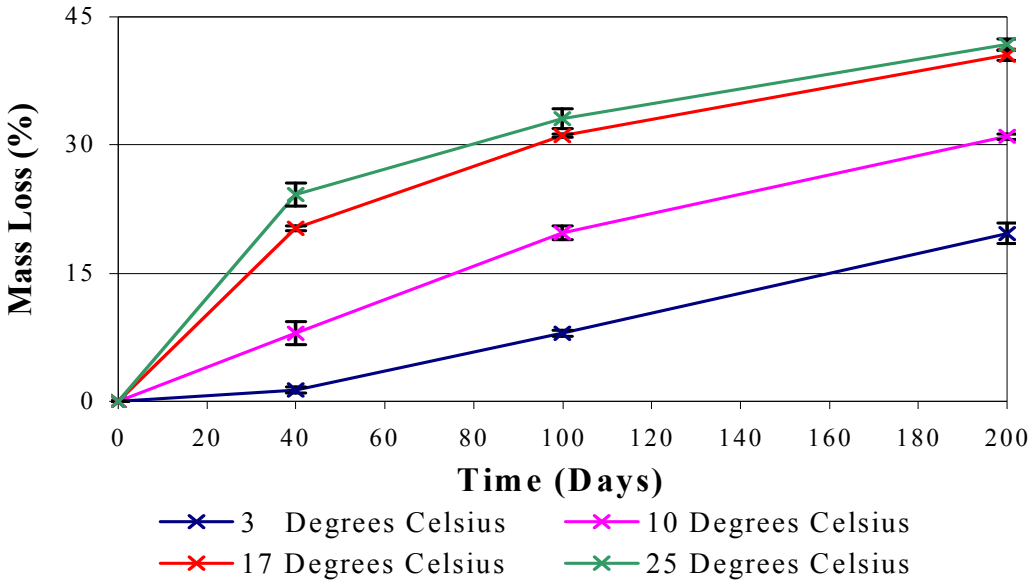


Table 3.10: Mass loss and decay rate constants for *Nothofagus fusca* floral litter after incubation at various temperatures

Temperature	% Mass Loss 40 Days	% Mass Loss 100 Days	% Mass Loss 200 Days	0-200 Days (*k*)
3°C	1.4 ± 0.4	8.0 ± 0.4	19.7 ± 1.2	0.40 ± 0.02
10°C	8.0 ± 1.3	19.7 ± 0.8	31.0 ± 0.3	0.68 ± 0.02
17°C	20.3 ± 0.3	31.1 ± 0.2	40.5 ± 0.7	0.95 ± 0.01
25°C	24.2 ± 1.4	33.1 ± 1.1	41.7 ± 0.7	0.99 ± 0.01

Note: Errors indicated are standard errors of the mean.

3.3.2 Nitrogen mineralisation at various temperatures

The amount of mineral nitrogen found in fresh *Nothofagus fusca* floral litter, expressed as a percentage of the total nitrogen, was found to be 0.500 ± 0.001%, calculated on an OD basis. Net percentage mineralisation of nitrogen from *Nothofagus fusca* floral litter over time at different temperatures is shown Figure 3.4 and in Table 3.11, calculated on an OD basis, where the levels of microbial density are also reported. Negative percentage values were determined in most cases, indicating net immobilisation, i.e. the microbial community assimilated more mineral nitrogen from the floral litter than it released. Mineralisation rates in the microcosms were highly variable, and consequently associated standard error values were also high.

The greatest amount of mineral nitrogen was found in microcosms incubated at 10^{o}C after 200 days, although net nitrogen mineralisation was first detected in microcosms incubated at 17^{o}C and 25^{o}C after 100 days. The amounts of mineral nitrogen in the microcosms incubated at 25^{o}C peaked and fell over time, shown graphically in Figure 3.4, as did the associated microbial growth density within the microcosms. The presence of volatilised ammonia was not detected in any of the acids traps placed in the microcosms, and the production of nitrates was not detected in any microcosm. The pH of the contents of the microcosms increased in all cases, except controls, and is shown in Table 3.12. Both pH increases and microbial growth density proved vastly more consistent across replicate microcosms than net nitrogen mineralisation rates.

Figure 3.4: Net nitrogen mineralisation from *Nothofagus fusca* floral litter over 200 days incubation at various temperatures

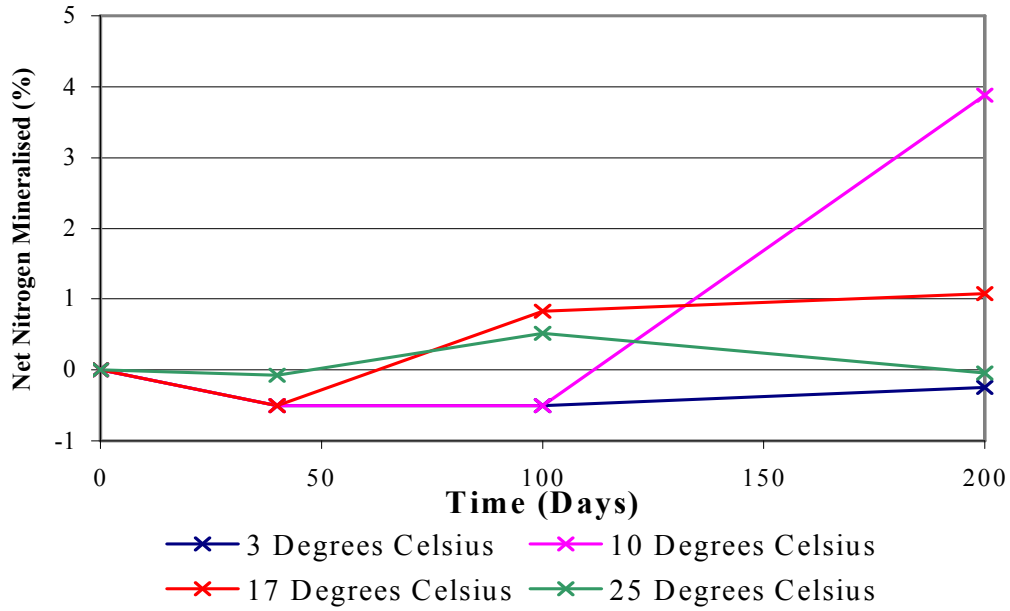


Table 3.11: Net nitrogen mineralisation and microbial growth on *Nothofagus fusca* floral litter at various temperatures

Temperature	40 Days		100 Days		200 Days	
	Nitrogen Mineralised (%)	MGD	Nitrogen Mineralised (%)	MGD	Nitrogen Mineralised (%)	MGD
3°C	-0.5	0	-0.5	+	-0.2 ± 0.2	+
10°C	-0.5	+	-0.5	++	3.8 ± 1.0	++
17°C	-0.5	++	0.8 ± 0.5	+++	1.1 ± 0.3	++
25°C	-0.1 ± 0.4	+++	0.5 ± 0.7	++++	0 ± 0.1	+++

Note: Errors indicated are standard errors of the mean.

Microbial growth density is abbreviated as MGD.

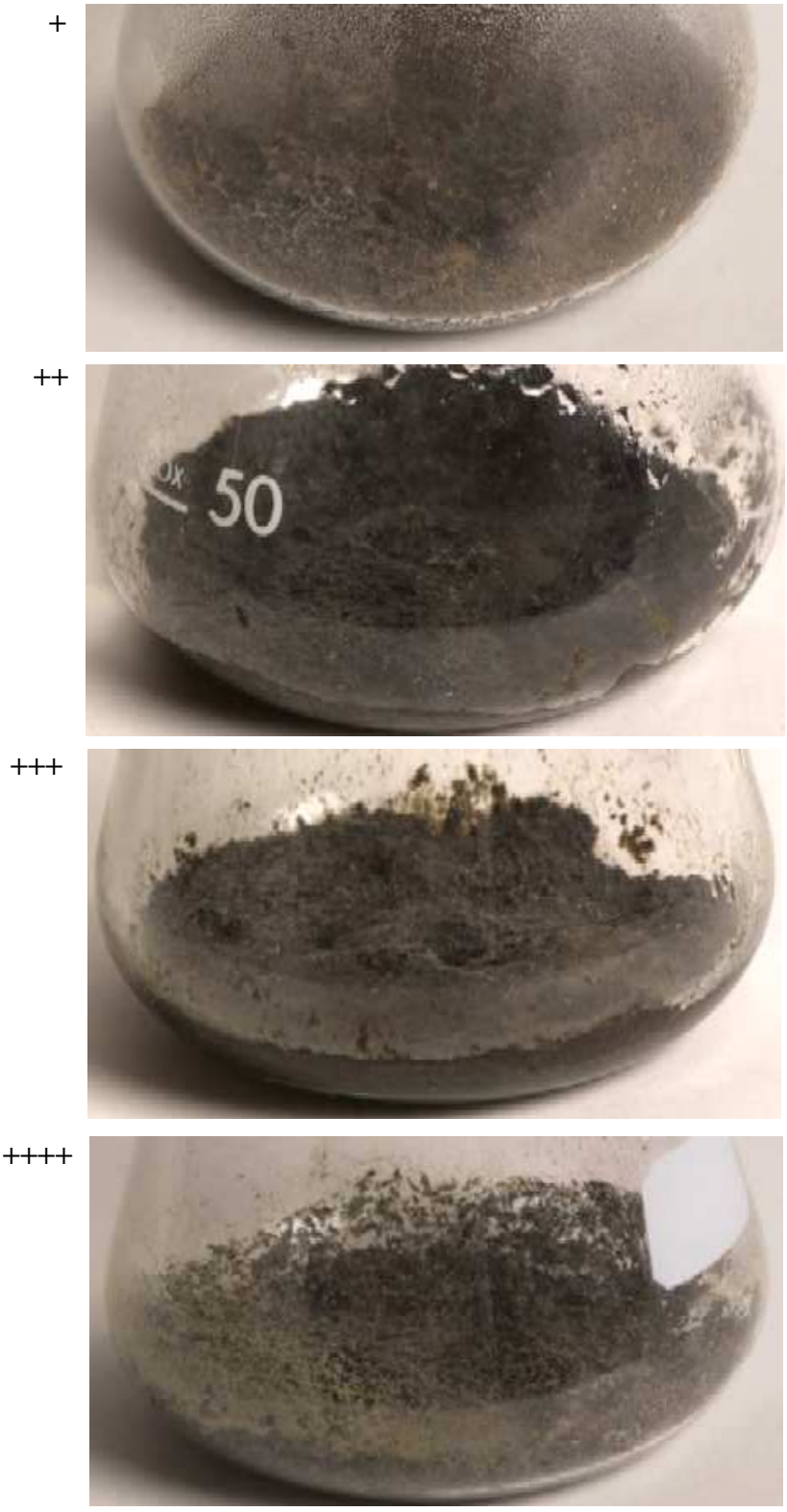
Table 3.12: pH of microcosms containing *Nothofagus fusca* floral litter incubated at various temperatures

Temperature	Day 0	Day 40	Day 100	Day 200
3	4.1	4.5	4.7	4.8 ± 0.1
10	4.1	4.5 ± 0.1	4.8	5.1 ± 0.1
17	4.1	4.6 ± 0.1	5.1 ± 0.1	5.1 ± 0.1
25	4.1	4.7 ± 0.1	5.2 ± 0.1	5.1 ± 0.1

Note: Error values given are standard errors of the mean.

Where no error is given all values were identical.

Figure 3.5: Microbial growth densities exhibited in microcosms containing *Nothofagus fusca* floral litter, ranked from + to ++++



3.3.3 Decomposition of floral litter in the field

Percentage mass loss over time from *Nothofagus fusca* floral litter incubated in the field, calculated on an ash free oven dry basis, is shown in Figure 3.6. Floral litter lost mass rapidly over the first 60 days in the field, but from this point onwards the rate of mass loss held relatively constant, evident in figures calculated for percentage mass loss in Table 3.13. After 60 days, 22.9% of the litter mass had been leached or mineralised, while in the next 140 days only a further 17.3% of the initial mass was lost. Over the entire 200 day period, k was calculated to be 0.94 ± 0.01. Mineral content, indicated by percentage ash content following ignition, is shown in Table 3.13. The ash content in floral litter after 200 days in the field was determined to 5.5%, compared to 2.5% initially. Scanning electron micrographs of the nylon mesh, prior to use in the field and after 200 days exposure (Figure 3.7), show no visibly obvious changes to the integrity of the mesh.

Changes to the concentration of nitrogen and absolute amount of nitrogen in the floral litter are shown in Figure 3.8, with values given in Table 3.14. Nitrogen concentration in the litter dropped rapidly over the first ten days in the field, then increased gradually until day 130, after which the nitrogen concentration fell again. Despite this, nitrogen concentration after 200 days in the field was still higher than initial levels. The absolute amount of nitrogen in the samples was more dynamic, twice showing increases in absolute content between sampling times, but eventually decreased to 64.2% of the initial absolute content after 200 days. Phosphorous concentration and absolute phosphorous content are shown in Figure 3.8. The concentration and absolute amount of phosphorous in the floral litter decreased initially, then increased after 60 days, and phosphorus concentration reached a maximum of 0.138%. Between day 130 and day 200 both concentration and absolute phosphorus content decreased rapidly, absolute content falling to 63.0% of initial content while the concentration of phosphorous fell to 0.118 percent, still slightly higher than phosphorous concentration at day 0, however.

Figure 3.6: Mass loss from *Nothofagus fusca* floral litter over time in the field

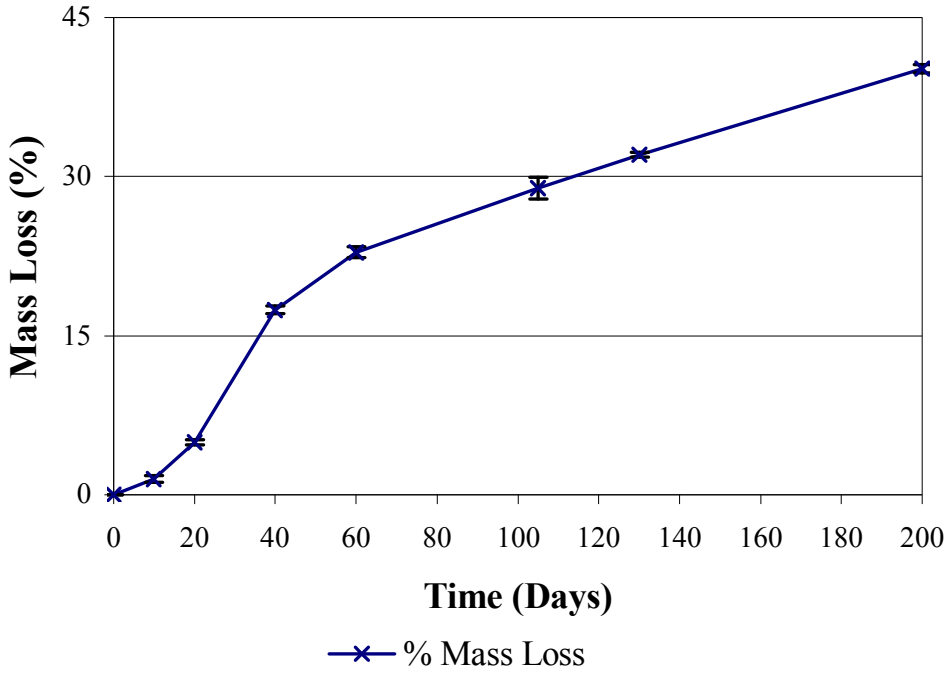


Table 3.13: Mineral contamination and mass loss from *Nothofagus fusca* floral litter over time in the field (ash free basis)

Days in Field	Ash Mass (%)	Mass Loss (%)
0	2.5	0
10	2.5 ± 0.1	1.4 ± 0.3
20	2.8 ± 0.1	5.0 ± 0.2
40	3.6 ± 0.1	17.5 ± 0.3
60	4.1 ± 0.2	22.9 ± 0.5
105	3.8 ± 0.1	28.9 ± 1.0
130	3.9 ± 0.1	32.1 ± 0.2
200	5.5 ± 0.1	40.2 ± 0.4

Note: Error values given are standard errors of the mean.

Figure 3.7 SEM showing nylon mesh prior to use in the field and after 200 days in the field.

(*a*) Nylon mesh prior to use. Bar indicates 100µm (bottom right corner)

(*b*) Nylon mesh after exposure to field conditions for 200 days. Bar indicates 100µm (bottom right corner)

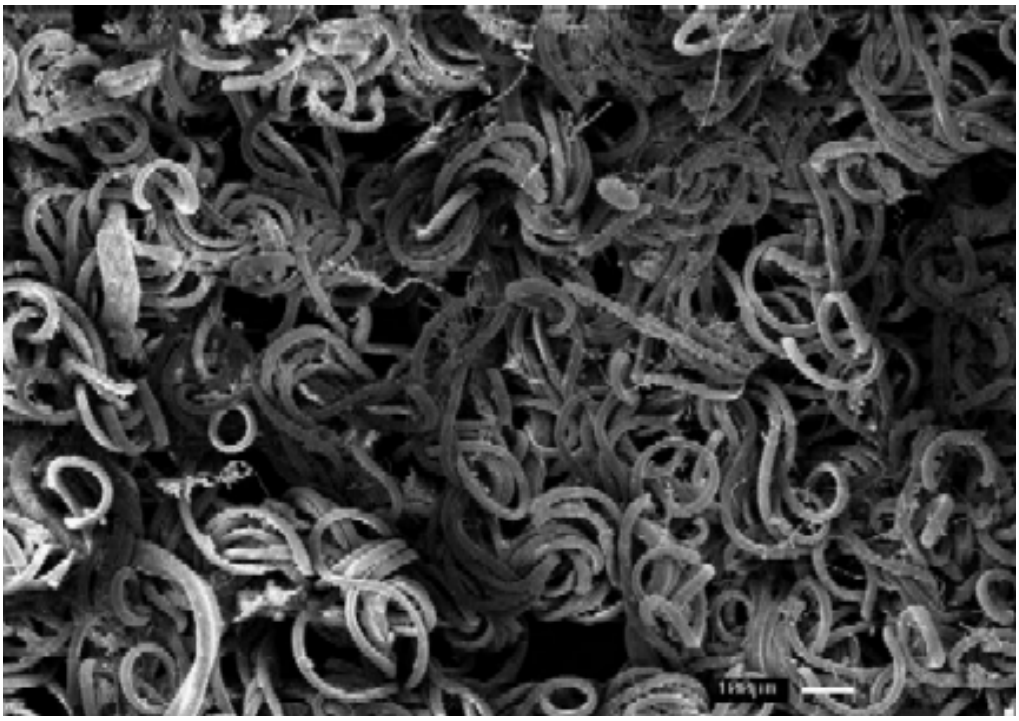


Figure 3.8: Nitrogen concentration and absolute nitrogen mass as a proportion of initial mass in *Nothofagus fusca* floral litter over time in the field

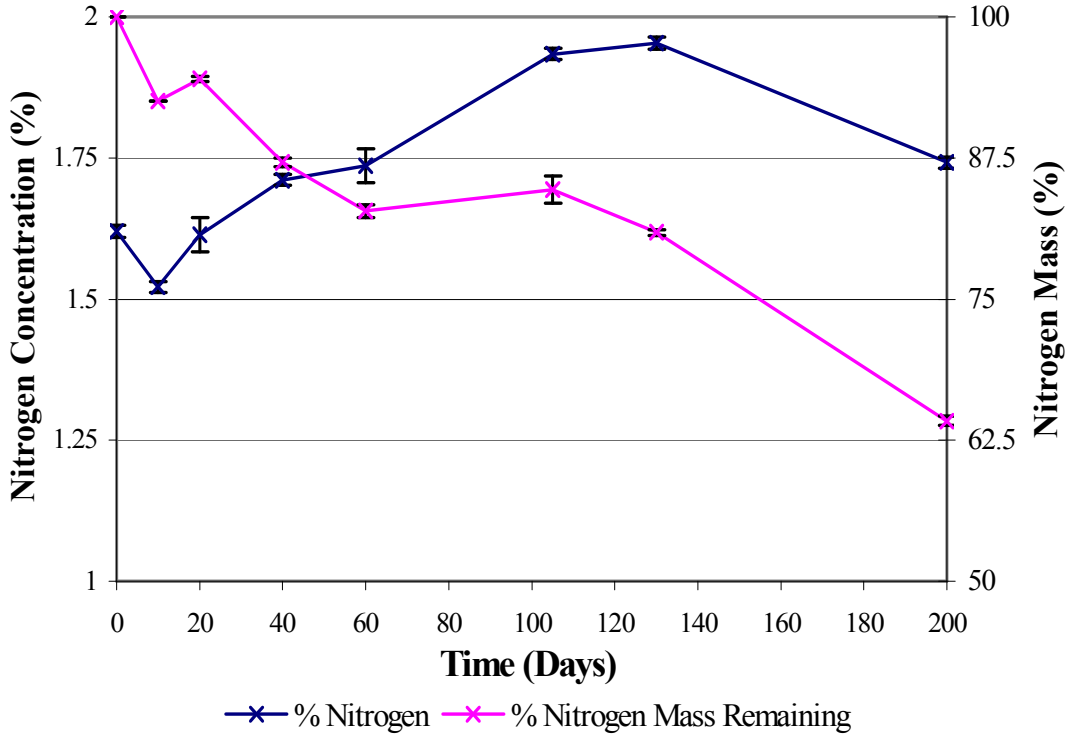


Table 3.14: Nitrogen concentration and absolute nitrogen mass as a proportion of initial mass in *Nothofagus fusca* floral litter over time in the field

Days in Field	Nitrogen Concentration (%)	Nitrogen Mass Remaining (%)
0	1.62 ± 0.01	100
10	1.52 ± 0.01	92.5 ± 0.3
20	1.61 ± 0.02	94.5 ± 0.2
40	1.71 ± 0.01	87.1 ± 0.4
60	1.74 ± 0.01	82.8 ± 0.6
105	1.93 ± 0.01	84.7 ± 1.2
130	1.94 ± 0.01	80.9 ± 0.3
200	1.77 ± 0.03	64.2 ± 0.4

Note: Error values given are standard errors of the mean.

Figure 3.9: Phosphorous concentration and absolute phosphorous mass as a proportion of initial mass in *Nothofagus fusca* floral litter over time in the field

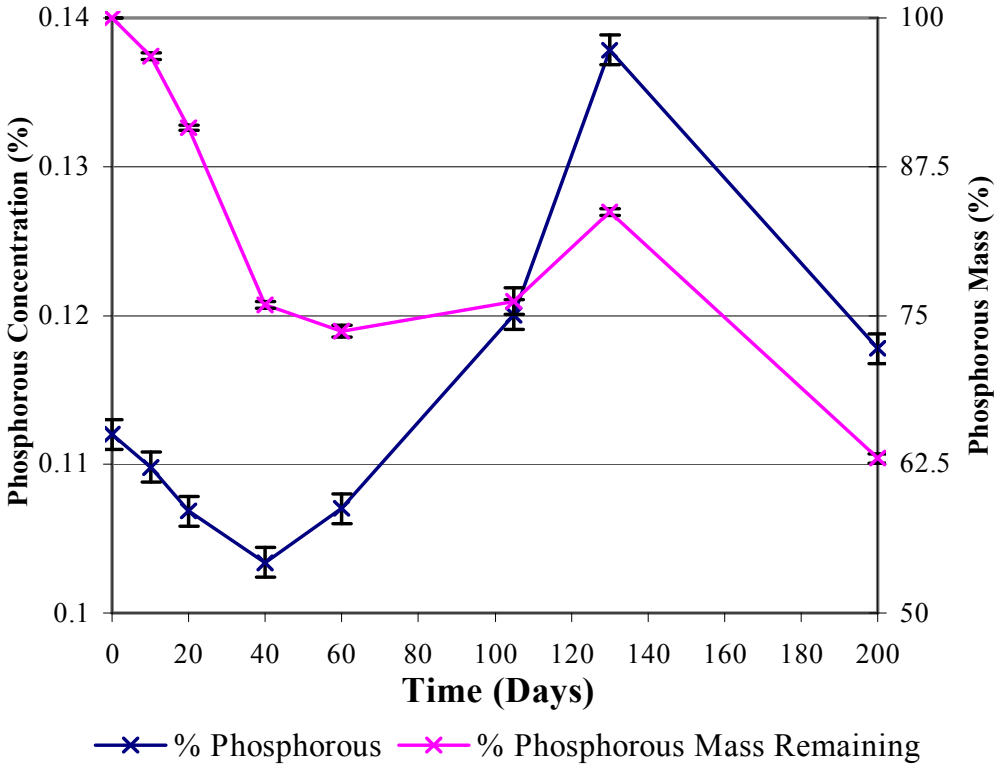


Table 3.15: Phosphorous concentration and absolute phosphorous mass as a proportion of initial mass in *Nothofagus fusca* floral litter over time in the field

Days in Field	Phosphorus Concentration (%)	Phosphorous Mass Remaining (%)
0	0.112 ± 0.001	100
10	0.110 ± 0.001	96.8 ± 0.3
20	0.107 ± 0.001	90.8 ± 0.2
40	0.103 ± 0.001	75.9 ± 0.3
60	0.107 ± 0.001	73.7 ± 0.5
105	0.120 ± 0.001	76.2 ± 1.1
130	0.138 ± 0.001	83.7 ± 0.4
200	0.118 ± 0.001	63.0 ± 0.2

Note: Error values given are standard errors of the mean.

3.4 Studies of *Nothofagus fusca* bark litter decomposition

3.4.1 Mass loss at various temperatures

Mass loss and decay rate constants for *Nothofagus fusca* bark litter types at a range of temperatures were determined on an OD, ash free basis, and are shown in Table 3.16. The greatest mass loss occurred in the microcosms containing *Nothofagus fusca* branch bark litter. This litter showed the fastest rate of mass loss, followed by young stem bark, then outer and inner old stem bark. The *k* values calculated indicated that 95% decomposition of all bark types would take at least a decade at any temperature, although this varied greatly, ranging from 11.5 years for branch bark to 59.9 years for old stem inner bark at 17^{o}C.

A notable characteristic was the comparatively large difference in decomposition rates between microcosms incubated at the two lower temperatures and the two higher temperatures. Although generally less pronounced after 100 days incubation, this division was highly evident after 200 days in the microcosms, and was common to all bark types. There was little difference between absolute mass loss and mass loss rates in the 3^{o}C-10^{o}C and 17^{o}C-25^{o}C gaps, and calculated error ranges were often found to be close or overlapping.

Table 3.16: Mass loss and decay rate constants (*k*) for *Nothofagus fusca* bark litter after incubation at various temperatures

Bark Type	Temperature	Mass Loss after 100 days (%)	Mass Loss after 200 days (%)	0-200 Days (*k*)
Branch	3°C	3.7 ± 0.3	6.0 ± 0.3	0.11 ± 0.01
	10°C	5.7 ± 0.2	6.7 ± 0.3	0.13 ± 0.01
	17°C	7.8 ± 0.3	13.3 ± 0.6	0.26 ± 0.01
	25°C	11.9 ± 0.8	15.6 ± 1.0	0.31 ± 0.02
Young Stem	3°C	1.5 ± 0.1	4.1 ± 0.1	0.08 ± 0.01
	10°C	2.0 ± 0.1	4.3 ± 0.5	0.08 ± 0.01
	17°C	4.5 ± 0.4	7.6 ± 0.3	0.14 ± 0.01
	25°C	4.9 ± 0.3	8.4 ± 0.6	0.16 ± 0.01
Old Stem Inner	3°C	1.7 ± 0.2	1.7 ± 0.1	0.03 ± 0.01
	10°C	1.4 ± 0.1	1.4 ± 0.1	0.03 ± 0.01
	17°C	2.6 ± 0.2	2.8 ± 0.1	0.05 ± 0.01
	25°C	2.7 ± 0.3	2.9 ± 0.1	0.05 ± 0.01
Old Stem Outer	3°C	1.8 ± 0.1	2.2 ± 0.1	0.04 ± 0.1
	10°C	1.9 ± 0.3	2.5 ± 0.1	0.05 ± 0.1
	17°C	4.3 ± 0.2	5.7 ± 0.1	0.11 ± 0.1
	25°C	4.6 ± 0.2	5.8 ± 0.1	0.11 ± 0.1

Note: Error values given are standard errors of the mean.

Figure 3.10: Mass loss from *Nothofagus fusca* branch bark after incubation at various temperatures

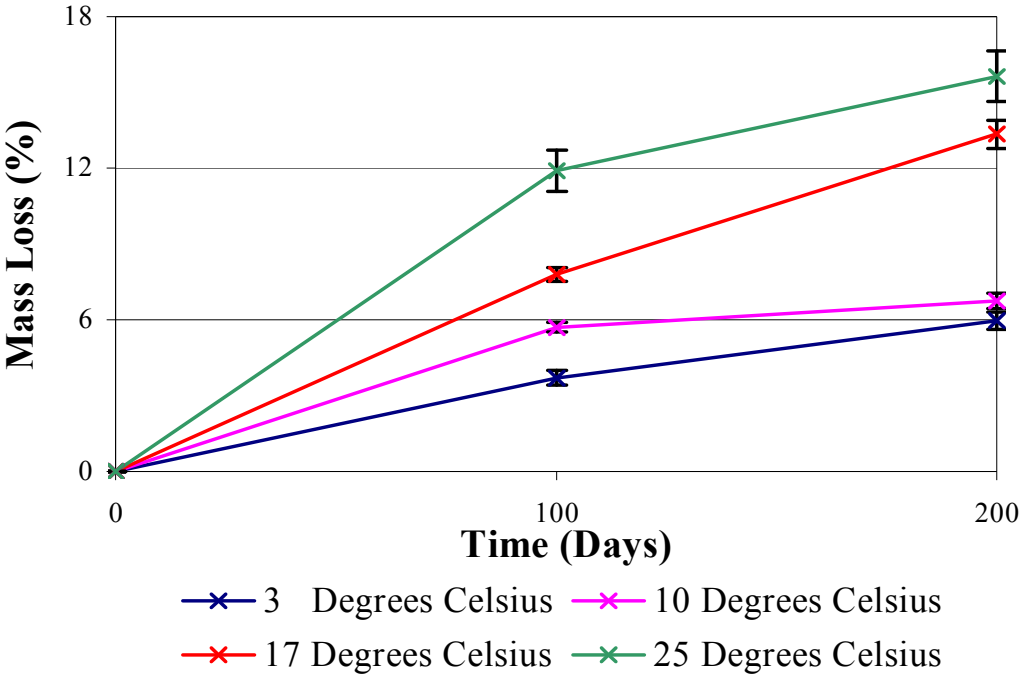


Figure 3.11: Mass loss from *Nothofagus fusca* young stem bark after incubation at various temperatures

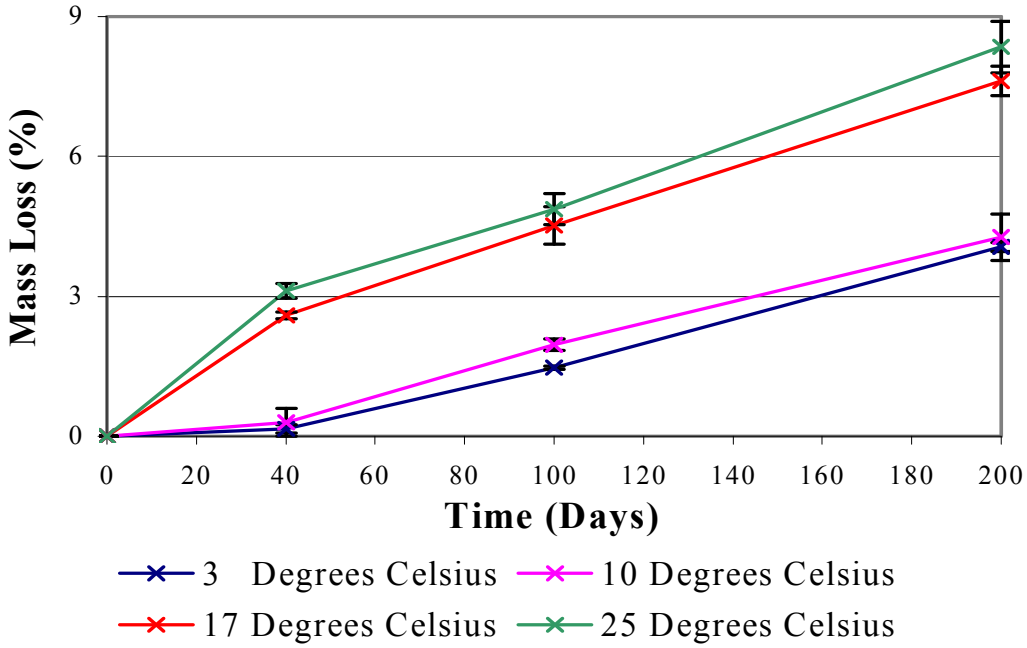


Figure 3.12: Mass loss from *Nothofagus fusca* old stem inner bark after incubation at various temperatures

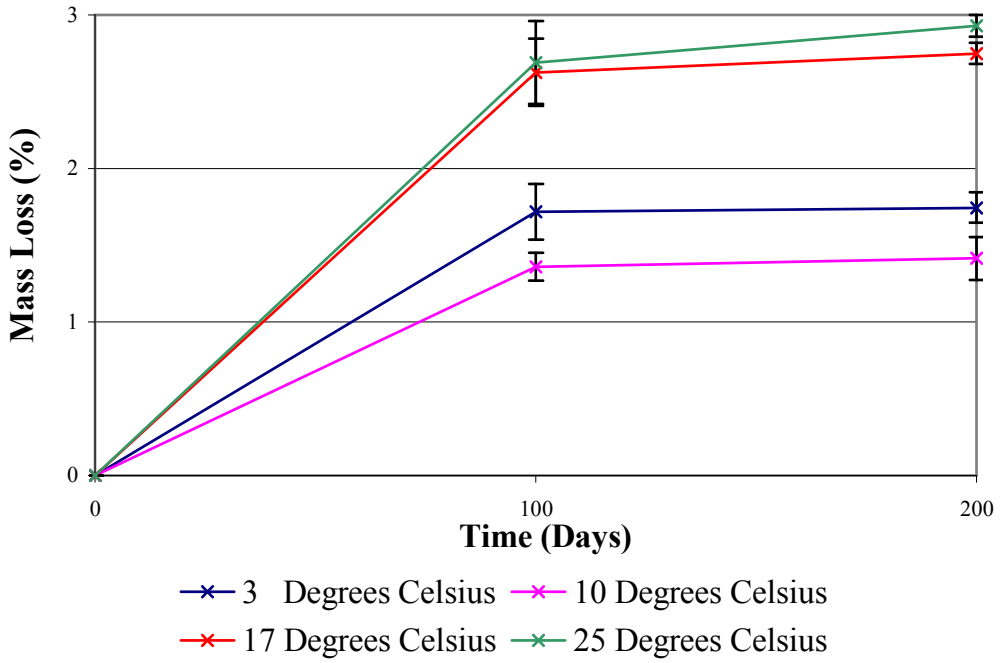
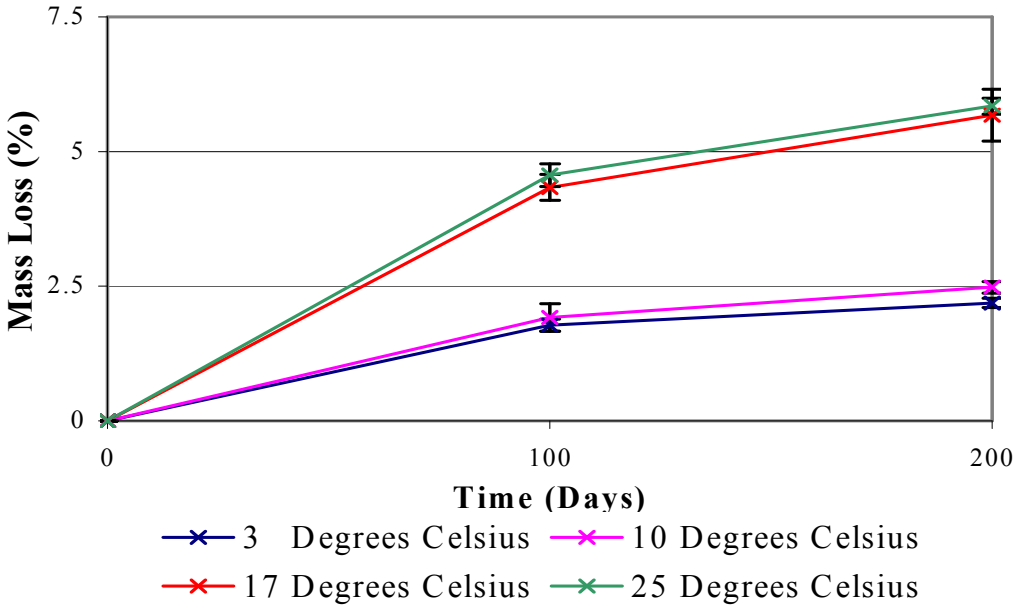


Figure 3.13: Mass loss from *Nothofagus fusca* old stem outer bark after incubation at various temperatures



3.4.2 Nitrogen mineralisation at various temperatures

Net mineralisation of nitrogen from the incubated bark litter was not detected in any of the microcosms. Mineral nitrogen present initially in the samples was immobilised even after 200 days (Table 3.17). Visible microbial colonisation developed in the microcosms, spreading at varying rates, but in no case was dense, abundant growth found to develop. Observations of the microcosms in the first few days of incubation indicated that some rapid growth did occur initially, but the development of these leading colonisers was arrested after approximately two weeks, and the colonies that had developed gradually disappeared, replaced by slower growing microorganisms. The pH of the microcosms was found to increase in almost every case over time (Table 3.18). Both pH increases and levels of observable microbial growth were found to be less variable between replicate microcosms than net nitrogen mineralisation figures.

Table 3.17: Net nitrogen mineralisation and microbial growth in microcosms containing *Nothofagus fusca* bark types at various temperatures

Bark Type	Temperature	100 Days		200 Days	
		Nitrogen Mineralised (%)	MGD	Nitrogen Mineralised (%)	MGD
Branch	3°C	-3.3	+	-2.8 ± 0.1	+
	10°C	-3.3	++	-2.4 ± 0.1	++
	17°C	-2.8 ± 0.3	+	-2.6 ± 0.1	++
	25°C	-3.3	++	-2.7 ± 0.1	++
Young Stem	3°C	-2.4 ± 0.0	+	-1.8 ± 0.1	++
	10°C	-2.1 ± 0.1	+	-1.5 ± 0.1	++
	17°C	-2.0 ± 0.0	++	-1.1 ± 0.1	+++
	25°C	-0.6 ± 0.1	++	-1.2 ± 0.1	+
Old Stem Inner	3°C	-3.0	0	-2.8 ± 0.1	+
	10°C	-3.0	0	-1.6 ± 0.3	+
	17°C	-3.0	0	-0.1 ± 0.2	+
	25°C	-3.0	0	0.0 ± 0.0	+
Old Stem Outer	3°C	-1.7	0	-1.7	+
	10°C	-1.7	0	-1.7	+
	17°C	-1.7	0	-1.7	+
	25°C	-1.7	++	-1.4 ± 0.2	+

Note: Error values given are standard errors of the mean.

Where no error is given values were identical

Microbial growth density is abbreviated as MGD.

Table 3.18: pH of microcosms containing *Nothofagus fusca* bark types incubated at various temperatures

Bark Type	Day 0 pH	Temperature	Day 100 pH	Day 200 pH
Branch	5.1	**3°C**	4.8 ± 0.1	5.4 ± 0.1
		10°C	5.0	5.6 ± 0.1
		17°C	5.4	6.0 ± 0.1
		25°C	6.2 ± 0.1	6.2 ± 0.1
Young Stem	5.4	**3°C**	6.4	6.3 ± 0.1
		10°C	6.5 ± 0.1	6.3 ± 0.1
		17°C	6.6 ± 0.1	5.4 ± 0.1
		25°C	6.5 ± 0.1	6.6 ± 0.1
Old Stem Inner	5.2	**3°C**	6.4 ± 0.1	7.0 ± 0.1
		10°C	7.0 ± 0.1	7.2
		17°C	7.5 ± 0.1	7.4
		25°C	7.4	7.1 ± 0.1
Old Stem Outer	4.1	**3°C**	4.9 ± 0.1	4.6 ± 0.1
		10°C	5.1 ± 0.1	4.9 ± 0.1
		17°C	5.3 ± 0.1	5.0 ± 0.1
		25°C	5.3 ± 0.1	5.2 ± 0.1

Note: Error values given are standard errors of the mean.

Where no error is given values were identical.

3.4.3 Decomposition and release of nutrients from bark litter in the field

Mass loss from the *Nothofagus fusca* young stem bark litter buried in the field was calculated on an oven dry, ash free basis, and varied significantly depending upon location (Table 3.19). Mass loss from the bark litter buried at the Lewis Pass Reserve site 5 (LPR) was consistently greater from the litter buried at the Ilam Campus grounds site (IC), although rates of mass loss from the IC litter were increasing in the latter time periods. Soil contamination tended to increase with time in the litter bags buried at the IC site, but no clear relationship between time and soil contamination was found in the LPR litter. In either case, the actual mass of soil imported into the samples was insignificant, never greater than a few milligrams. Decay rate constants, k, calculated over the 130 day period, were 0.69 ± 0.1 for the litter buried at the LPR site and 0.48 ± 0.1 for the IC litter.

The concentration of nitrogen in the bark litter buried at the LPR site, calculated on an OD, ash free basis, dropped rapidly over the first ten days in the field, then increased until day 60, surpassing the initial nitrogen concentration. After this, the nitrogen concentration fell slightly, then increased, reaching 0.5%. The absolute amount of nitrogen in the litter, also calculated on an OD, ash free basis and expressed as a percentage of the initial absolute nitrogen content, tended to follow nitrogen concentration, although the greatest absolute amount of nitrogen was reached at day 60, when nitrogen content was 106.4% of the initial amount. Nitrogen concentration and absolute nitrogen content in the litter buried at the IC site conformed approximately to the same trends as the bark litter buried at the LPR site, but tended to take more time, peaking after 80 days had elapsed.

Phosphorous concentration and absolute phosphorous content, again expressed as a percentage of the initial phosphorus content on an oven dry ash free basis, decreased rapidly over the first 20 days in the field, then increased gradually at the LPR site. After 130 days, phosphorous concentration was

determined to be 0.05%, while the absolute amount of phosphorous was 53.1% of the initial amount, and both had been increasing slowly over the past 110 days. Changes to the phosphorus concentration and content in the litter buried at the IC site did not follow the same trend, rising and falling apparently at random over time.

Figure 3.14: Mass loss from *Nothofagus fusca* young stem bark over time in the field

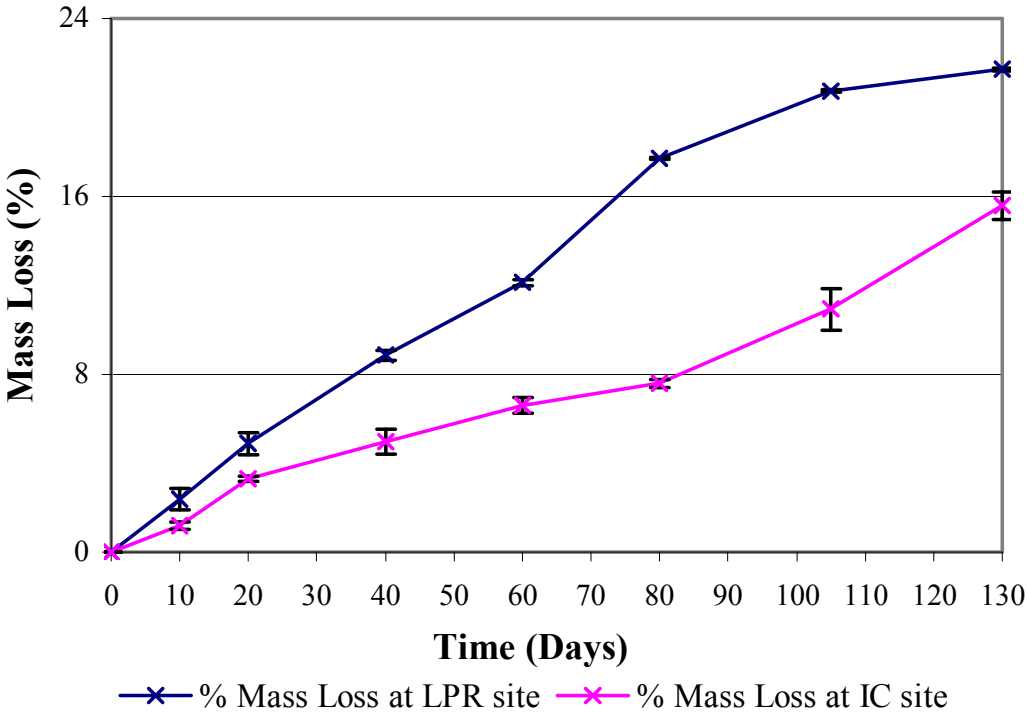


Table 3.19: Mass loss from *Nothofagus fusca* young stem bark in the field over time on an ash free basis

Days in Field	Mass Loss at Lewis Pass Reserve Site (%)	Mass Loss at Ilam Campus Site (%)
0	0	0
10	2.4 ± 0.5	1.2 ± 0.2
20	4.9 ± 0.5	3.3 ± 0.1
40	8.9 ± 0.2	5.0 ± 0.6
60	12.1 ± 0.1	6.6 ± 0.4
80	17.7 ± 0.1	7.6 ± 0.2
105	20.7 ± 0.3	10.9 ± 0.9
130	21.7 ± 0.3	15.6 ± 0.6

Note: Error values given are standard errors of the mean.

Figure 3.15: Nitrogen concentration and absolute nitrogen mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Lewis Pass Reserve site 5 over time

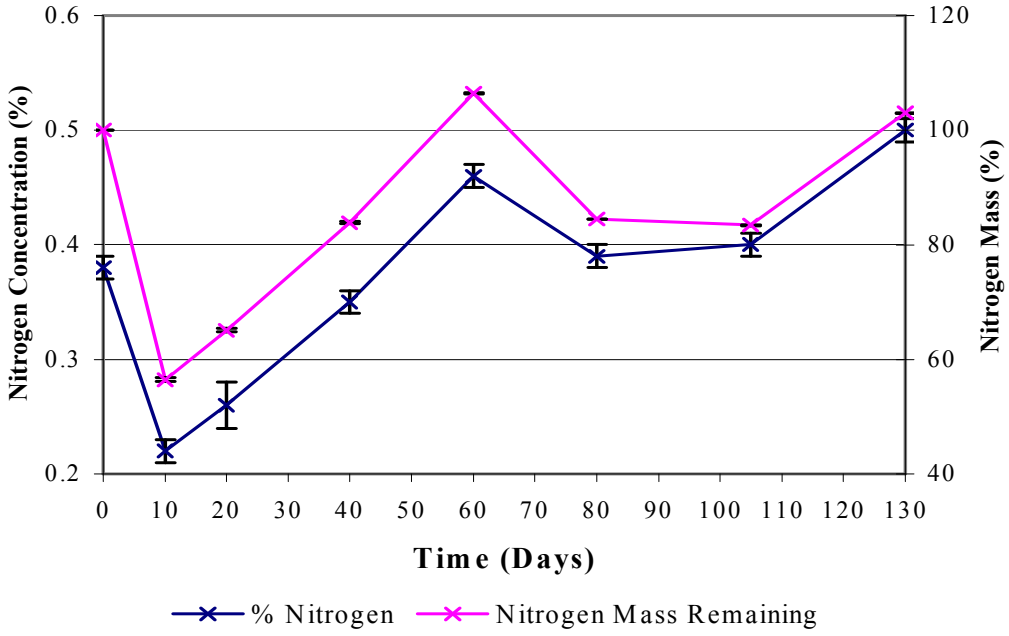


Table 3.20: Nitrogen concentration and absolute nitrogen mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Lewis Pass Reserve site 5 over time

Days in Field	Nitrogen concentration (%)	Nitrogen Mass Remaining (%)
0	0.38 ± 0.01	100
10	0.22 ± 0.01	56.5 ± 0.3
20	0.26 ± 0.02	65.1 ± 0.3
40	0.35 ± 0.01	83.9 ± 0.2
60	0.46 ± 0.01	106.4 ± 0.2
80	0.39 ± 0.01	84.5 ± 0.1
105	0.40 ± 0.01	83.4 ± 0.1
130	0.50 ± 0.01	103.0 ± 0.1

Note: Error values given are standard errors of the mean.

Figure 3.16: Nitrogen concentration and absolute nitrogen mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Ilam Campus site over time

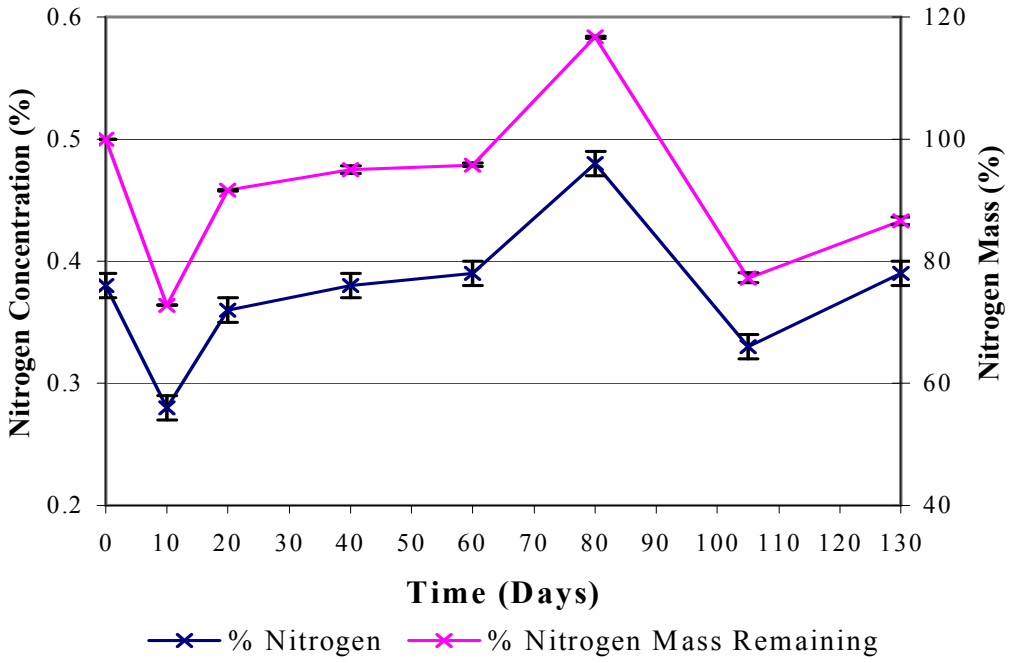


Table 3.21: Nitrogen concentration and absolute nitrogen mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Ilam Campus site over time

Days in Field	Nitrogen concentration (%)	Nitrogen Mass Remaining (%)
0	0.38 ± 0.01	100
10	0.28 ± 0.01	72.8 ± 0.1
20	0.36 ± 0.01	91.6 ± 0.1
40	0.38 ± 0.01	95 ± 0.6
60	0.39 ± 0.01	95.8 ± 0.4
80	0.48 ± 0.01	116.7 ± 0.2
105	0.33 ± 0.01	77.3 ± 0.8
130	0.39 ± 0.01	86.64 ± 0.7

Note: Error values given are standard errors of the mean.

Figure 3.17: Phosphorous concentration and absolute phosphorous mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Lewis Pass Reserve site 5 over time

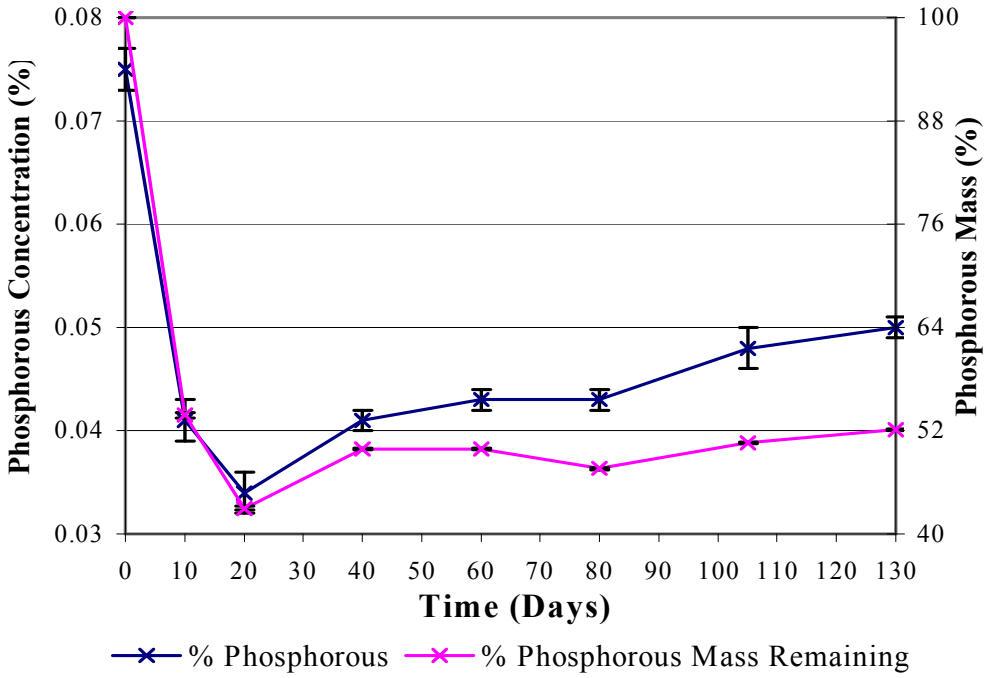


Table 3.22: Phosphorous concentration and absolute phosphorous mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Lewis Pass Reserve site 5 over time

Days in Field	Phosphorous concentration (%)	Phosphorous Mass Remaining (%)
0	0.075 ± 0.002	100
10	0.041 ± 0.002	53.8 ± 0.2
20	0.034 ± 0.002	43.0 ± 0.1
40	0.041 ± 0.001	49.9 ± 0.1
60	0.043 ± 0.001	49.9 ± 0.1
80	0.043 ± 0.001	47.6 ± 0.1
105	0.048 ± 0.002	50.6 ± 0.1
130	0.050 ± 0.001	52.1 ± 0.1

Note: Error values given are standard errors of the mean.

Figure 3.18: Phosphorous concentration and absolute phosphorous mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Ilam Campus site over time

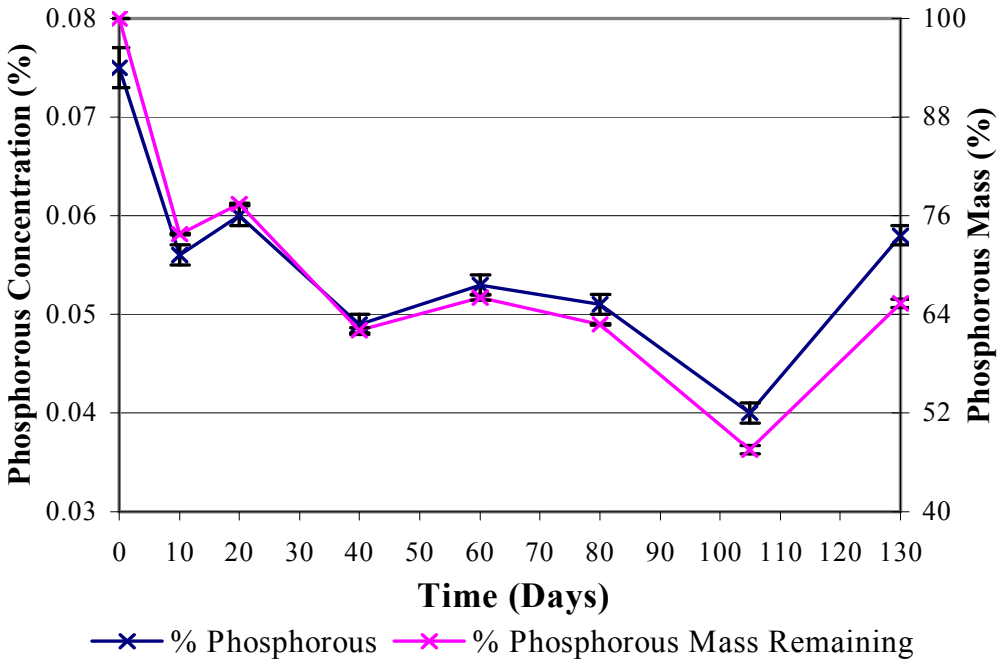


Table 3.23: Phosphorous concentration and absolute phosphorous mass as a proportion of initial mass in *Nothofagus fusca* young stem bark buried at Ilam Campus site over time

Days in Field	Phosphorous concentration (%)	Phosphorous Mass Remaining (%)
0	0.075 ± 0.002	100
10	0.056 ± 0.001	73.8 ± 0.1
20	0.060 ± 0.001	77.4 ± 0.1
40	0.049 ± 0.001	62.1 ± 0.3
60	0.053 ± 0.001	66.0 ± 0.3
80	0.051 ± 0.001	62.8 ± 0.1
105	0.040 ± 0.001	47.5 ± 0.5
130	0.058 ± 0.001	65.3 ± 0.5

Note: Error values given are standard errors of the mean.

3.5 Decomposition of *Nothofagus fusca* litter mixtures

Differences between actual and expected mass losses occurred in several of the microcosms containing mixtures of *Nothofagus fusca* litter, as shown in Table 3.24. Substantial variations in the amount of mass loss between replicates were identified in many cases, resulting in the calculation of comparatively large error values. For the leaves-twigs and leaves-flowers-twigs-bark combinations, error values were particularly large, as in both cases one microcosm showed approximately twice the amount of mass loss as the other two replicates. Only one litter combination produced a statistically significant non-additive result at α=0.05. This combination was the leaves-flowers mixture, and as actual mass loss was less then expected, the effect was considered to be antagonistic. No change in litter mass was detected in the control microcosms.

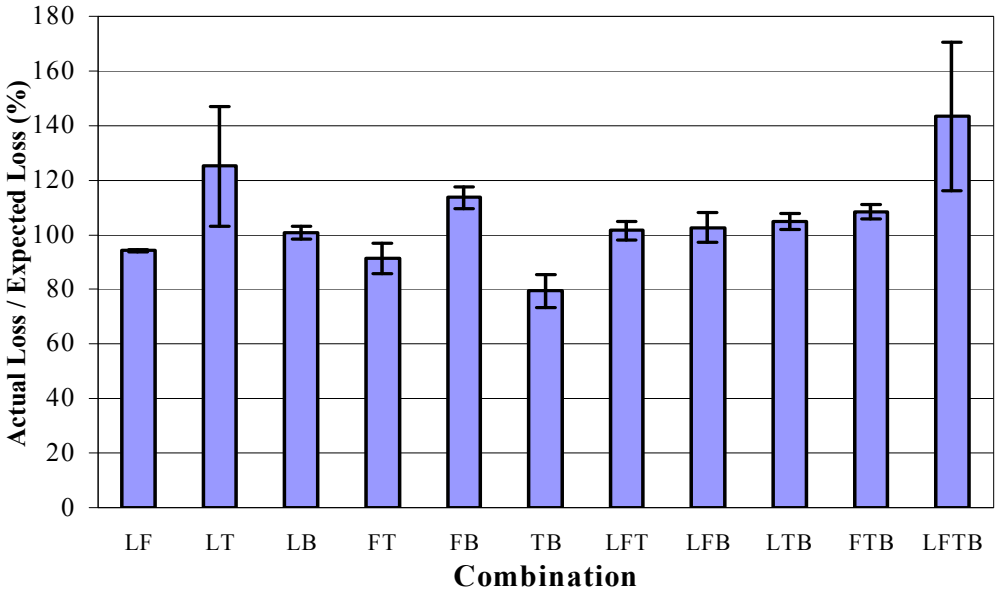
Table 3.24: Expected and actual mass loss from mixed *Nothofagus fusca* litter after incubation in microcosms for 200 days

Litter Combination	Expected mass loss (%)	Actual Mass Loss (%)
LF	27.0	25.4 ± 0.1
LT	18.6	23.2 ± 4.1
LB	16.2	16.3 ± 0.4
FT	21.2	19.4 ± 1.2
FB	18.8	21.3 ± 0.7
TB	10.7	8.5 ± 0.6
LFT	22.2	22.5 ± 0.8
LFB	20.6	21.1 ± 1.1
LTB	15.1	15.9 ± 0.4
FTB	16.8	18.3 ± 0.4
LFTB	18.7	26.8 ± 5.1

Note: Error values given are standard errors of the mean.

Litter types are abbreviated as Leaves (L), Flowers (F), Twigs (T) and Young Stem Bark (B).

Figure 3.19: Proportion of actual mass loss to expected mass loss in mixed *Nothofagus fusca* litter microcosms



Note: Error bars indicate standard errors of the mean.

Litter types are abbreviated as Leaves (L), Flowers, (F), Twigs (T) and Young Stem Bark (B).

CHAPTER FOUR: DISCUSSION

4.1 Floral and Bark litter production

Rochow (1974) discussed the inherent difficulties in conducting forest litter surveys to a standardised procedure due to the natural variability of the forest floor surface. This study was affected by these problems, as the placement of quadrats for litter collection was biased towards relatively flat areas, avoiding sampling on fallen logs and branches, to make collections more easily accomplished. Observations indicated fallen logs tended to have less litter accumulated on top, but more around the sides, as litter falling on logs tended to slide off, so the consequences of this bias to the accuracy or results was not considered to be significant.

The majority of litter collected was identified as originating from *Nothofagus fusca*. The greatest proportion of material from species other than *Nothofagus fusca* was found to be leaves (mostly from *Nothofagus menziesii*), although this was determined to be less than 2% of the total leaves sorted from any one collection of litter. Sites 1, 2, 5 and 7 all produced similar floral masses, while values for sites 3, 4 and 6 were significantly higher (refer Table 3.1).. Variability in litter production between sites can be caused by differences in soil fertility (Lamb and Florence, 1975), and the accumulation of litter can be influenced by the predominant wind direction (Orndorff and Lang, 1981; Shure and Gottschalk, 1985). However, these factors were not assessed in this study, and were not considered in relation to differences in litter masses collected. All sites were old-growth *Nothofagus fusca – Nothofagus menziesii* stands (Stewart and Burrows, 1994), minimising variability in litter production due to differences in stand age (Odum, 1969).

Flowering in *Nothofagus fusca* has been reported as occurring from September to October (Ogden *et al*., 1996), and observations at the 7 sites in November supported this since there was little floral material extant on the trees. Very little discernible floral material was present in samples collected during the May 2000 survey, indicating that most floral litter changed beyond recognition in 6 months or less on the forest floor, due to weathering and/or microbial decomposition. This also implied that it was highly unlikely that floral litter produced in the 1998 flowering season remained in a recognisable form long enough to be included in the November 1999 survey. Hence, it seems reasonable to suggest that the estimated standing crop of floral material on the forest floor represents the actual production of floral material by *Nothofagus fusca* in the 1999 season, and was therefore 734 ± 76 kg ha^{-1}.

Estimation of floral litter production by *Nothofagus fusca* has not been reported in other studies. Sweetapple and Fraser (1992) studied litter production from a mixed *Nothofagus fusca – Nothofagus menziesii* forest in the central North Island of New Zealand, but floral litter masses were presented in combination with seeds, bud scales, mosses, lichens and various other materials. Floral litter was mentioned as being a major component of litter production from October to January, but no numerical data on floral production alone was given. Floral production in *Nothofagus fusca* was similar to the estimate of 720 ± 61 kg ha^{-1} determined by Alley *et al*. (1998) for *Nothofagus truncata* floral production in a mast season in 1994.

Estimates of annual floral production by other species vary widely. Stocker *et al*. (1995) estimated floral litter fall in lowland and tableland rain forests to be 320 kg ha^{-1} and 600 kg ha^{-1} respectively, while Gosz *et al*. (1972) estimated annual floral litter fall in the Hubbard Brook Experimental Forest to be 23 kg ha^{-1}. Estimates as high as 3829 kg ha^{-1} of annual floral litter have been calculated for *Camellia japonica* (Walker, 1994), while 2400 kg ha^{-1} was produced in a Venezuelan rain forest (Cuevas and Medina, 1986). At the other extreme, Jensen (1974) reported annual floral production by *Fagus sylvatica* to

be only 2 kg ha^{-1}, based on unpublished data. Annual floral production is mentioned in various other studies, but the tendency to combine all reproductive material prevents determination of floral production alone (Whittaker *et al*., 1974; Kunkel-Westphal and Kunkel, 1979; Proctor *et al*., 1983; Scott *et al*., 1992).

Ogden *et al*. (1996) reported *Nothofagus fusca* leaf fall peaks from September to November. However, the standing crop of recognisable *Nothofagus fusca* foliar litter was approximately 1 Mg ha^{-1} less in mid-November 1999 than in May 2000 (refer Table 3.1). *Nothofagus fusca* does not have two peak litter fall periods as do other *Nothofagus* species (Ogden *et al*., 1996), hence peak foliar litter production must have shifted, as more leaf litter was present after November, rather than before. Alley *et al*. (1998), studying *Nothofagus truncata* and *Nothofagus menziesii* litter fall patterns in the Orongorongo Valley, New Zealand, also found that annual peaks of leaf fall shifted significantly in both species during years of prolific flowering. Peaks in leaf fall were found to occur earlier, with comparatively little leaf fall occurring when the majority of floral litter fell. As no data on litter layer composition prior to November 1999 was generated by this study, it cannot be determined if peak leaf litter production in *Nothofagus fusca* occurred earlier in the year as with other *Nothofagus* species.

The shift in maximum leaf fall in *Nothofagus fusca*, no matter the direction, may be considered the result of changes to the internal allocation of nutrients and energy reserves in *Nothofagus fusca* from the production of vegetative to reproductive structures, including flowers and seeds. Bazzaz *et al*. (1987) discussed this phenomenon, concluding that plants carry out various nutrient allocation strategies to alter internal nutrient utilisation. Alley *et al*. (1998) came to the same conclusion, deducing that significant internal redistribution of energy and nutrient reserves from leaf to reproductive material occurred in *Nothofagus truncata* and *menziesii* in mast flowering years. Pregitzer and Burton (1991), studying *Acer saccharum*, also found similar changes to foliar

litter production during mast years, and likewise concluded alterations to resource allocation strategies were responsible.

Miller and Hurst (1957), studying *Nothofagus truncata*, and Alley *et al*. (1998) identified another effect of mast events in *Nothofagus*. Both studies reported significant decreases in foliar litter production in the year subsequent to mast flowering, i.e. the year of mast seeding. The time limitations of this study did not allow investigation to determine if this phenomenon occurred in *Nothofagus fusca* after mast flowering.

As *Nothofagus fusca* does not shed bark in significant quantities (Wardle, 1984), the amount of bark material on the forest floor was assumed to be dependent upon the production of coarse woody debris (CWD). The total standing crop of CWD on the forest floor, not including standing dead trees (snags) was estimated to be 73 ± 5 Mg ha^{-1}. This was less than the figure of 91.7 Mg ha^{-1}, calculated from surveys performed in 1991-1992 by Stewart and Burrows (1994) for Rough Creek (refer Figure 2.1). The difference between these figures can be partially explained by the continued presence of large masses of CWD on the forest floor produced from mass mortality of *Nothofagus fusca* in 1978-1980 (Hosking and Kershaw, 1985).

Amounts of CWD from *Nothofagus menziesii* were estimated to be a small percentage of *Nothofagus fusca* CWD, while unidentified CWD was in the order of 25% of *Nothofagus fusca* CWD by volume. It was possible that a large proportion of the unidentifiable volume was unrecognisable *Nothofagus fusca* material, due to the small percentage of CWD from other species. Stewart and Burrows (1994), working at Rough Creek, determined the volumes of fallen *Nothofagus menziesii* CWD and unidentifiable CWD to be 4-8% and 18% of *Nothofagus fusca* volume respectively. *Nothofagus menziesii* CWD volumes were similar to those calculated in this study, but the volume of unidentifiable CWD was notably larger. This was considered a consequence of the gradual decomposition of *Nothofagus fusca* CWD, produced as a result of mass mortality (Hosking and Kershaw, 1985), making positive identification more difficult.

The mass of fallen *Nothofagus fusca* CWD in 1991-1992 was also estimated in two areas in the Maruia Valley by Stewart and Burrows (1994), and these were determined to be 77.5 and 119.4 Mg ha^{-1} for Station Creek and Fergies Bush respectively. These values were notably different to the 91.7 Mg ha^{-1} determined for Rough Creek, indicating CWD accumulation was affected by site. Stand age at the three sites were considered to be the same, and was therefore not a source of variance. However, as uncertainties in these values were not provided, the significance of the differences in standing crops of *Nothofagus fusca* CWD between sites cannot be determined. Standing crops of fallen CWD in other ecosystems vary considerably. Harmon *et al*. (1986) determined standing crops of CWD in temperate forest ecosystems of various ages to range from 10 to 511 Mg ha^{-1}, based on a large number of studies. CWD accumulation in *Nothofagus fusca* forest ecosystems was roughly in the middle of this range.

The mass of bark associated initially with fresh CWD was determined to be approximately 18% of the total mass. This was determined using a bark thickness formula, calculated using volume measurements, and the specific gravity of bark on standing *Nothofagus fusca* and fresh CWD (Appendix B). Wardle (1984) presented similar bark thickness formulae for three other *Nothofagus* species, and commented that bark thickness in *Nothofagus fusca*, although not given, was observed to be equal or greater than other *Nothofagus* species. This was found to be the case, as bark thickness in *Nothofagus fusca* was determined to be roughly twice that of *Nothofagus solandri* var. *solandri* (Black Beech) and *Nothofagus solandri* var. *cliffortioides* (Mountain Beech).

Miller (1963) found bark mass in live standing *Nothofagus truncata* to range from 13% to 28% of associated wood mass, depending upon the sampling height, although the average bark to wood mass proportion over the entire tree was calculated to be 17%. Comparisons to other species are of limited use, since bark masses are highly variable between different species (Olsson, 1978; Harmon *et al*., 1986), ranging from 8% in *Pinus contorta* (Fahey, 1983) to 27% in *Pinus pinaster* (Brown *et al*., 1996).

Relating the mass of *Nothofagus fusca* CWD on the forest floor to bark mass on the forest floor was not straightforward. Fahey (1983), working with *Pinus contorta*, and Brown *et al*. (1996), studying the decomposition of CWD from six species, determined that mass loss from bark occurred at approximately the same rate as mass loss from the associated wood. If *Nothofagus fusca* bark and wood lost mass at the same rate, then the bark thickness formula would predict the proportion of bark mass in CWD, regardless of the level of decay.

Conversely, Schowalter (1992) determined that mass loss from inner and outer bark of *Quercus* species was 71% and 62% respectively over two years in the field, while mass loss from sapwood and heartwood over the same time was 31% and 45%. Additionally, Grier (1978) concluded that approximately 50% of initial mass loss from *Tsuga heterophylla* CWD in the field was due to the decay of bark. Since bark mass initially comprised substantially less than 50% of *Tsuga heterophylla* CWD mass, it was concluded that the bark proportion of CWD mass decayed faster than the wood in this species.

The loss of bark from CWD can also occur via sloughing, wherein whole bark fragments detach from the wood surface, due to weathering and microbial or animal activity, and fall to the forest floor (Grier, 1978; Krankina *et al*., 1999). Sloughed bark fragments can therefore cause overestimates in bark decay if not accounted for, as the bark may not have undergone substantial mass loss prior to falling off. It was noted, however, that once in contact with the forest floor, fragments of bark tend to decompose more rapidly than when attached to CWD, and this is considered to be the result of increased exposure to the soil microbial community (Olsson, 1978; Fahey, 1983).

Inspections of *Nothofagus fusca* CWD on the forest floor indicated that although bark mass may have initially been 18% of total CWD mass, bark mass (i.e. the external surface of the CWD naturally covered by bark in living trees) decreased markedly with age, and bark was frequently absent on smaller (<200mm in diameter) pieces of CWD. Few pieces of fresh CWD with a complete bark layer were observed. The proportion of bark remaining on *Nothofagus fusca*

CWD in varying stages of decay was assessed (Appendix C), and it was postulated that the proportion of bark to wood mass decreased over time, agreeing with Grier (1978) and Schowalter (1992). However, the mass of sloughed *Nothofagus fusca* bark present on the forest floor in an identifiable form was unable to be determined. Observations in the field indicated only a small mass of material recognisable as sloughed *Nothofagus fusca* bark was present in the litter layer around CWD, indicating that little bark sloughed off *Nothofagus fusca* CWD and / or any sloughed bark fragments decayed relatively rapidly (Olsson, 1978; Fahey, 1983). Consequently, it was not possible to accurately estimate the proportion of bark that sloughed off during decomposition.

The mass of bark material attached to fallen wood was estimated to be approximately 10% of CWD mass, equal to 7.3 Mg ha^{-1}, based on the bark mass remaining on CWD (Appendix C). It must be stressed that confidence in the accuracy of this figure was very low, due to the number of assumptions and the unknown influences of sloughing on the derivation of this value.

As with all other facets of bark dynamics, bark litter inputs in forest ecosystems were generally highly variable, and significantly influenced by disturbances such as windthrow and pathogen activity that affect CWD production (Harmon *et al*., 1986). For example, Whittaker *et al*. (1974) estimated annual stem bark production in the Hubbard Brook forests from 1956-1960 and 1961-1965 to be 292 and 243 kg ha^{-1} respectively, while Gosz *et al*. (1972) determined annual bark litter fall from 1968-1969 in the same area to range from 45-141 kg ha^{-1}. Consequently, comparisons to figures for annual bark production calculated for other ecosystems are of limited value.

Natural bark production of *Nothofagus fusca* was not determined by this study, since CWD inputs of any significance were not detected over the six month monitoring period. This was considered a result of the discontinuous nature of CWD production, as well as the small geographical area and limited time frame of the study (Harmon *et al*., 1986; Rayner and Boddy, 1995). Stewart and Burrows (1994) estimated the annual volume of CWD production in a *Nothofagus fusca*

dominated forest to be 3.2 m^3 ha^{-1} across six years, producing approximately 236 kg ha^{-1} of bark annually. Analysis of the data presented indicated the value was highly variable, and an associated standard error of the mean for CWD inputs calculated from the data was found to be 1.7 m^3 ha^{-1}, or 125 kg ha^{-1} in terms of bark mass.

4.2 Characteristics of Floral and Bark material

The samples of *Nothofagus fusca* floral material used to determine characteristics such as moisture, ash content and nutrient content were carefully scrutinised for any signs of decomposition or leaching prior to use. The concentration of nitrogen and phosphorous in fresh floral litter of *Nothofagus fusca* was determined to be 1.58% and 0.11% respectively, while the ratios of these nutrients to organic carbon were found to be 40.8 for nitrogen and 585 for phosphorus on a moisture free basis. These ratios are considered critical to determining the availability of nutrients within the substrate, and hence also determine the quality of litter. This can be used to infer the relative ease of decomposition (Swift *et al*., 1979).

Comparison to C:N and C:P ratios in the other litter types indicated floral litter was a relatively good quality substrate. Pugh (1974), studying various litters, determined C:N ratios in better quality litters to be around 30, increasing to 200 in very poor quality litters, while Witkamp (1966) inversely related the rate of microbial decomposition to the C:N ratio of the substrate. Nutrient concentrations determined in the floral material of a number of other plant species are given in Table 4.1, while Walker (1994) determined the mean nitrogen concentration in floral litter from 26 species to be 1.9%, ranging from 0.4% for *Grevillea* sp. to 5.0% for *Magnolia stellata*.

Table 4.1: Nitrogen and phosphorous concentrations in fallen flowers

Species	%N	%P	Reference
Acer saccharum and *Fagus grandifolia* (mixed)	0.8	0.0	Gosz *et al*. (1972)
Quercus coccinea	1.5	0.2	Woodwell *et al*. (1975)
Quercus alba	2.6	0.2	Woodwell *et al*. (1975)
Pinus rigida	1.1	0.2	Woodwell *et al*. (1975)
Gaylussacia baccata	1.7	0.2	Woodwell *et al*. (1975)
Vaccinium vacillans	1.7	0.2	Woodwell *et al*. (1975)

Staaf and Berg (1982) commented that nitrogen may be held in various organic components, and the form in which nitrogen is bound influences the availability of that nitrogen to microbes. This inferred that C:N ratios were not absolute indicators of substrate quality, as a variable fraction of nitrogen may be held internally in recalcitrant substances. Consequently, determining the distribution of nitrogen in litter may be important to determining substrate quality (Staaf and Berg, 1982; Wardle and Greenfield, 1991). Acid hydrolysis of floral litter identified that 61% of the nitrogen was in the form of α-amino nitrogen. Greenfield (1992) suggested that the majority of the hydrolysable unidentifiable nitrogen fraction consisted of non α-amino acids and imino acids, while NH_4-nitrogen was largely derived from amides (Greenfield, 1999). Consequently, it was estimated that approximately 90% of nitrogen in *Nothofagus fusca* floral litter was proteinaceous, or, to a lesser extent, in the form of free amino acids, again indicating high substrate quality (Swift *et al*., 1979)

Mass loss from whole *Nothofagus fusca* floral litter due to the leaching of water soluble substances was calculated to be approximately 9% after ten days exposure to water. Absolute losses of nitrogen and phosphorous from the floral litter over the same time were determined to be 13% and 24% of the initial mass respectively.

The leachate from floral litter was shown to support extensive microbial growth. Consequently, it was considered unlikely that water soluble allelopathic or inhibitory substances (Wardle *et al*., 1998) were produced in *Nothofagus fusca* floral material, as inhibition of microbial development would be expected if any were present (Wardle *et al*., 1998). It was considered unlikely that floral litter would undergo leaching to same extent over the first ten days in the field, so this degree of mass and nutrient loss was not expected to be seen after the initial period of incubation for field based experiments.

Floral litter was the best quality substrate when compared to other *Nothofagus fusca* litter types in terms of C:N and C:P ratios (refer Table 3.7). Consequently, when *Nothofagus fusca* floral litter was produced in large quantities, as in the 1999 season, the commensurate allocation of nutrients by *Nothofagus fusca* to floral litter was also considerable, and this will be discussed later in greater detail.

The initial criteria for determining the different types of *Nothofagus fusca* bark were based purely on physical appearance. Branch bark and young stem bark were not split into inner and outer components, since accurate separation was not possible due to the thinness of both materials. Old stem bark was easily split into inner and outer fractions, due to the thickness and obvious division in tissue types, apparent to both the naked eye and under microscopic examination (refer Figure 2.2; Appendix D). The ratio of old stem inner bark to old stem outer bark for *Nothofagus fusca* in terms of mass was large, in the order of 10:1. Olsson (1978), working with pine, birch and spruce bark, determined this particular characteristic was dependent upon species, and was highly variable.

All bark material was sound prior to use in characteristic and nutrient analysis procedures. Substantial differences in nitrogen concentration and distribution, phosphorous concentration and organic carbon content indicated the four bark types were distinct in terms of chemical composition (Table 4.2). Branch bark litter, on the basis of nitrogen and phosphorous content, and C:N and C:P ratios, was the greatest quality substrate of the bark types (Pugh, 1974; Swift

et al., 1979), although the overall range of nitrogen concentrations between all bark types was only 0.4%. The distribution of nitrogen as determined by acid hydrolysis revealed that the greatest protein content was also found in branch bark, further suggesting branch bark was the highest quality substrate of the bark types examined (Greenfield, 1992; Greenfield, 1999). The amounts of nitrogen and phosphorous in the other *Nothofagus fusca* bark types were more variable, and no clear indication of comparative litter quality between young stem bark, old inner stem bark and old outer stem bark was determined (refer Table 4.2).

Table 4.2: Nutrient concentrations and C:nutrient ratios of *Nothofagus fusca* bark

Bark Type	% Nitrogen	C:N	% Phosphorous	C:P
Branch Bark	0.65 ± 0.01	89	0.118 ± 0.004	488
Young Stem Bark	0.38 ± 0.01	153	0.073 ± 0.002	796
Old Stem Inner Bark	0.25 ± 0.01	220	0.084 ± 0.001	656
Old Stem Outer Bark	0.34 ± 0.03	141	0.027 ± 0.001	2041

Note: Errors indicated are standard errors of the mean.

Concentrations of nutrients in the bark of other species are presented in Table 4.3. It should be noted that all values presented were determined from material described as either “bark” or “stem bark”, with no distinction between different bark types on the same species (e.g. branch bark, young stem bark, old stem bark). Nitrogen concentrations varied from 0.16% for *Nothofagus truncata* to 0.56% for *Quercus ilicifolia*, while phosphorous concentrations ranged from 0.015% to 0 .081% for *Quercus marilandica* and *Vaccinium vacillans* respectively. Comparisons with *Nothofagus fusca* bark indicated that nitrogen and phosphorous concentrations in young stem bark and both old stem bark types

were not unusual, although nitrogen and phosphorous content in *Nothofagus fusca* branch bark was greater than any of the values compiled in Table 4.3.

Table 4.3: Nutrient concentrations in bark

Species	%N	%P	Reference
Nothofagus truncata	0.20	0.04	Miller (1963)
Quercus stellata	0.55	0.016	Johnson and Risser (1974)
Quercus marilandica	0.48	0.015	Johnson and Risser (1974)
Quercus coccinea	0.32	0.042	Woodwell *et al*. (1975)
Quercus alba	0.42	0.047	Woodwell *et al*. (1975)
Pinus rigida	0.23	0.060	Woodwell *et al*. (1975)
Quercus ilicifolia	0.56	0.063	Woodwell *et al*. (1975)
Gaylussacia baccata	0.47	0.044	Woodwell *et al*. (1975)
Vaccinium vacillans	0.55	0.081	Woodwell *et al*. (1975)
Kalmia angustifolia	0.43	0.026	Woodwell *et al*. (1975)
Psuedotsuga menziesii	0.19	ND	Fogel and Cromack (1977)

Note: ND indicates value was not determined

Brown *et al*. (1996) determined nitrogen and phosphorous concentrations in two types of bark from six different species. The bark types were identified as "small bark" and "large bark", and were considered equivalent to branch bark and young stem bark respectively, based on physical descriptions provided. These are shown in Table 4.4, and indicated that nitrogen and phosphorous concentrations in small bark were generally greater than in large bark, as was found to be the case for *Nothofagus fusca* branch and young stem bark.

Table 4.4: % Concentration of nitrogen and phosphorous in bark types of various species on dry weight basis (adapted from Brown *et al*., 1996)

Species	Nitrogen (%)		Phosphorous (%)	
	Small Bark	Large Bark	Small Bark	Large Bark
Allocasuarina fraseriana	0.49	0.39	0.009	0.006
Banksia grandis	0.25	0.09	0.013	0.005
Eucalyptus calophylla	0.25	0.20	0.031	0.018
Eucalyptus diversicolor	0.16	0.15	0.011	0.011
Eucalyptus marginata	0.19	0.14	0.026	0.015
Pinus pinaster	0.17	0.12	0.014	0.006

Comparisons between old stem inner and outer bark of *Nothofagus fusca* revealed inner bark held less nitrogen, but significantly more phosphorous, and this was also shown in C:N and C:P ratios. This contradicted the conclusions of a number of other studies, which reported greater nitrogen concentrations in inner bark (Olsson, 1978; Harmon *et al*., 1986). For example, Schowalter (1991) found the concentration of nitrogen in outer bark across a range of *Quercus* species to be approximately 17% less than in inner bark. Little difference in the distribution of nitrogen in inner and outer bark following acid hydrolysis was detected in this study (refer Table 3.5), and this was also considered to contradict the prevalent theory that inner bark is a better substrate than outer bark (Olsson, 1978; Schowalter, 1992).

Phosphorous content in old stem outer bark of *Nothofagus fusca* was 32% of that in old stem inner bark. This agreed qualitatively with other studies (Woodwell *et al*., 1975; Schowalter, 1992), but the difference in phosphorous content was greater in *Nothofagus fusca* when compared to other species, barring *Pinus rigida*, which was found to have a phosphorous concentration in outer bark only 28% of that in inner bark.

Olsson (1978) produced the only other study found reporting the results of leaching on mass loss in bark material. Water soluble materials in *Picea abies* (Norway spruce), *Pinus silvestris* (Scots pine) and *Betula verrucosa* (birch) were

found to comprise 15-25% of total bark mass, while the mass of water soluble substances in inner bark and outer bark from these species was 20-25% and 2-3% respectively. Mass loss via the leaching of water soluble substances from *Nothofagus fusca* bark types (refer Table 3.8) was less than in other species, ranging from 8.2-13.3%, while the similarity between inner and outer bark in water soluble content (8.2% in both cases) again contradicted the conclusions of Olsson (1978).

Substantial proportions of the total amount of nitrogen in all bark types were soluble in water, ranging from 25% for old stem inner bark to 44% for branch bark, and were roughly correlated to the initial mass of nitrogen in the bark. The proportion of phosphorous held in water soluble substances in *Nothofagus fusca* bark was determined to be very large, since any phosphorous present in bark material after leaching could not be detected (refer Table 3.8).

Olsson (1978) identified one potential artefact of the leaching procedure employed in this study. Semipermeable membrane integrity greatly influences the movement of water soluble substances from bark cells, hence conditions that result in damage to this membrane, such as desiccation or freeze-thaw cycles, which cause cells to become “leaky”, increasing rates of leaching. As all *Nothofagus fusca* litter was air dried prior to use in leaching experiments, it was assumed that the observed rates of leaching were increased by this phenomenon. As desiccation should not radically alter the nature of the chemicals within the bark tissue, it was presumed that air drying should have had little effect on the total content of water soluble substances in the bark.

Microbial growth in the leachates of the *Nothofagus fusca* bark types developed rapidly, except in the case of old stem inner bark, in which microbial growth was markedly slower and less extensive (refer Table 3.8). Anti-fungal substances have been found in the wood of various tree species (Bultman and Southwell, 1976), including *Nothofagus* (Rayner and Boddy, 1988), but no evidence was produced from this study to indicate water soluble substances extracted from *Nothofagus fusca* bark possessed antimicrobial capacities (Wardle,

1998). As with floral litter, exposure of bark material to water in the field would most likely be less extensive than in the leaching experiments, hence the export of water soluble substances in the field was expected to take longer.

4.3 Decomposition of floral and bark material in microcosms

Determination of decay rates of the floral litter in microcosms indicated that 95% mass loss would have occurred in 4.4 years at 10^{o}C, or in 3.2 years if maintained at 17^{o}C, using a constant fractional mass loss model with no litter inputs to determine *k* (Olson, 1963). Swift *et al*. (1979) suggested that a linear model allowed the best estimation of *k* for fast decomposing litter types, citing reproductive material as an example, but this was not appropriate in this case due to the curvilinear mass loss kinetics displayed at higher temperatures (refer Figure 3.3). *k* values and estimated time for 95% mass loss for Nothofagus *fusca* bark material in microcosms were calculated using the same model (Olson, 1963), and are shown in Table 4.5, which also includes values for floral litter decomposition. Only data from incubation at 10^{o}C and 17^{o}C is presented in this table, as the greatest difference in decomposition dynamics was generally found between these temperatures. Moisture levels in all microcosms were maintained at a level considered to be optimal for microbial activity throughout incubation.

Mass loss from *Nothofagus fusca* litter types incubated in microcosms was compared to initial litter qualities using stepwise multiple regression analysis, and the most important factor for determining mass loss was found to be C:N ratios ($t = 10.34$, $P < 0.0005$). Water soluble nitrogen contents and C:P ratios were also significant at $P < 0.0005$, but were less important for predicting mass loss as the *t* statistics calculated were smaller. Temperature of incubation was also included in the regression, and was significant at $P < 0.001$, less than any of the litter characteristics.

Table 4.5: *Nothofagus fusca* floral and bark decay constants

Litter Type	Temperature	*k*	Mass Loss After 1 Year (%)	95% Mass Loss (Years)
Floral	10°C	0.68 ± 0.02	49.3	4.4 ± 0.1
	17°C	0.95 ± 0.02	61.3	3.2 ± 0.1
Branch Bark	10°C	0.13 ± 0.01	12.2	23 ± 2
	17°C	0.26 ± 0.01	22.9	11.5 ± 0.5
Young Stem Bark	10°C	0.08 ± 0.01	7.7	37 ± 6
	17°C	0.14 ± 0.01	13.1	21 ± 2
Old Stem Inner Bark	10°C	0.03 ± 0.01	3.0	100 ± 50
	17°C	0.05 ± 0.01	4.9	60 ± 15
Old Stem Outer Bark	10°C	0.05 ± 0.01	4.9	60 ± 15
	17°C	0.11 ± 0.01	10.4	27 ± 3

Note: Errors given are standard errors of the mean

The majority of studies investigating the relation between substrate quality and decomposition rates have concluded lignin:N ratios provide the best prediction of mass loss based on substrate quality (Fogel and Cromack, 1977; Meentemeyer, 1978; Keenan *et al*. 1996). As lignin content was not determined in this study, it is possible that lignin:N ratio could have provided a better estimate of decomposition rates. It was noted, however, that Taylor *et al*. (1989) concluded C:N ratios provided the most accurate predictive capacity for decomposition after comparing the effect of lignin:N and C:N ratios on decomposition in microcosms. The correlation between decomposition rates and the content of water soluble nitrogen has also been identified previously (Nykvist *et al*., 1959).

Data on the decomposition of floral litter in microcosms was only available from one source (Walker, 1994), and the comparatively rapid decomposition of *Nothofagus fusca* floral litter agreed with these findings. No comparative data on mass loss from bark litter incubated in microcosms was

found, but results agreed with the consensus that bark decomposition is slow (Fogel and Cromack, 1977; Olsson, 1978; Brown *et al*., 1996; Scowcroft, 1997).

Figures for mass loss were underestimates, since microbial biomass was not removed from the litter prior to weighing (Jones and Worrall, 1995). Samples taken from the microcosms during decomposition indicated that although microbial growth in the tubes may have been visually dense, the actual microbial biomass in the microcosms was very low. Estimations of microbial mass in the microcosms ranged up to 4 mg, and the underestimate was therefore considered slight. Consequently, the overall effect of the underestimation on mass loss results was considered to be negligible.

Interpreting the net nitrogen mineralisation rates of *Nothofagus fusca* floral and bark litter in microcosms was not so straightforward. Net nitrogen mineralisation from floral litter was found to be approximately 4% and 1% after 200 days at 10^{o}C and 17^{o}C respectively, while net mineralisation of nitrogen was not detected from any bark litter type.

These figures do not take into account the mass of nitrogen that was mineralised from the litter and immediately assimilated into microbial biomass, rather than released as mineral nitrogen. The amount of microbial biomass in the microcosms can be quantified by determination of the amount of microbial growth, while increases in the alkalinity of the contents of the microcosm can be used to infer the extent of microbially mediated decomposition that has occurred (Jensen, 1974). Since both significant pH increases and extensive microbial growth occurred in the microcosms containing floral litter, it was suggested that mineralisation of nitrogen from *Nothofagus fusca* floral litter occurred at a faster rate than was determined. The amount of assimilated nitrogen can be calculated by determining the nitrogen concentration in the microbial tissue, but as microbial biomass in the tubes could not be accurately determined, this figure could not be quantified.

Clinton *et al* (1999) indicated nitrogen concentration in fungal sporocarp tissue ranged from 1 - 6%. From this, it was calculated that 1mg of microbial

biomass may contain up to 60μg of nitrogen. Although microbial biomass was not estimated, it was determined that the nitrogen released from floral litter and assimilated into microbial tissue of nitrogen can constitute a large proportion of total nitrogen release. For example, it was calculated that the mineralisation of 10% of the total nitrogen content of 500 mg of floral litter was required to support the growth of only 4 mg of microbial biomass. As 4% net nitrogen mineralisation was detected in microcosms containing an estimated 4 mg of microbial growth, actual net nitrogen mineralisation may have been as high as 14%. However, this figure is presented only to illustrate the potential for underestimation of net nitrogen mineralisation without accurate determination of microbial nitrogen content, rather than as a precise value.

Consideration of this factor with regards to mineralisation from bark litter indicated that net mineralisation was also underestimated (refer Table 3.17). Less extensive growth was generally observed in bark microcosms, however, so the magnitude of the underestimate in the case of the bark litter types was considered to be less.

Actual mass loss differed from expected mass loss in many of the microcosms containing mixtures of *Nothofagus fusca* litter, and large variances were identified between replicates. Consequently, significant non-additive effects were statistically indicated at $\alpha = 0.05$ for only the leaves-flowers combination, and as mass loss was lower than expected, an antagonistic effect was concluded to have occurred in this mixture of litter types. Large differences to expected mass loss were observed in other combinations, particularly the leaves-twigs, twigs-bark and leaves-flowers-twigs-bark mixtures, but could not be supported at $\alpha = 0.05$ due to the substantial variance between replicates (refer Figure 3.20).

The reasons for the large variance in mass loss between mixed litter microcosm replicates compared to single litter microcosm replicates is unknown, and cannot be explained. All replicates were inoculated with the same soil solutions, and incubated under identical temperature and moisture conditions, as were all microcosm replicates from any portion of this study.

Wardle *et al*. (1997), commenting on the findings of mixing leaf litter from up to eight different species in the field, identified litter mixing as capable of producing large, if unpredictable results. The similarly idiosyncratic results obtained by this study prevent any conclusions regarding non-additive effects of mixing *Nothofagus fusca* litter being made with any confidence. Although one antagonistic effect was statistically significant, further effects may have been proven statistically significant if additional replicate microcosms had been utilised.

Microcosms used in this study did not simulate various environmental factors (Pomeroy, 1970), such as temperature and moisture cycles, leaching or the effects of microfauna, all of which can influence rates of litter decomposition (Swift *et al*., 1979; Meentemeyer, 1978; Day, 1983; Williams and Alexander, 1991). Other criticisms of microcosm based studies have been made regarding artefacts arising from this technique. Daubenmire (1963) reported decomposition of litter in microcosms was an artefact of temperature of incubation, negating any influence of litter quality on decomposition processes. This finding was refuted somewhat, as three measures of substrate quality (water soluble nitrogen content, C:N ratios and C:P ratios) were all determined to be statistically more important than ambient temperature in predicting mass loss from *Nothofagus fusca* litter incubated in microcosms. Anderson (2000) highlighted the accumulation of microbial waste products and the development of anaerobic microsites in the microcosms, results of the static nature of the microcosm environment, as other effects which could influence microbial activity, and hence decomposition rates.

The majority of these effects were recognised before experimental work commenced. The purpose of examining mass loss and nitrogen mineralisation in microcosms was not to approximate decomposition rates in the field, but to determine comparative amounts of decay under identical, controllable conditions.

4.4 Decomposition of floral and bark material in the field

Litter bag experiments produced a range of data on the dynamics of both mass loss and nutrient transfers from *Nothofagus fusca* floral and bark litter over time in the field. Ashing of samples taken from the litterbags indicated that soil contamination in the litterbags was minimal. Despite this, all estimations of mass loss and nutrient change were calculated on an ash free basis, to eliminate this source of interference with results.

Rapid initial mass loss via the leaching of water soluble substances from plant litter has been identified by various workers (Gosz *et al*., 1973; Swift *et al*., 1979; Day, 1983), but this was not clearly distinguishable from mass loss attributed to microbial activity in the data generated by this study. Only a fraction of the total mass of *Nothofagus fusca* floral and young stem bark was determined to be water soluble after extensive leaching in the laboratory (refer Table 3.8). As higher values were determined for litter from other species after less rigorous exposure to water (Day, 1983), rapid mass loss from the *Nothofagus fusca* litter via leaching in the field was not considered to occur, but could still be significant over time. As with microcosms, microbial biomass was noted in the litter bags, but not removed from the litter, so mass losses were considered slight underestimates.

The decay rate constant, *k*, for floral material after 200 days in the field was calculated to be 0.94 ± 0.01. From this it was estimated that 95% mass loss from *Nothofagus fusca* floral litter would occur after 3.2 ± 0.1 years at the Lewis Pass Reserve site. This value was similar to that determined for mass loss from floral litter in microcosms incubated in the laboratory at 17^{o}C and 25^{o}C, but substantially greater than that for mass loss in microcosms incubated at 10^{o}C. Little comparative information was available on *in situ* floral decomposition, other than data generated by Walker (1994), using whole flowers from four species buried in litterbags. From the data provided in the aforementioned study, decay rate constants were calculated, ranging from 2.41 for *Broussonetia*

papyrifera floral litter (2.0% nitrogen) to 1.02 for *Grevillea* spp. floral litter (0.4% nitrogen). This indicated *Nothofagus fusca* floral litter was slow to decompose compared to floral litter from other species, although further data from a wider range of flower types are required to determine this conclusively.

It was noted that the decomposition periods used by Walker (1994) were approximately 10% less than in this study. As rates of mass loss from litter tend to decrease over time (Swift *et al*., 1979), the decay rates calculated from the data of Walker (1994) were considered to be slightly inflated compared to the findings of this study. The soil type used by Walker (1994) to incubate litter bags was also different to that used in this study, and it is possible this can influence decay rates, as identified in this study for bark decomposition, and by others (Florence and Lamb, 1974).

Mass loss from the floral litter bags appeared to follow sigmoid kinetics initially, then levelled out to a relatively constant rate of mass loss (refer Figure 3.6). This was interpreted as rapid decomposition of the readily metabolised materials in the floral litter (Swift *et al*., 1979) followed by slower, more consistent decomposition, presumed to occur as a result of the exhaustion of higher quality substances in the litter by decomposition and leaching, leaving only more recalcitrant materials. (Swift *et al*., 1979).

Decay rate constants calculated for *Nothofagus fusca* young stem bark after 130 days in the field at the Lewis Pass Reserve and Ilam Campus sites were 0.45 ± 0.01 and 0.31 ± 0.01 respectively. From these values it was calculated 95% mass loss from the young stem bark litter in the field would occur after 6.7 ± 0.2 and 9.7 ± 0.3 years at the Lewis Pass and Ilam Campus sites respectively. Decay rates in the field were found to be substantially higher than in microcosms. Ninety five percent mass loss was calculated to occur three times faster at the Lewis Pass Reserve site than in microcosms incubated at 17^{o}C, while 95% mass loss at Ilam Campus site was calculated to occur twice as fast (refer Table 4.6). This point indicated that conditions in microcosms were not conducive to young stem bark decay, since decomposition was markedly slower than in the field.

Fogel and Cromack (1977) determined decay rate constants (*k*) for *Pseudeotsuga menziesii* bark litter after two years in the field in litter bags (mesh size 1mm) to range from 0.03 to 0.04. Scowcroft (1997), working with *Acacia koa* and *Metrosideros polymorph*, calculated decay rate constants for the bark material from these trees to be 0.13 and 0.26 respectively, after 252 days in the field in litter bags (mesh size 1.5mm). Both the aforementioned studies incubated material in the native soils of the plant material, but used litter bags with larger mesh sizes than used in this study. Comparison of decay rate constants indicated the decomposition of *Nothofagus fusca* young stem bark was much more rapid than *Pseudeotsuga menziesii* bark decomposition, and also considerably faster than *Acacia koa* and *Metrosideros polymorph* bark decomposition. One factor not discussed by Fogel and Cromack (1977) or Scowcroft (1997) was the size of the bark material placed in the litter bags and decomposed. Bark fragment size influences rates of decomposition (Olsson, 1978) as many small fragments generally decompose faster than a single fragment of equal mass, due to the greater available surface area providing a larger area for leaching and microbial colonisation (Swift *et al*., 1979). This factor may explain some of the difference in results, but cannot be resolved due to the lack of data.

Another potential source of variance was the differences in the length of incubation, which, as already discussed, potentially influenced the accuracy of comparisons between decay rate constants (Swift *et al*., 1979). The *Nothofagus fusca* bark material was only incubated for 130 days, as opposed to periods of 252 days and two years for the other bark types mentioned. Consequently, it was postulated that the decay rate constant for *Nothofagus fusca* young stem bark would have been less over a longer incubation period. This had, in fact been planned, but the sets of long term (>200 days) litter bags at both the Lewis Pass Reserve and Ilam Campus sites were destroyed in the field by animal disturbance, and were not able to be replaced due to time constraints.

The kinetics of mass loss from young stem bark were generally linear at both sites, although the rate of mass loss was significantly greater at the Lewis

Pass Reserve site (refer Figure 3.14). This indicated that the rate of decomposition of the young stem bark over 130 days in the field was relatively constant, although it was considered probable that decay rates would slow down after longer exposure in the field (Swift *et al*., 1979).

The initial decrease in nitrogen concentration in *Nothofagus fusca* floral and bark material incubated in the field was most likely due to the leaching of water soluble nitrogenous substances (Berg and Staaf, 1981; Staaf and Berg, 1982). This was also seen in absolute nitrogen content in the litter, which decreased after ten days in the field. At the completion of the final time period for floral litter (200 days) and young stem bark litter (130 days), nitrogen concentrations were found to be higher than initial levels. In the case of floral litter, increased nitrogen concentration was considered to be predominantly the result of the mineralisation of non-nitrogenous substances (Gosz *et al*., 1973; Swift *et al*., 1979), rather than inputs of nitrogen (Bocock, 1963; Swift *et al*., 1979). This was concluded since the absolute content of nitrogen in the floral litter increased over only one time period, and that increase was only 1.9% (refer Figure 3.8).

The increase in nitrogen concentration in the young stem bark was determined to be substantially influenced by nitrogen inputs, unlike floral material. This was concluded from the repeated increases in absolute nitrogen content of the young stem bark litter at both sites, occasionally beyond initial levels, indicating that significant nitrogen inputs had occurred (refer Figures 3.15; 3.16). Various mechanisms for nitrogen import have been suggested, including precipitation (Grier, 1978), throughfall and stemflow deposition (Parker, 1983), translocation, biological nitrogen fixation, movement of organisms (microbial or otherwise) and absorption of leachates (Heal *et al*., 1982), but it was not possible to determine which of these pathways was responsible for the increases in nitrogen content.

The analysis of nitrogen content was performed after samples had been oven dried at 105^{o}C, and Bremner (1965a) commented that this may cause the

loss of ammonium from soil samples. However, Wardle *et al*. (1997), referring to unpublished data, stated that only negligible nitrogen loss occurred from plant material during drying at 70°C and 105°C. The results of comparisons between the nitrogen content of fresh and oven dried *Nothofagus fusca* floral and bark litter indicated that changes in nitrogen content did not occur (Appendix E), supporting the conclusion of Wardle *et al*. 1997.

Changes to the phosphorous concentration and content of the *Nothofagus fusca* floral and bark litter were more difficult to explain. Rapid initial decreases in phosphorous concentration and absolute content over the first 40 days in the field were attributed to the leaching of water soluble substances (Lousier and Parkinson, 1978; Prescott *et al*., 1993). The results of the laboratory based leaching study determined that 24% of the phosphorous content of floral litter was present in water soluble substances, and this agreed closely with the figure for phosphorous mass loss in the field after 40 days (refer Table 3.15).

Subsequent increases in phosphorous concentration in floral litter were attributed to the mineralisation of carbonaceous substances (Swift *et al*., 1979) and the import of phosphorous from the environment (Gosz *et al*., 1973). The rapid decrease in phosphorous content and concentration in floral litter during the last time interval (refer Figure 3.9) was on a par with loss rates from leaching, although little water soluble phosphorous was expected to be present in the floral litter after 130 days in the field. Consequently, microbial activity is the most likely explanation for this rapid movement of phosphorous out of the substrate.

Phosphorous in young stem bark was largely water soluble, reflected in its rapid loss from young stem bark at the Lewis Pass Reserve site, although not to the same extent at the Ilam Campus grounds site (refer Figures 3.17; 3.18). Subsequent phosphorous dynamics also differed, as concentration and content increased slowly at the Lewis Pass Reserve site, while both fluctuated significantly in young stem bark at the Ilam Campus site. Consequently, phosphorous dynamics in young stem bark litter, in terms of both release and accumulation, were considered to be influenced by site conditions.

Nutrient dynamics in decomposing litter have been discussed in various other studies. Gosz *et al*. (1973) determined the concentration of various nutrients in branches of *Acer saccharum, Fagus grandifloia and Betula allegheniensis* after twelve months incubation in the field. The concentration of nitrogen in the branches of all three species was found to increase, compared to initial values, while phosphorous concentration decreased in all species of branch litter, agreeing with the results of this study. Both nitrogen and phosphorous concentrations increased over time in decomposing leaf litter examined by Gosz *et al*. (1973), the latter contrasting with findings for both *Nothofagus fusca* floral and bark litter. Grier (1978) identified nitrogen and phosphorous dynamics similar to those described in this study during the decomposition of *Tsuga heterophylla* and *Picea sitchensis* fallen logs after up to 38 years in the field. Nitrogen concentration rose gradually over time, while phosphorous concentration in the fallen logs decreased.

Prescott *et al*. (1993) studied the nutrient dynamics of cone, foliar, wood, and root litter produced by *Pinus contorta*, *Picea glauca* and *Abies lasiocarpa* in the field over four years. Nitrogen concentration in litter generally tended to increase for a period of 2-3 years, as did the absolute content of nitrogen, indicating that inputs of nitrogen to the litter were occurring. Phosphorous dynamics were found to fluctuate considerably over time, both in terms of content and concentration, regardless of litter type. Prescott *et al*. (1993) concluded that phosphorous availability did not limit decomposition in the aforementioned study, due to the fluctuations in phosphorous levels, but nitrogen content was a limiting factor.

Brown *et al*. (1996) determined that the concentration of both nitrogen and phosphorous increased in bark from six different species during decomposition in the field. Nitrogen concentrations were approximately 150-220% of initial values after five years in the field, while phosphorous concentrations were approximately 150% of initial levels after the same period of time. No other data on nutrient dynamics during bark decomposition in the field could be found.

In comparing the mass loss and nutrient dynamics in young stem bark between the two sites, differences in moisture levels were considered a possible cause of variation. Average precipitation at the Lewis Pass Reserve site over the time of incubation was determined to be at least three times greater than at the Ilam Campus site (New Zealand Meteorological Service, 2000), potentially leading to higher soil moisture content (Slatyer, 1967). Early loss of nutrients was more substantial in *Nothofagus fusca* young stem bark incubated at the Lewis Pass Reserve site. This suggested that the leaching of water soluble substances occurred more rapidly at this site, agreeing with the differences between sites in rainfall and soil moisture levels. Puri and Ashman (1998) identified soil moisture levels as the most important environmental influence on nitrogen mineralisation, concluding that rates of mineralisation increased in soils with higher moisture content. Any difference in the rate of nitrogen mineralisation from young stem bark litter between sites was not able to be distinguished, since nitrogen accumulation, rather than mineralisation, was found to occur. It is possible that differences in the rate of mineralisation may have been detected over a longer time period.

The two sites used for *Nothofagus fusca* young stem bark decomposition in this study had different nitrogen and phosphorous contents. Soil nitrogen and phosphorous concentrations were 0.53% and 0.070% respectively from the Lewis Pass Reserve site, while nitrogen and phosphorous concentrations in Ilam campus site soil were 0.30% and 0.084%. However, as the organic and inorganic distribution of these nutrients was not determined, the availability and influence of soil nitrogen and phosphorous on the decomposing young stem bark litter was largely unknown (Florence and Lamb, 1974). Nevertheless, nitrogen concentration after 130 days was higher in the bark incubated at the Lewis Pass Reserve site, while phosphorous concentration was higher at the Ilam Campus site, reflecting the differences in soil nitrogen and phosphorous concentration between sites.

Litter bag experiments were originally intended to be carried out sequentially, i.e. all bags buried at the same time, then recovered upon completion. Interference with litter bags at the Lewis Pass Reserve site, most likely from the large rodent population, occurred several times. The source of interference at the Ilam campus site was probably animal, and it was consequently necessary to bury more litter bags at both sites on several occasions. This prevented the possibility of correlating mass loss and nutrient release rates with temporal climatic effects, as had been intended, and these effects were therefore not considered. It was assumed that the animal population, rodent or otherwise, did not affect results in any other way, although as animal excreta generally contains large amounts of nitrogen and phosphorous (Swift *et al*., 1979), large nutrient imports could have occurred in this way.

4.5 Nutrient flux through floral litter

The loss of nitrogen in 1999 from *Nothofagus fusca* trees via the production of floral litter was estimated to be 12 ± 1 kg ha^{-1}, whilst phosphorous loss was estimated to be 0.8 ± 0.1 kg ha^{-1}. This does not indicate flux from *Nothofagus fusca* floral litter from plant to soil, since only a portion of the nutrient contents of the floral litter was mineralised within a year. The rate of nitrogen release from floral litter was estimated using a linear mass loss model described by Swift *et al*. (1979), as this best suited the kinetics shown in Figure 3.8. From this, it was calculated that 7.8 ± 0.7 kg ha^{-1} of the nitrogen content of the floral litter was released in the first year on the ground, using a release constant calculated from nitrogen release in the field after 200 days. This was calculated to be equivalent to 65% of the nitrogen exported through *Nothofagus fusca* floral litter in 1999.

Phosphorous release from floral litter was calculated on the same basis, and was estimated to be 0.55 ± 0.05 kg ha^{-1} in the first year in the field, equal to 69% of the phosphorous export from *Nothofagus fusca* in the production of floral

litter in 1999. However, the generally variable results for phosphorous movement from floral litter determined over time (refer Figure 3.9) suggest that this value should be treated with caution. Lack of data on release rates after 200 days prevents accurate estimation of nutrient release rates after the first year.

It should be noted that these nutrient export data do not include the flux of nutrients through pollen produced by *Nothofagus fusca*, which has been shown to contain 4.1% nitrogen by mass (Greenfield, 1999), and may also impact on phosphorous cycling (Doskey and Ugoagwu, 1989). Wardle (1984) reported the frequency of mast events in *Nothofagus fusca* to be every 3-10 years, so it was concluded that this increased nutrient export through floral litter is a relatively common occurrence.

The export of nutrients from *Nothofagus fusca* in 1999 through floral litter was compared to export through foliar litter. Although data on the annual leaf litter production of *Nothofagus fusca* was not determined in this study, Sweetapple and Fraser (1992) gave a mean of 1562 ± 78 kg ha^{-1}, based on leaf litter production from *Nothofagus fusca* in central North Island, New Zealand, over two years. The forest stand type used by Sweetapple and Fraser (1992) was described as the same as that used in this study by Wardle (1984), based on soil characteristics, associated plant species and stand development. Variation in leaf litter production between the central North Island site studied by Sweetapple and Fraser (1992) and the Lewis Pass Reserve site used in this study was possible despite these similarities, therefore the values derived from this figure are given as estimates, rather than precise data. A mast event did not occur during the study period of Sweetapple and Fraser (1992), but other studies have concluded that leaf litter production by *Nothofagus* species in mast flowering years is not significantly different to average annual leaf litter production (Miller and Hurst, 1957; Alley *et al*., 1998). Consequently, this factor was not considered a potential influence on the assumption of equivalent leaf litter production at the different sites.

Nitrogen concentration in fallen *Nothofagus fusca* leaf litter was found to be 0.66%, similar to the value obtained by Heine (1973) for freshly fallen *Nothofagus fusca* leaves. No other figures could be found to compare with the figure of 0.07% for phosphorous concentration in fallen foliar *Nothofagus fusca* litter determined by this study. From these data, the annual export of nitrogen and phosphorous from *Nothofagus fusca* foliar litter was estimated to be 10 ± 1 kg ha^{-1} and 1.1 ± 0.1 kg ha^{-1} respectively. Using these figures, it was calculated that the export of nitrogen through floral litter in 1999 was 117% of the export through leaf litter, while phosphorous export through floral litter production was 73% of that through leaf litter in the same year. It is emphasised that these figures are estimates, as leaf litter production in 1999 was not accurately determined.

Pregitzer and Burton (1991) determined nitrogen export through reproductive litter production from *Acer saccharum* over two years to range up to 174% of nitrogen export through leaf production in a mast year, although the average percentage was 67%, and nitrogen exported in seed production was also included in these figures. Consideration of this information suggests the findings presented in this study for nitrogen export from *Nothofagus fusca* through floral litter in a mast year are comparatively large, although the value of comparisons to a different species may be limited.

Data on the nutrient export involved in the fall of twig litter from *Nothofagus fusca* was not calculated, since the annual production of twigs was not determined in this study, and was unavailable elsewhere. Consequently, total nutrient export from *Nothofagus fusca* in 1999 could not be estimated.

Floral litter production in the 2000 season was not accurately determined due to time constraints. Observations of floral material on standing *Nothofagus fusca* and in the forest floor litter layer indicated that substantially less floral litter was produced, estimated to be 1% of 1999 production, or 7.3 kg ha^{-1}. Alley *et al*. (1998) determined floral litter production in *Nothofagus truncata* and *Nothofagus menziesii* in non-mast years to be 0 – 2% of floral production in a mast year, agreeing with this estimate. Based on this figure for floral production in 2000, the

export of nitrogen and phosphorous from *Nothofagus fusca* through floral litter was approximately 0.1 kg ha^{-1} and 0.01kg ha^{-1}. Since the floral production figure was a broad estimate, these values are best considered indications of the variation in nutrient export through *Nothofagus fusca* floral litter in different years.

The apparently massive increase (approximately 10000%) in nutrient allocation to the production of floral material by *Nothofagus fusca* in a mast year represents a considerable change in resource allocation (Bazzaz *et al*., 1988; Pregitzer and Burton, 1991). This drain on nutrient reserves is not rapidly recouped from the decomposition of the fallen floral litter, as it was determined that 65% and 69% respectively of the nitrogen and phosphorous content of the floral litter were released within a year. It can also be assumed that a proportion of the nutrients released would be assimilated by other species in the ecosystem, decreasing the mass of nutrients available for return to *Nothofagus fusca*.

This drain on the nutrient reserves of *Nothofagus fusca* may potentially limit the production of plant tissue following a mast event. This is suggested by the findings of Miller and Hurst (1957) and Alley *et al*. (1998), who reported diminished foliar production in *Nothofagus* species the year after mast flowering. The amount of nutrients allocated to seed production by *Nothofagus fusca*, although not determined in this study, is also potentially important, possibly greater than nutrient allocation to floral production, as determined in other *Nothofagus* species (Alley *et al*., 1998).

It has often been suggested that the occurrence of mast flowering and seeding are related to the control of seed predator population numbers (Webb and Kelly, 1993). However, the data on the nutrient masses involved in the production of floral litter as determined by this study, let alone the nutrient allocation to seeds and other reproductive structures, suggests nitrogen and phosphorous availability and reserves of the species in question may also be influential to determining when mast events occur.

4.6 Nutrient flux through bark litter

From the data compiled in this study, it was apparent that accurate estimation of nutrient flux through bark material was not possible, due to the large uncertainty in the figure for CWD calculated from Stewart and Burrows (1994). This situation was exacerbated by the differences in nutrient concentrations in the bark types, since the bark production data did not distinguish one type of bark from another. The proportion of old stem inner bark to old stem outer bark on fully grown trees was identified to be approximately 10:1. However, the proportion of branch and young stem bark inputs from fallen branches and younger *Nothofagus fusca* could not be determined due to the variability of production.

Overall nitrogen (0.37%) and phosphorous concentrations (0.085%) for *Nothofagus fusca* bark were estimated by averaging the nutrient concentrations of each bark type, weighted to estimated relative masses of 4:6:10:1, for branch, young stem, old stem inner and old stem outer bark. The basis for the estimation of these proportions were observations of bark mass on fresh *Nothofagus fusca* CWD from trees of various ages, but these are regarded as crude calculations.

Using these concentration figures, it was estimated that the annual input of nitrogen to the litter layer via *Nothofagus fusca* bark was 1.0 kg ha^{-1}, while annual input of phosphorous was 0.22 kg ha^{-1}. These inputs are dependent upon CWD production, and hence events that increase branch fall or tree mortality, such as storms, droughts or pathogen activity, will increase the input of bark, and the nutrients contained within. It was difficult to determine nitrogen and phosphorous dynamics of bark in the field, as data was only available up to 130 days in the field. This prevented the extrapolation of results over long periods of time, but broad conclusions regarding initial periods of decomposition can be made.

Since large proportions of bark nutrients were soluble in water and readily leached, as determined by laboratory and field work, it was estimated that 34% of the nitrogen in bark was water soluble, equivalent to 0.34 kg ha^{-1} annually. This figure was determined using the same proportional calculations used for overall bark nutrient concentrations. The nutrient analysis of *Nothofagus fusca* young stem bark incubated in the Lewis Pass Reserve indicated that approximately 40% of nitrogen was released from young stem bark after the first 10 days in the field, so it is possible that this nitrogen release can occur rapidly.

After one year in the field, however, it was concluded that young stem bark litter would immobilise more nitrogen than was released. This was determined from laboratory microcosms, where net nitrogen mineralisation was not detected after 200 days, although the artefacts arising from this microcosm based study compromise the validity of extrapolation to nitrogen dynamics in the field (Pomeroy, 1970; Anderson, 2000). Field based experiments at the Lewis Pass Reserve provided more relevant information, and from these it was determined the absolute content of nitrogen in *Nothofagus fusca* young stem bark increased after 130 days, although this increase was only 3% of the initial nitrogen content. However, as the majority of bark litter was found to have a lower nitrogen concentration than young stem bark, it was determined that immobilisation in most bark material would occur.

The water soluble phosphorous content of *Nothofagus fusca* bark was found in laboratory studies to be a large proportion of total phosphorous content, but was not numerically determined due to the extent of leaching, as discussed earlier. This indicated that the initial flux of phosphorous from bark litter could be substantial. Fifty five percent of the phosphorous content of young stem bark was released from the bark material after 20 days in the field at the Lewis Pass Reserve, agreeing with this suggestion. After 130 days in the field, phosphorous content in young stem bark was approximately 50% of the initial mass, indicating phosphorous immobilisation occurred between day 20 and day 130, but it was slight. It was concluded that, due to the extent of initial phosphorous leaching, the

net release of phosphorous would occur from *Nothofagus fusca* bark over the first year in the field, although predictions regarding release and immobilisation after this period cannot be made.

Overall conclusions on the importance of nutrient flux through bark are difficult to make due to the uncertainty in bark proportions and lack of longer term field data. It would appear, based on results in the laboratory and in the field, that a large proportion of nitrogen and phosphorous content in *Nothofagus fusca* bark is water soluble, and is readily leached. However, as total nitrogen and phosphorous concentrations in bark are relatively low, and natural bark production was determined to be small, the comparative importance of these leached nutrients to ecosystem wide function is likely to be minimal, although localised effects around a fallen tree may possibly occur.

Relating the nitrogen and phosphorous loss through bark litter production to nutrient budgets and reserves for *Nothofagus fusca* is difficult, since natural bark production is irregular, and virtually always the result of branch fall or tree mortality. Hence, nutrient movement through the production of bark litter cannot be related to the annual nutrient demands for standing *Nothofagus fusca*, as the vast bulk of bark litter is produced from dead or dying trees.

The significance of these results is perhaps greater when applied to studying nutrient dynamics in an area of *Nothofagus fusca* after large inputs of CWD due to mass mortality resulting from windthrow or pathogen activity (Harmon *et al*., 1986). In these circumstances, the input of significantly larger amounts of bark than normal could result in a rapid commensurate increase in nutrient availability in the area, particularly phosphorous, due to the potential for the leaching of water soluble substances from the bark. After this initial nutrient release, however, large scale immobilisation of nitrogen may occur, again altering nutrient dynamics, potentially for several decades (Zimmerman *et al*., 1995).

Although the logging of *Nothofagus fusca* in the geographical area studied is currently restricted, the collection of information on the characteristics of *Nothofagus fusca* bark can be used to ascertain the impact upon forest nutrient

levels of bark removal (Jorgensen, 1975) and likely effects of bark accumulation (Olsson, 1978) if logging recommences. This information is also important due to the general lack of understanding on the fate and role of bark in many natural and managed ecosystems.

The removal of bark material from *Nothofagus fusca* forests, ignoring the nutrient content of the associated wood, would most likely have few immediate consequences for ecosystem nitrogen and phosphorous levels, as bark contains low concentrations of nitrogen and phosphorous, and accounts for a fraction of annual CWD inputs. This also suggests that leaving bark at clearfelled sites would have little impact on remediating the eventual impact of nitrogen and phosphorous loss from the removal of wood, but may result in rapid fluxes of water soluble nutrients from the bark if enough moisture is available.

Another consequence of logging is the physical decrease in the mass of wood that will fall to the forest floor. The decrease of CWD inputs can potentially decrease the capacity of an ecosystem to store nutrients through immobilisation in CWD, increasing the availability of nutrients from soil (Harmon *et al*., 1986; Zimmerman *et al*., 1995). This can result in increased nutrient export from the ecosystem via leaching, and alter the biodiversity of the ecosystem by providing altered conditions better suited to plant species not indigenous to the ecosystem, with even further potential implications for ecosystem wide nutrient cycling (Scowcroft, 1997). The immobilisation of nutrients by bark left on site could remediate this effect somewhat, but the overall decrease in CWD mass and nutrient storage capacity over time would still be significant.

The stockpiling of *Nothofagus fusca* bark on a large scale could result in the release of substantial amounts of leached nutrients if moisture availability is sufficient, with possible consequences for nutrient cycling in the immediate area. Although bark accumulation may occur outside of the geographical area of the ecosystem, Olsson (1978) observed that large amounts of bark, approximately 40% of total the bark litter produced from logging in Swedish forests, accumulated on the side of logging roads. Duplication of this phenomenon could

result in alteration to nutrient dynamics in the area around logging roads, due to the potential for initial leaching and long term immobilisation of nutrients in bark.

The use of bark as a soil amendment in agriculture and horticulture has been studied (Bollen and Glennie, 1963; Allen and Low, 1973), but the effectiveness of using *Nothofagus fusca* bark in this way is unknown, since this was not investigated in this study and data is not available from other sources. It is suggested that bark may have some uses as a slow release fertiliser, after the absorption of nutrients by immobilisation. It is possible that the release of nutrients can be controlled through the use of different types of bark, as suggested by the different rates of nitrogen mineralisation from the different bark types in microcosms, as determined by this study.

4.7 Overall Conclusions

The mass of nitrogen and phosphorous exported from *Nothofagus fusca* to the litter layer via the production of floral litter in 1999 was substantial. It was also determined that the release of the nitrogen and phosphorous from floral litter would take longer than one year. The export of nitrogen through floral litter was estimated to be greater than that through foliar litter. Although the nitrogen and phosphorous input through *Nothofagus fusca* floral litter in non-mast years was estimated to be significantly less, data on floral litter production and decomposition in mast flowering years was concluded to be necessary for the accurate comprehension of overall nitrogen and phosphorous dynamics in the ecosystem. The influences of mast events on other facets of *Nothofagus fusca* behaviour was also discussed, and the timing of peak foliar litter production was concluded to be different in 1999 when compared to non-mast flowering years.

The characteristics of *Nothofagus fusca* bark were found to be dependent upon the age of the tree, and the part of the tree from which the bark was obtained. The importance of bark litter to nitrogen and phosphorous cycling was

therefore difficult to determine, although it was concluded that nitrogen was immobilised in fallen bark within one year, while net phosphorous release from bark occurred after one year. The significance of bark litter inputs to nitrogen and phosphorous dynamics was dependent upon bark production, and consequently events that influence bark production, such as climatic conditions, pathogen activity or land management practices. The basal level of bark production determined in this study indicated bark litter was of little significance to nitrogen and phosphorous cycling on an ecosystem wide level. However, large accumulations of *Nothofagus fusca* bark could rapidly produce significant effects from the release of water soluble substances, particularly to phosphorous dynamics, while the immobilisation of nitrogen in large bark masses could also have serious consequences for nitrogen availability.

Although *Nothofagus fusca* floral and bark litter were very different in terms of characteristics, it can be concluded that when they are produced in large quantities due to natural or anthropogenic events, both can have a significant impact on the cycling and availability of nitrogen and phosphorous.

4.8 Further work suggested

Data on floral production in normal and mast years by *Nothofagus fusca* over more years is required to identify the increase in nutrient allocation to floral production with greater accuracy. Further data on foliar production over the same time frame would also be important for accurate comparisons of nutrient allocation to these two litter types in various years.

Further study of bark decomposition in the field is also recommended, as the decomposition of only one type of bark was examined in detail. Data on mass loss and nutrient dynamics for a longer period would also be important, allowing longer range predictions of the decomposition dynamics of bark to be made.

The concentration or decomposition dynamics of cations, such as calcium and potassium, in *Nothofagus fusca* floral and bark litter was not determined. Data

on the flux of these elements would enable the significance of production and nutrient release from floral and bark litter to be better understood. This may be particularly important in the case of bark, which has been found in various species to contain substantial masses of cations (Gosz *et al*., 1972; Woodwell *et al*., 1975; Allen *et al*., 1997).

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ACKNOWLEDGMENTS

I would like to thank Dr Laurence Greenfield and Dr Peter Clinton for their time and advice over the course of this thesis, and I also acknowledge and thank David Wardle and Jo Anderson for their contributions. I extend my gratitude to the staff of the Plant and Microbial Sciences Department and the Forest Research Institute, particularly Craig Galilee, Nic Cummings, Matt Walters, and Neil Andrews. Thanks go out to my lab group for ideas and discussions regarding the production of a thesis (amongst other things).

Finally, I would like to acknowledge the support and encouragement of my partner Andi and my friends and family, and thank them deeply for putting up with me.

APPENDICIES

A Phosphorous Analysis Calibration Curve

Absorption values produced from the phosphorous solutions of known phosphorous concentration are given in Table A.1. From these values, excluding the data for 0 PPM phosphorous, a regression equation relating the absorbency of solutions to phosphorous content was formulated. This was:

$$\text{PPM Phosphorous} = (0.0206 \times \text{Adjusted Reading}) - 0.0719$$

R^2 for this regression was 0.998, indicating the equation was highly linear.

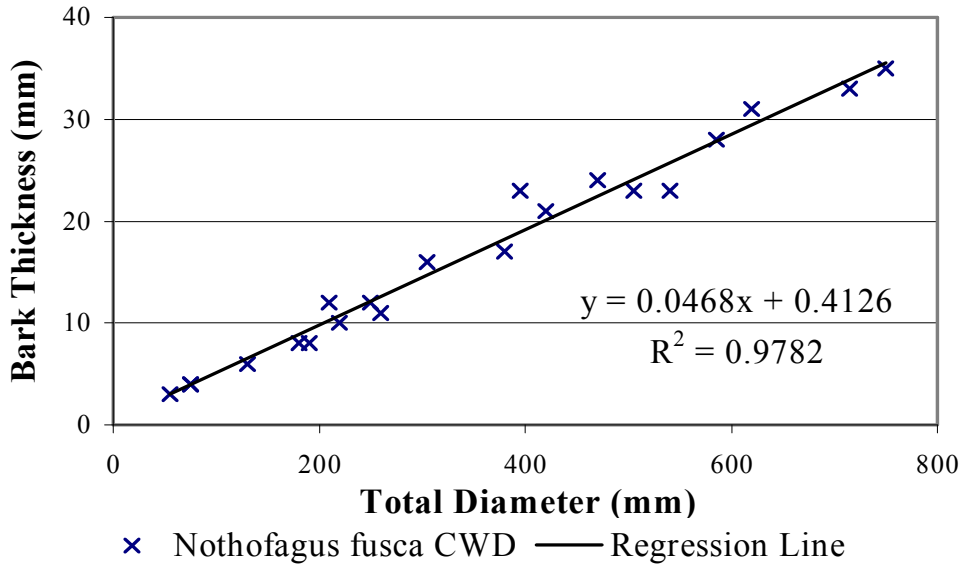
Table A.1 Phosphorous calibration curve data

PPM Phosphorous	Reading	Adjusted Reading
0	9.825	0
4	9.84	0.015
8	9.93	0.105
10	9.95	0.125
12	9.99	0.165
16	10.085	0.26
20	10.16	0.335
24	10.259	0.434
32	10.413	0.588

B Bark thickness and specific gravity

The thickness of fresh bark *Nothofagus fusca* CWD was measured, and compared to the total CWD diameter. The results of this, and the regression equation calculated, are shown in Figure A.1. From this equation, the volume of bark in the CWD was calculated to be approximately 18% of total volume.

Figure A.1: Bark thickness versus total diameter



Specific gravity was determined by measuring the water displacement of a known mass of bark or wood. From this, it was determined that the specific gravity of fresh *Nothofagus fusca* bark and wood was approximately equal, and hence the fraction of bark mass in CWD mass was equal to the fraction of bark volume in CWD volume.

C Bark mass remaining on decomposing CWD

The average mass of bark left remaining on 16 samples of *Nothofagus fusca* CWD in various stages of decomposition was determined to be 10 ± 1%, expressed as a percentage of total CWD mass. CWD was ranked according to comparative decay. CWD was selected based on size and decay to attempt to duplicate a selection representative of forest floor CWD, although whether this was successful is unknown, and a significant source of uncertainty.

Table A.2: Percentage mass of bark on *Nothofagus fusca* CWD

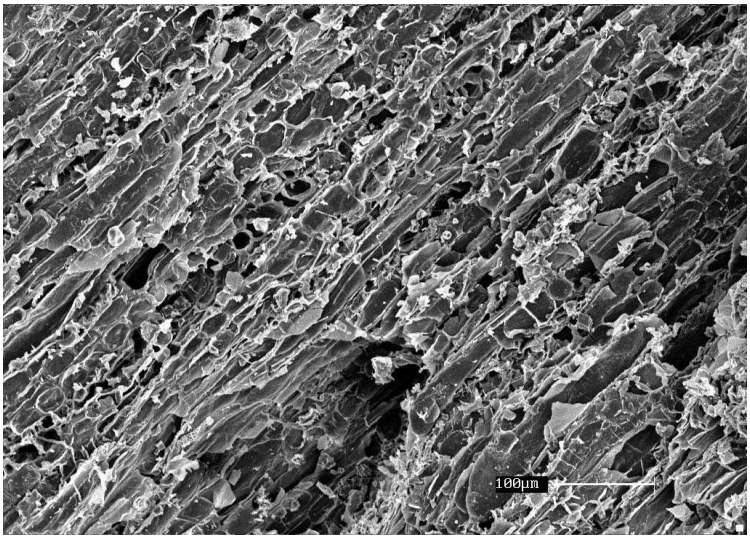
Type of CWD	Decay Rating	Bark Mass as % of CWD mass
Branch	0	18
Thick Stem	0	18
Branch	1	11
Young Stem	1	13
Thick Stem	1	16
Branch	2	11
Young Stem	2	12
Thick Stem	2	15
Branch	3	5
Young Stem	3	8
Thick Stem	3	11
Branch	4	0
Branch	4	2
Young Stem	4	4
Thick Stem	4	9
Thick Stem	4	11

D Scanning Electron Micrographs of Inner and Outer Bark

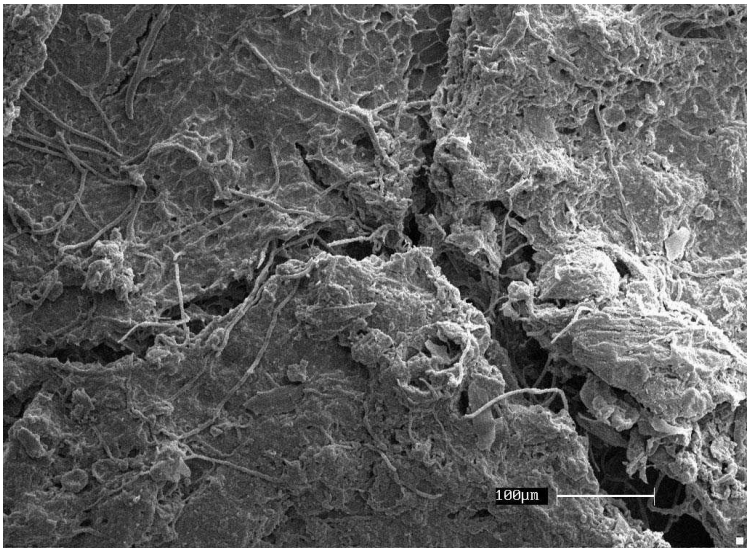
The surface of inner bark (exposed when outer bark is removed) and the external surface of outer bark were examined under high magnification. Inner bark structure was highly organised, forming fibers, while outer bark structure was comparatively random.

Figure A.3: SEM of *Nothofagus fusca* inner bark (*a*) and outer bark (*b*)

(*a*)



(*b*)



Note: Fungal hyphae are visible on the external surface of the outer bark

E Effect of oven drying on total nitrogen content (Kjeldahl)

Statistical analysis (Students *t*-test) indicated that oven drying did not cause a significant change to the nitrogen concentration of various types of *Nothofagus fusca* litter, replicated three times each.

Table A.3: *Nothofagus fusca* litter nitrogen content after oven drying

Litter Type	Initial Nitrogen concentration (%)	Nitrogen concentration after oven drying (%)
Flowers	1.58 ± 0.1	1.58 ± 0.2
Branch Bark	0.65 ± 0.1	0.64 ± 0.2
Old Stem Inner Bark	0.25 ± 0.1	0.25 ± 0.1
Twigs	0.45 ± 0.1	0.45 ± 0.1

Note: Errors indicated are standard errors of the mean.