Decomposition and nutrient dynamics of green and freshly fallen radiata pine (*Pinus radiata*) needles

G.K. Girisha, L.M. Condrona,*, P.W. Clintoob, M.R. Davisb

aSoil, Plant, and Ecological Sciences Division, P.O. Box 84, Lincoln University, Canterbury, New Zealand
bNew Zealand Forest Research Institute, P.O. Box 29237, Fendalton, Christchurch, New Zealand

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Abstract

Thinning and pruning operations in radiata pine (*Pinus radiata*) plantation forests result in the addition of large amounts of green needles to the forest floor. The decomposition of green and freshly fallen radiata pine needles and the effects of adding green needles to freshly fallen needles were examined in a microcosm experiment. Green needles lost 72% of the original mass after 10 months, compared with 27% for freshly fallen needles. The corresponding mass losses for 1:1 ratios of green and freshly fallen needles were 55% when mixed and 53% when layered. Nutrient concentrations generally increased during decomposition while total amounts of nutrients decreased with time. Decomposition was primarily influenced by needle lignin and N content, and by the holocellulose to lignocellulose quotient (HLQ). The results of this study indicate that addition of green needles does not significantly affect the decomposition of freshly fallen needles. This outcome was attributed to substrate preference by decomposer microorganisms. It is, therefore, concluded that forest management practices (thinning, pruning and harvesting) which result in significant inputs of carbohydrates and nutrients in the form of green needles will have little impact on decomposition of existing forest floor materials.

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Keywords: *Pinus radiata*; Green needles; Freshly fallen needles; Decomposition; Nutrient release

1. Introduction

Plantation forestry in New Zealand is based mainly on radiata pine (*Pinus radiata*) and currently covers approximately 1.7 million ha (7% total land area). Extensive thinning is carried out in most forests, while over half are pruned to varying degrees (Maclaren, 1993). Thinning and pruning operations add a large amount of fresh plant residue material to the forest floor as fresh (green) needles and coarse woody debris. Green needles are rich in carbohydrates and nutrients and low in lignin and are, therefore, qualitatively very different from most forest floor litter materials (e.g. Sanger et al., 1998; Hyvonen et al., 2000). The addition of green needles may also affect the decomposition and nutrient dynamics of dead (or freshly fallen) pine needles on the forest floor. Litter decomposition and nutrient release is controlled by a combination of factors including litter quality, the physico-chemical environmental, and the nature and activity of decomposer organisms (Swift et al., 1979). The principle objective of this study was to investigate the decomposition of green and freshly fallen radiata pine needles, either separately, or in mixtures or discrete layers, to improve our understanding of the impact
of common management practices on nutrient cycling processes in the forest floor of radiata pine plantations.

2. Materials and methods

2.1. Microcosm experiment

In this study, mass loss and change in chemical composition were determined in green and freshly fallen pine needles incubated on a forest soil in controlled environment microcosms for periods of up to 10 months. Green needles were collected from freshly pruned trees in an 8-year-old radiata pine silvopastoral (agroforestry) trial established in 1990 at Lincoln University, New Zealand (43°38′S, 172°30′E) (Mead et al., 1993; Chang et al., 2002). The final stocking rate on this trial is 200 stems ha⁻¹ (pruned to 6 m), and it includes four different understorey treatments (bareground, lucerne (*Medicago sativa* L.), perennial ryegrass (*Lolium perenne* L.), white clover (*Trifolium repens* L.)). Green needles (comprising buds, current needles and needles, aged 1 year and older) were separated from twigs and branches immediately after pruning. Freshly fallen needles were collected from the forest floor beneath the unpruned trees from the same plots. The freshly fallen needles appeared intact and showed little or no decomposition. The soil used in microcosms was the top 2.5 cm of a Lismore stony silt loam (Udic ustochrept) collected from under a 14-year-old stand of second rotation radiata pine at Eyrewell Forest (43°25′S, 172°16′E). The soil was passed through a 4 mm sieve and stored at 4 °C prior to use. Selected chemical and physical properties are shown in Table 1.

A modified version of the laboratory microcosm design described by Taylor and Parkinson (1988) was used. The microcosms were incubated in controlled environment chambers at a constant temperature of 22 °C and 55% relative humidity with an 18:6 light:dark cycle.

![Cross-section of the microcosm chamber](image)

**Table 1**

Selected chemical and physical properties of the Eyrewell forest soil (0–2.5 cm) used in the microcosms

<table>
<thead>
<tr>
<th>Property</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH (water)</td>
<td>5.1</td>
</tr>
<tr>
<td>Organic C (%)</td>
<td>3.2</td>
</tr>
<tr>
<td>Total N (%)</td>
<td>0.20</td>
</tr>
<tr>
<td>Total S (%)</td>
<td>0.02</td>
</tr>
<tr>
<td>Total P (mg kg⁻¹)</td>
<td>293</td>
</tr>
<tr>
<td>Olsen P (mg kg⁻¹)</td>
<td>5.0</td>
</tr>
<tr>
<td>Cation exchange capacity (c mol kg⁻¹)</td>
<td>13.0</td>
</tr>
<tr>
<td>Exchangeable Ca (c mol kg⁻¹)</td>
<td>1.90</td>
</tr>
<tr>
<td>Exchangeable K (c mol kg⁻¹)</td>
<td>0.40</td>
</tr>
<tr>
<td>Exchangeable Mg (c mol kg⁻¹)</td>
<td>1.00</td>
</tr>
<tr>
<td>Exchangeable Na (c mol kg⁻¹)</td>
<td>0.10</td>
</tr>
<tr>
<td>Base saturation (%)</td>
<td>26</td>
</tr>
<tr>
<td>Dry bulk density (t m⁻³)</td>
<td>0.80</td>
</tr>
<tr>
<td>Field capacity (%)</td>
<td>24.3</td>
</tr>
<tr>
<td>Porosity (%)</td>
<td>51.1</td>
</tr>
</tbody>
</table>

Fig. 1. Cross-section of the microcosm chamber (lid closed).
used for this study (Fig. 1). Half of the microcosm was filled with acid-washed sand, and a 2.5 cm layer of soil (80% field capacity) was placed on top of the sand separated by 0.1 mm nylon mesh. The pine needles were placed on the soil surface, again separated by 0.1 mm nylon mesh. The experiment comprised 20 microcosms of each of the following four treatments: green needles, freshly fallen needles, 1:1 mixture (by weight) of green and freshly fallen needles, and green needles layered over freshly fallen needles (1:1). The total amount of needles in each treatment was 18.5 g (oven dry equivalent). This amount is equivalent to the total amount of needles in each treatment was 18.5 g (oven dry equivalent). This amount is equivalent to

In order to compare the mass loss and the parameters of decay in different substrates it was necessary to find the mathematical function that best fitted the data. The function with the higher $R^2$ was taken as the function which fitted the data best. The most frequently used model to describe decomposition is the single exponential decay function (Olson, 1963):

$$W_t = W_0 e^{-kt}$$

where $W_t$ is the mass of litter remaining at time $t$; $W_0$ the initial litter mass; $k$ the decay constant; $t$ the time in years.

In addition, a double exponential model was fitted to test the assumption that litter was composed of labile and recalcitrant components that have different rates of decomposition, whereby lignin was considered as the recalcitrant component and all other components were considered to be labile (Berg and Agren, 1984). The double exponential decay function used was:

$$W_t = W_L e^{-k_L t} + W_R e^{-k_R t}$$

where $W_t$ is the mass of litter remaining at time $t$; $W_L$ the labile fraction mass at time $t = 0$; $W_R$ the initial lignin mass; $k_L$ the decay constant for the labile fraction; $k_R$ the decay constant for the lignin fraction; $t$ time in years.

3. Results

As expected, there was a marked difference in the chemical properties of green and freshly fallen needles (Table 2). Concentrations of soluble carbohydrates,
polyphenols, and hemicellulose were greater in green needles but concentrations of cellulose and lignin were significantly greater in freshly fallen needles. Nitrogen, P and K concentrations were significantly greater in green needles, while there were no significant differences in C, Ca and Mg concentrations. Green needles had greater holocellulose to lignocellulose quotient (HLQ), but with the exception of C; divalent cation ratios, had lower values for all other litter quality indices compared with freshly fallen needles (Table 3).

Green needles alone lost 70% of the original dry mass during the first 4 months of incubation and, thereafter the rate of decomposition was slow (Fig. 2). Freshly fallen needles alone had the slowest decomposition of all the treatments, and the mixed and layered treatments had similar mass loss rates that were close to the average rate of green and freshly fallen needles alone.

Table 2
Initial chemical characteristics (mg g\(^{-1}\) dry weight) of green and freshly fallen radiata pine needles used in the microcosm experiment

<table>
<thead>
<tr>
<th></th>
<th>Green</th>
<th>Freshly fallen</th>
<th>L.S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soluble carbohydrates</td>
<td>96.3</td>
<td>34.2</td>
<td>1.48</td>
</tr>
<tr>
<td>Polyphenols</td>
<td>27.2</td>
<td>15.9</td>
<td>3.00</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>127.4</td>
<td>70.7</td>
<td>42.87</td>
</tr>
<tr>
<td>Cellulose</td>
<td>171.6</td>
<td>244.3</td>
<td>11.11</td>
</tr>
<tr>
<td>Holocellulose</td>
<td>298.9</td>
<td>315.0</td>
<td>32.36a</td>
</tr>
<tr>
<td>Lignin</td>
<td>239.8</td>
<td>373.8</td>
<td>35.50</td>
</tr>
<tr>
<td>C</td>
<td>483.8</td>
<td>469.4</td>
<td>16.23a</td>
</tr>
<tr>
<td>N</td>
<td>17.1</td>
<td>7.3</td>
<td>0.44</td>
</tr>
<tr>
<td>P</td>
<td>1.7</td>
<td>0.7</td>
<td>0.14</td>
</tr>
<tr>
<td>C(^a)</td>
<td>10.8</td>
<td>10.6</td>
<td>6.13a</td>
</tr>
<tr>
<td>Mg</td>
<td>1.6</td>
<td>1.5</td>
<td>1.01a</td>
</tr>
<tr>
<td>K</td>
<td>7.4</td>
<td>1.8</td>
<td>1.63</td>
</tr>
</tbody>
</table>

\(^a\) Difference between green and freshly fallen needles is not significant.

Fig. 2. Mass loss of four litters in microcosms during a 10-month incubation period (standard errors are shown by vertical bars).
### Table 3

Initial litter quality parameters determined for green and freshly fallen radiata pine needles used in the microcosm experiment

<table>
<thead>
<tr>
<th></th>
<th>Green  (±standard error)</th>
<th>Freshly fallen  (±standard error)</th>
<th>L.S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>C:N</td>
<td>28.44 ± 0.62</td>
<td>64.74 ± 2.82</td>
<td>1.68</td>
</tr>
<tr>
<td>C:P</td>
<td>277.27 ± 30.02</td>
<td>679.68 ± 39.81</td>
<td>132.70</td>
</tr>
<tr>
<td>C:Ca</td>
<td>44.89 ± 2.68</td>
<td>44.49 ± 2.21</td>
<td>25.92*</td>
</tr>
<tr>
<td>C:Mg</td>
<td>312.01 ± 23.74</td>
<td>320.79 ± 14.65</td>
<td>207.90*</td>
</tr>
<tr>
<td>C:K</td>
<td>65.04 ± 7.74</td>
<td>251.2 ± 6.79</td>
<td>47.42</td>
</tr>
<tr>
<td>Polyphenols:N</td>
<td>1.6 ± 0.02</td>
<td>2.2 ± 0.05</td>
<td>0.23</td>
</tr>
<tr>
<td>Lignin:N</td>
<td>14.09 ± 0.53</td>
<td>51.56 ± 0.46</td>
<td>2.54</td>
</tr>
<tr>
<td>Lignin:P</td>
<td>137.43 ± 25.09</td>
<td>541.36 ± 35.69</td>
<td>68.95</td>
</tr>
<tr>
<td>Lignin:carbohydrates</td>
<td>2.49 ± 0.89</td>
<td>10.93 ± 0.29</td>
<td>0.55</td>
</tr>
<tr>
<td>Lignin:cellulose</td>
<td>1.4 ± 0.22</td>
<td>1.53 ± 0.05</td>
<td>0.11</td>
</tr>
<tr>
<td>HLQ</td>
<td>0.55 ± 0.01</td>
<td>0.46 ± 0</td>
<td>0.05</td>
</tr>
<tr>
<td>(Lignin + polyphenols):N</td>
<td>15.69 ± 0.54</td>
<td>53.76 ± 0.46</td>
<td>2.38</td>
</tr>
</tbody>
</table>

* Difference between green and freshly fallen needles is not significant.

![Graph](https://via.placeholder.com/150)

**Fig. 3.** Changes in concentration and total amounts of water-soluble carbohydrates and polyphenols in four litters during 10-months incubation in microcosms (standard errors are shown by vertical bars).
Concentrations of water-soluble carbohydrates and polyphenols in green, freshly fallen, mixed and layered materials declined markedly during the first 2 months of incubation, and declined more slowly or remained constant thereafter (Fig. 3). The concentration of water soluble carbohydrates declined to 22, 56, 51 and 39% of the original in green, freshly fallen, mixed and layered treatments, respectively, after the first 2 months. The concentration of polyphenols declined to 11, 29, 22, 2% of the original in green, freshly fallen, mixed and layered treatments, respectively, after the first 2 months. The percent of the original water-soluble carbohydrates remaining in the green, mixed and layered treatments after 10 months was significantly less than freshly fallen needles. Only 2% of the original polyphenols remained in the green needles after 10 months compared with 13% for freshly fallen needles.

The holocellulose fraction (i.e. cellulose + hemicellulose) decomposed slowly compared to soluble carbohydrates. The holocellulose concentration of green needles decreased from 300 to 153 mg g\(^{-1}\) over 10 months, compared with a decrease from 315 to 55 mg g\(^{-1}\) in freshly fallen needles (Fig. 4). Mixed and layered samples recorded intermediate declines in concentration between green and freshly fallen needles. The concentration of holocellulose in mixed and layered treatments decreased to 26, 34, 45, 59 and

![Graphs showing changes in concentration of holocellulose and lignin over time.](image-url)
71% of time at zero concentration. During the first 4 months of incubation total holocellulose decreased rapidly in all treatments. Green needles and layered and mixed green and freshly fallen needles showed a marked increase in lignin concentration during the first 4 months of incubation compared with freshly fallen needles alone (Fig. 4). Lignin concentration in mixed treatments was significantly greater than green needles at 2 and 6 months. However, the layered treatment lignin concentration did not differ significantly from green needles throughout the incubation. Lignin concentration was significantly greater in mixed than layered treatment samples at 4, 6 and 10 months. Freshly fallen needles lost only 17% of the original lignin compared to 43% for green needles over 10 months, while the mixed and layered treatments lost around 25% over the same period.

Carbon concentrations did not vary much over the 10 months duration of the incubation experiment, although N concentrations increased initially in the green and mixed needle treatments (Fig. 5). On the other hand, P concentrations decreased with time in all the treatments (Fig. 6). Ca and Mg concentrations in green, mixed and layered treatments, and K in green needles, increased in the initial 2 months of incubation but decreased thereafter (Figs. 6 and 7). However, in freshly fallen needles Ca concentrations continuously declined, while Mg concentrations increased during

![Graphs showing changes in concentration and total amounts of carbon and nitrogen in four litters during 10-months incubation in microcosms (standard errors are shown by vertical bars).](image-url)
the incubation period. There was a net release of C and nutrients in all the treatments (Figs. 5–7). Except for Mg in freshly fallen needles, the rate of release was rapid during the initial 2 months and decline was gradual thereafter in all the treatments. Green needles released C, N, P, Ca, Mg and K in greater amounts compared to other treatments.

Simple linear regression analysis of pooled data (mass loss of all the treatment versus quality parameters) indicated that among the quality parameters lignin content explained 73% of the variation in mass loss, followed by the polyphenols:N ratio (67%), N (51%), C:N ratio (48%), soluble carbohydrates (45%), cellulose (36%), and HLQ (35%). Stepwise multiple linear regression indicated that lignin, N, and HLQ together explained 96% of the variations in mass loss according to the following:

\[
\text{mass loss} = -51.052 + 1.410\% \text{lignin} + 32.977\% \text{N} - 60.929 \text{HLQ} \quad (R^2 = 0.962)
\]

When analysed separately marked differences between green and freshly fallen treatments were observed. While C:N ratio, lignin:N ratio, (lignin + poly phenols):N ratio, N, soluble carbohydrates, and lignin:-cellulose ratio explained variations in mass loss in green needles well, cellulose and lignin:soluble carbohydrates ratio better explained the variability in freshly
fallen needle mass loss. Lignin, HLQ, lignin:P ratio, and soluble carbohydrates explained mass loss well in both the treatments.

Model fitting showed that the double decay function fitted data better (i.e. higher $R^2$) than the single exponential function (Table 4). The $R^2$ between the estimated and the actual amount of litter remaining at different times was highly significant ($P < 0.001$), supporting the assumption that litter is composed of labile and recalcitrant fractions with different exponential kinetics. Decomposition of the labile component was more than 5 and 2 times faster than the recalcitrant component for green and freshly fallen needles, respectively (Table 4). The decay constants for both components of the mixed and layer treatments were similar.

4. Discussion

The mass loss in the mixed (55%) and layered (53%) treatments was similar to the average of pure green (72%) and pure freshly fallen needle (27%) treatments. The rate of mass loss was fastest for green needles, slowest for freshly fallen needles and intermediate for mixed and layered treatments (Table 4).
Thus, if it is assumed that green needles decomposed at the same rate alone as when mixed or layered with freshly fallen needles, the results of the present study indicate that addition of green needles did not significantly affect the decomposition of freshly fallen needles. The effect of one litter type on the decomposition of other has been reported by others (Klemmedson, 1987; Blair et al., 1990; Ineson and McTierran, 1992). These studies have shown that certain litter mixtures exhibit positive interactions in increasing litter decay rates over the pure litter types. This positive interaction between litter types has been largely attributed to nutrient translocation (Taylor et al., 1989) and increase in the activity of soil faunal activity (Chapman et al., 1988). However, in the present study there was no interaction between green needles and freshly fallen needles. Lack of interaction observed in the present study may be attributed to lack of nutrient transfers between the litter types and lack of soil faunal activity. The decay rates determined in the microcosm experiment were broadly similar to rates determined in a related field experiment (Girisha, 2001).

Green needles were richer in the labile (non-lignin) organic fraction than freshly fallen needles and, therefore lost mass faster than freshly fallen needles. Carbohydrates are a relatively energy-rich and readily available substrate for litter decomposers, and they are one of the litter components first decomposed. Therefore, high initial concentrations of soluble carbohydrates probably caused the higher mass loss for green needles. This is supported by the results of simple regression analysis. High coefficients of determination ($R^2$) for N and parameters derived from N (e.g. lignin:N ratio) and readily available compounds such as soluble carbohydrates and cellulose explains the control of N and easily degradable compounds in the early stages of decomposition. The results of present study are supported by the findings of other studies. In field studies Prescott et al. (1993) reported that the labile fraction of litter was rapidly metabolised by microorganisms or lost through leaching. Although some of the labile material is water soluble, research indicates that microbial metabolism rather than leaching is responsible for the greatest part of mass loss (Parsons et al., 1990). Swift et al. (1979) and Berg et al. (1982) confirmed that during plant residue decomposition the most rapid loss was of monosaccharides (soluble sugar) fractions, followed by the polysaccharides (holocellulose) and, finally, lignin. The soluble polyphenol content of needles, in the present study, decreased rapidly in the first 2 months and stabilised thereafter. Loss of polyphenols could have been due to either leaching (as a result of re-moistening the litter in microcosms) or microbial decomposition (Martin and Haider, 1980).

The results of this study clearly showed that there was an inverse relationship between cellulose degradation and lignin content. Lignin and cellulose are intimately associated within the cell wall of litter material. Although there is no chemical interaction between the two, the physical proximity of the lignin may retard enzymatic attack on the cellulose (Melillo et al., 1982). In the present study, green needles had significantly lower lignin concentration and content than freshly fallen needles. Rapid mass loss in green needles driven by loss of easily degradable compounds (such as carbohydrates) a sharp increase in lignin concentration. As the lignin concentration increased in green needles the rate of decay decreased significantly from the second month onwards. Similarly, significantly greater concentration of lignin in freshly fallen needles explains the slow rate of decomposition of freshly fallen needles compared to green needles.

### Table 4
Double and single exponential decay constants determined for mass loss of green and freshly fallen radiata pine needles after 10 months decomposition

<table>
<thead>
<tr>
<th></th>
<th>Double</th>
<th>Single</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Labile $k_L$</td>
<td>Recalcitrant $k_R$</td>
</tr>
<tr>
<td>Green</td>
<td>5.365</td>
<td>0.931</td>
</tr>
<tr>
<td>Standard error</td>
<td>1.391</td>
<td>0.168</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.86</td>
<td>0.74</td>
</tr>
<tr>
<td>Freshly fallen</td>
<td>0.537</td>
<td>0.232</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.027</td>
<td>0.004</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Mixed</td>
<td>2.319</td>
<td>0.341</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.443</td>
<td>0.012</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.82</td>
<td>0.75</td>
</tr>
<tr>
<td>Layered</td>
<td>2.072</td>
<td>0.359</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.385</td>
<td>0.005</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.82</td>
<td>0.77</td>
</tr>
</tbody>
</table>

$^a$ For difference between estimated and actual mass loss.
Different nutrients in decomposing litter have different patterns of release over time and nutrients are retained with different strength in the litter structures. One mechanism behind this is microbial immobilisation (Rutigliano et al., 1998). The status of a nutrient, whether it is limiting or non-limiting to microbial growth, determines its release dynamics. The nutrients which are in limiting amounts (where the C:element ratio is above the critical limit) will be retained resulting in immobilisation, whereas, elements in surplus (where the C:element ratio is below the critical limit) will be released during decomposition (Berg and Staaf, 1981). Nutrient release and turnover are further influenced by the nature of chemical bonds that attach the elements to organic matter.

Nutrients like Mg and K, which are not structural components, are susceptible to initial leaching losses (Staaf, 1980). The significant increases in N and Mg concentrations in green and freshly fallen needles indicated that they were limiting to decomposers (Figs. 5 and 7). The significant positive correlations between mass loss and accumulated N \((R^2 = 0.64\) and \(0.52\) for green and freshly fallen needles) and Mg \((R^2 = 0.98\) for freshly fallen needles) confirm this. In the case of freshly fallen needles, Mg was retained more strongly than N indicating that it was probably the most limiting element to the decomposer community. The fact that Mg was immobilised in both green and freshly fallen needles and K was immobilised in green needles suggests that the impact of leaching on the loss of nutrients especially Mg and K from litters was minimal.

The change in absolute amount of a nutrient element during decomposition (net immobilisation or the net release of nutrients) is a function of both mass loss and change in the relative concentrations of the element in the residual litter. In the present study, net mineralisation (net release) of nutrients was observed for all elements studied (Figs. 5 and 7). This may be explained as follows. The assimilation ratio of the decomposer community is believed to be 0.2 (Bosatta et al., 1980). This means that for each molar unit of organic C decomposed 0.8 is respired and 0.2 U are utilised for the production of microbial biomass. Thus, a balanced substrate decomposed by microbes having a C:element ratio of \(x\) should then have a C:element ratio of \(5x\). Thus, microbes can utilise substrate having C:element ratio up to five times its own. This value theoretically corresponds to the critical ratio for that particular element. Any C:element ratio higher than the critical ratio should theoretically result in net immobilisation of that particular element. However, critical ratios for different elements vary under different conditions.

Table 5 includes C:element ratios in microbial biomass from the literature and the initial C:element ratios of different litter materials used in this study. Though the C:element ratios are variable amongst fungi, it is clear that the C:element ratios of green and freshly fallen needles are below the theoretical critical ratios (five times of microbial C:element ratio) for the respective nutrient elements. Therefore, in the present study, net mineralisation (nutrient release in absolute terms) occurred for all the nutrients studied (Figs. 5–7).

The results of multiple regression analysis support the hypothesis that for litter materials with low N (less than 3%) and high lignin (more than 15%), N and lignin are better predictors among the quality parameters of decomposition (Mafongoya et al., 1998). According to Berg (1986) decomposition of ‘labile’ fractions (water-soluble components, non-lignified cellulose and hemicellulose) is primarily controlled by nutrient concentrations (e.g. N, P, S). Decomposition of recalcitrant fractions, composed mainly of lignin, depends on the initial lignin content and increases as cellulose content increases. Fast growing microorganisms that degrade labile compounds are active in the early stage of the decomposition and their activity is enhanced by the availability of N. During this phase lignin content usually increases. During the later stages of decomposition, lignin regulates

<table>
<thead>
<tr>
<th>Table 5</th>
<th>Carbon:element ratios determined for green and freshly fallen radiata pine needles compared with literature values for decomposing fungi</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C:N</td>
</tr>
<tr>
<td>Needles</td>
<td></td>
</tr>
<tr>
<td>Green</td>
<td>28</td>
</tr>
<tr>
<td>Freshly fallen</td>
<td>65</td>
</tr>
<tr>
<td>Fungi</td>
<td></td>
</tr>
<tr>
<td>Scots pine(^a)</td>
<td>12</td>
</tr>
<tr>
<td>Jeffrey pine(^b)</td>
<td>20</td>
</tr>
<tr>
<td>Mixed deciduous forest(^c)</td>
<td>16</td>
</tr>
</tbody>
</table>

\(^a\) Baath and Soderstrom (1979).
\(^b\) Stark (1972).
\(^c\) Ausmus and Witkamp (1973).
decomposition (Couteaux et al., 1991). High coefficient of determinations observed for lignin and HLQ in the present study support the change of control of decomposition from soluble carbohydrates and nutrients in the initial stages to changes in insoluble organic compounds in the latter stages.

5. Conclusions

The study demonstrated that decomposition of radiata pine needle material is determined by chemical composition (i.e. quality). Thus, green needles which contained a greater proportion of non-lignin fractions than freshly fallen needles, decomposed at a much faster rate than freshly fallen needles. It was apparent that different stages of decomposition of litter materials were governed by different quality parameters. Accordingly nutrients and soluble organic constituents controlled the decomposition during the initial stages of decomposition, lignin and HLQ components influenced the later stages of decomposition. As expected, green needles released nutrients at a faster rate compared with freshly fallen needles. The faster decomposition rate of green needles did not significantly influence the decomposition rate of freshly fallen needles in either the mixed and layered treatments. This finding indicates that addition of green needles to the forest floor through various forest management practices (thinning, pruning and harvesting) will have little impact on decomposition of existing forest floor material. However, further work involving separation of green and freshly fallen needles in mixed and layered treatments is needed to confirm this conclusion.

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