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THE IMPACT OF SELECTIVE BEECH (*NOTHOFAGUS* SPP.)
HARVEST ON LITTER-DWELLING INVERTEBRATES AND
THE PROCESS OF LITTER DECOMPOSITION

A thesis submitted in partial fulfilment of
the requirements for the Degree
of
Doctor of Philosophy
at
Lincoln University,
New Zealand.

Alison Evans
Lincoln University
1999
The conclusion I draw is optimistic: to the degree that we come to understand other organisms, we will place a greater value on them, and on ourselves.

(Edward Wilson, 1984)

Maruia state forest - showing clear-felling management in the forefront and sustainably managed forest behind.
Minimising the potential impact of forest management requires an understanding of the key elements that maintain forest diversity and its role in ecological processes. Invertebrates are the most diverse of all biota and play important roles in maintaining forest processes. However, little is known about invertebrates in New Zealand’s beech forests or the degree to which selective beech harvest might impact on their diversity and ability to carry out ecosystem processes. Studying ecosystem responses to disturbance is considered vital for understanding how ecosystems are maintained. One of the main objectives of this research was to assess whether litter-dwelling invertebrates were susceptible to the impacts of selective harvest and, if so, whether they could be used as indicators of forest health. Changes in invertebrate diversity could have important implications for nutrient cycling and primary production in forests. Litter-dwelling invertebrates contribute to the process of decomposition by increasing the surface area of the leaves, mixing soil organic matter and by infecting leaf particles with soil microbes. This investigation into the function of invertebrates in beech forest was carried out in the context of ecological theories which relate diversity to ecosystem stability and resilience.

A replicated study was established in Maruia State Forest (South Island, New Zealand) to assess the potential biotic and abiotic impacts of sustainable beech harvest. Litter-dwelling invertebrates and environmental factors were monitored during 1997, before harvest, to determine how much variability there was between study sites. Specifically, litter pH, light intensity, litter fall, litter temperature, moisture as well as invertebrate abundance and diversity were compared before and after selective harvest.
On 17 January 1998, two to three trees were selectively harvested from three of the nine study sites. On 15 February 1998 a similar number of trees were winched over or felled manually to create artificial windthrow sites. The remaining three undisturbed sites were used as controls. Invertebrates belonging to the detritivore guild were assessed from litter samples and a series of litter-bags containing pre-weighed leaf litter which were placed in each of the sites to assess rates of litter decomposition.

Millipedes (Diplopoda: Polyzoniidae, Schedotrigonidae, Dalodesmidae, Habrodesmidae, Sphaerotheridae), earthworms (Oligochaeta: Annelida), tipulid larvae (Diptera: Tipulidae), weevils (Coleoptera: Curculionidae), moth larvae (Lepidoptera: Oecophoridae, Tortricidae and Psychidae), slaters (Isopoda: Styloniscidae), Oribatid mites (Acarina: Cryptostigmata) and landhoppers (Crustacea: Amphipoda) were extracted from the litter-bags and their abundance and diversity was compared between the three treatments. Weight loss from the litter-bags and the carbon and nitrogen content of litter were used to measure the rate of decomposition in each treatment. An additional study investigated whether exclusion of invertebrates from leaf litter resulted in reduced rates of decomposition.

The results indicated that there was an increase in light intensity and a small increase in temperature following selective harvest and artificial windthrow. There was no significant difference in litter moisture or the amount of litter fall between the treatments. Invertebrate abundances were significantly affected by season but did not appear to be affected by selective harvest or artificial windthrow. The diversity of invertebrates remained relatively constant throughout the year, as did the rate of decomposition. When invertebrates were excluded from the leaf litter there was no consequential effect on the rate of litter decomposition. This suggests that there may be compensatory mechanisms taking place between the trophic levels of the food web to maintain processes and that direct links between invertebrates and decomposition are relatively weak.

In conclusion, it appears that the effects of selective beech harvest on forest-floor processes were minimal and are comparable to those created by natural windthrow disturbance. It also appears that macroclimatic effects such as seasonal climatic effects have a large effect on
forest biota. As none of the invertebrates studied appeared to be detrimentally affected by selective harvest and as there was no direct link demonstrated with decomposition, it was considered inappropriate to advocate the use of this group of invertebrates as indicators of sustainable forest management. The results from this study provide information which may help inform decisions on the future management of diversity in beech forest ecosystems.

Keywords: *Nothofagus*, beech, forest, sustainability, diversity, decomposition, ecosystem processes, selective harvest, disturbance, invertebrates, detritivores, litter-bags, indicator species, taxa.
Acknowledgements

I would like to sincerely thank my supervisors Prof. Steve Wratten and Dr. Rowan Emberson of Lincoln University and Dr. Gordon Hosking of Hosking Research for their contributions towards this thesis. All gave me good humoured guidance and allowed me the freedom to develop my own research ideas.

Dr Chris Frampton and Dr David Wardle provided constructive advice regarding research design and interpretation of the results reported in this thesis. Dr Glenn Stewart gave valuable discussion and editorial comments on parts of this thesis and gave me a crash course in *Coprosma* spp. identification. Dr Richard Duncan also gave up his time to comment on parts of this thesis. Dr John Dugdale, Dr Peter Johns and Dr Rowan Emberson were instrumental in identification of the invertebrates studied in this thesis.

Dr John Hunt and Dr Rob Allen gave me advice in the critical early phases of this research and have continued to take an interest in the results.

The staff at AgResearch kindly lent me their Tullgren funnels for the duration of the research - without which the research would have been very restricted. Karen Bonner, Mike Bowie and John Marris all offered their technical services and taught me new laboratory techniques. Phillipa Gardner and Marie Neal are both loyal friends and colleagues who demonstrated perseverance while assisting with the collection and the sorting of invertebrate samples. I also thank Murray Edmonds for his late night help with the graphics presented in this thesis.

Many people helped me to collect “bugs” in the forest during this study. I would like to thank: Rhonda Pearce, Nicolette Was, Simon Hodge, Margaret Gray, Jason Smith, Alisdair Freeman and Bill Frampton for scratching like chickens on the forest floor.

The staff at Timberlands West Coast Ltd, particularly Rob Dalley and Kit Richards were extremely professional and organised for the trees to be harvested with military precision.
John Moore of Forest Research (Rotorua, N.Z.) defeated gravity and managed to winch over some ‘rather large’ beech trees during the creation of the artificial windthrow gaps. Vaughan Keesing climbed gallantly up tall beech trees to attach the winching equipment and I wish to acknowledge his bravery.

I would also like to thank my dear friends Martin Journeaux, Jacqui Nevell, Gabrielle Hillebrandt, Eleanor Dodd, Catherine Gardner and Dr Nadine Berry for their encouragement while working on this research project. Finally, I would like to thank my husband Chris and my family for teaching me “aim high and achieve well”. Their love and support provided the foundation from which to complete this thesis.
# Table of Contents

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Title</td>
<td>i</td>
</tr>
<tr>
<td></td>
<td>Frontispiece</td>
<td>ii</td>
</tr>
<tr>
<td></td>
<td>Abstract</td>
<td>iii</td>
</tr>
<tr>
<td></td>
<td>Acknowledgements</td>
<td>vi</td>
</tr>
<tr>
<td></td>
<td>Table of Contents</td>
<td>viii</td>
</tr>
<tr>
<td></td>
<td>List of Figures</td>
<td>x-xii</td>
</tr>
<tr>
<td></td>
<td>List of Tables</td>
<td>xiv</td>
</tr>
<tr>
<td></td>
<td>List of Plates</td>
<td>xv</td>
</tr>
<tr>
<td></td>
<td>Chapter 1 General Introduction</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduction and literature review</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Concluding remarks</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Research objectives</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Chapter 2 Research area description</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Experimental design</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Site description</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Chapter 3 Abiotic and biotic changes following selective harvest and artificial windthrow.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduction</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Methods</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Results</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>Discussion</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>Chapter 4 Responses of litter-dwelling invertebrates to selective harvest and artificial windthrow.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Introduction</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>Methods</td>
<td>41</td>
</tr>
</tbody>
</table>
Chapter 5  The effect of selective harvest and artificial windthrow on litter-dwelling invertebrates and litter decomposition.

Introduction  58
Methods  61
Results  65
Discussion  77

Chapter 6  The effect of excluding invertebrates on decomposition rate and the effect of selective harvest on microbial respiration.

Introduction  82
Methods  85
Results  87
Discussion  90

Chapter 7  General Discussion

Addressing the research objectives  93
Limitations of the research  97
Concluding remarks  99

References  101

Appendices
# List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Rainfall in the Maruia District in 1997.</td>
<td>13</td>
</tr>
<tr>
<td>2.2</td>
<td>Rainfall in the Maruia District 1998 and in January and February, 1999.</td>
<td>13</td>
</tr>
<tr>
<td>2.3</td>
<td>Placement of the nine sites at Station Creek.</td>
<td>18</td>
</tr>
<tr>
<td>2.4</td>
<td>The basal area in each site- preharvest and postharvest.</td>
<td>20</td>
</tr>
<tr>
<td>3.1</td>
<td>The mean litter fall recorded in Control, Harvested and Windthrow sites</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>during the preharvest and postharvest years.</td>
<td></td>
</tr>
<tr>
<td>3.2</td>
<td>Mean, minimum and maximum bimonthly leaf litter temperatures from all nine</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>sites in the preharvest year.</td>
<td></td>
</tr>
<tr>
<td>3.3</td>
<td>Mean, minimum and maximum bimonthly leaf litter temperatures from the</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>control sites in the postharvest year.</td>
<td></td>
</tr>
<tr>
<td>3.4</td>
<td>Mean, minimum and maximum bimonthly leaf litter temperatures from the</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>harvested sites in the postharvest year.</td>
<td></td>
</tr>
<tr>
<td>3.5</td>
<td>Mean, minimum and maximum bimonthly leaf litter temperatures from the</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>windthrow sites in the postharvest year.</td>
<td></td>
</tr>
<tr>
<td>3.6</td>
<td>The mean bimonthly leaf litter temperatures for each treatment in the</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>postharvest year.</td>
<td></td>
</tr>
</tbody>
</table>
3.7 Mean water content of leaf litter samples at two monthly intervals: preharvest.

3.8 Mean water content of leaf litter samples at two monthly intervals: postharvest.

4.1 The proportion of each detritivore family collected in all nine sites during the preharvest study.

4.2 The proportion of each detritivore family collected on 5 December, 1997 during the preharvest study and 16 December, 1998 during the postharvest study.

4.3 Detritivore family richness in control, harvest and windthrow sites during the preharvest and postharvest year.

4.4 Oribatid mite richness in control, harvest and windthrow sites during the preharvest and postharvest years.

4.5 Detritivore diversity in the proposed control, proposed harvest and proposed windthrow sites during the preharvest year.

4.6 Oribatid mite diversity in the proposed control, proposed harvest and proposed windthrow sites during the preharvest year.

4.7 Biplot showing how invertebrate families were influenced by temperature, moisture and litter fall in the preharvest and postharvest years combined.

4.8 Biplot showing how invertebrates in the preharvest study sites (No. 1-9) and postharvest study sites (No. 10-18) are influenced by temperature, moisture and litter fall two months after selective harvest and artificial windthrow.
4.9 Biplot showing how invertebrates in the preharvest study sites (No. 1-9) and postharvest study sites (No. 10-18) are influenced by temperature, moisture and litter fall 12 months after selective harvest and artificial windthrow.

5.1 Canonical Correspondence Analysis ordination of the detritivore families in each of the nine sites in relation to environmental variables following two months’ and 12 months’ decomposition in the preharvest year.

5.2 Canonical Correspondence Analysis ordination of the detritivore families in each of the nine sites in relation to environmental variables following two months’ and 12 months’ decomposition in the postharvest year.

5.3 Canonical Correspondence Analysis ordination of the nine sites in relation to environmental variables following two months (Nos. 1-9) and 12 months (Nos. 10-18) decomposition in the preharvest year.

5.4 Canonical Correspondence Analysis ordination of the nine sites in relation to environmental variables following two months (Nos. 1-9) and twelve months (Nos. 10-18) decomposition in the postharvest year.

5.5 The richness of detritivore families in litter-bags collected at two monthly intervals from control, harvested and artificial windthrow sites.

5.6 The richness of oribatid mites in litter-bags collected at two monthly intervals from control, harvested and artificial windthrow sites.

5.7 The evenness of detritivore distributions in control, harvested and windthrow sites in preharvest and postharvest years.
5.8 The evenness of oribatid mite distributions in control, harvested and windthrow sites in preharvest and postharvest years. 72

5.9 The mean diversity of detritivore families in litter-bags collected at two month intervals from control, harvested and artificial windthrow sites. 73

5.10 The mean diversity of oribatid mites in litter-bags collected at two month intervals from control, harvested and artificial windthrow sites. 73

5.11 The percentage weight remaining in litter-bags collected at two-monthly intervals from control, harvested and artificial windthrow sites in the preharvest year. 74

5.12 The percentage weight remaining in litter-bags collected at two-monthly intervals from control, harvested and artificial windthrow sites in the postharvest year. 75

5.13 The mean carbon:nitrogen ratio of leaf litter in litter-bags in control, harvested and artificial windthrow sites at two-monthly intervals during the preharvest year. 75

5.14 The mean carbon:nitrogen ratio of leaf litter in litter-bags in control, harvested and artificial windthrow sites at two-monthly intervals during the postharvest year. 76

5.15 The percentage of carbon and nitrogen per litter-bag in control, harvest and windthrow sites during the preharvest study. 76

6.1 The mean weight remaining in large mesh litter-bags, small mesh litter-bags and small mesh litter-bags treated with insecticide after 0, 2, 4, 8 and 12 months litter decomposition. 89
List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Inventory of trees harvested from three study sites.</td>
<td>16</td>
</tr>
<tr>
<td>2.2</td>
<td>Inventory of trees that were winched over or felled to simulate windthrow damage.</td>
<td>17</td>
</tr>
<tr>
<td>2.3</td>
<td>The number of trees and saplings (&gt;5cm DBH) in the proposed control, harvest and artificial windthrow sites.</td>
<td>19</td>
</tr>
<tr>
<td>2.4</td>
<td>The mean acidity (pH) of leaf litter in nine sites - preharvest and postharvest.</td>
<td>20</td>
</tr>
<tr>
<td>3.1</td>
<td>Amount of light intercepted by the canopy in Control (C), Harvested (H) and Artificial windthrow (W) sites.</td>
<td>29</td>
</tr>
<tr>
<td>6.1</td>
<td>The total abundance of detritivore families from five small mesh litter-bags with insecticide, five small mesh litter bags without insecticide and five large mesh litter-bags collected from harvested and control sites.</td>
<td>87</td>
</tr>
<tr>
<td>6.2</td>
<td>The total abundance of Oribatid mites from five small mesh litter-bags with insecticide, five small mesh litter-bags without insecticide and five large mesh litter-bags collected from harvested and control sites.</td>
<td>88</td>
</tr>
<tr>
<td>6.3</td>
<td>The mean (± SE) for microbial substrate induced respiration for litter collected from control, harvested and windthrow sites (n = 15 samples/treatment).</td>
<td>90</td>
</tr>
</tbody>
</table>
List of Plates

<table>
<thead>
<tr>
<th>Plate</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Maruia State Forest.</td>
</tr>
<tr>
<td>2.2</td>
<td>A Mil 17 helicopter lifting the harvested trees from one of the study sites.</td>
</tr>
<tr>
<td>2.3</td>
<td>Trees manually winched over to simulate windthrow damage.</td>
</tr>
<tr>
<td>3.1</td>
<td>A litter-funnel being emptied in one of the study sites.</td>
</tr>
<tr>
<td>3.2</td>
<td>A datalogger used to monitor leaf litter temperature.</td>
</tr>
<tr>
<td>4.1</td>
<td>The Tullgren funnels used to extract invertebrates from leaf litter.</td>
</tr>
<tr>
<td>4.2</td>
<td>Leaf litter samples.</td>
</tr>
<tr>
<td>5.1</td>
<td>One of the litter-bags used in this study.</td>
</tr>
</tbody>
</table>
Chapter 1

General Introduction

1.1 Introduction and literature review

In 1992, the United Nations Conference on Environment and Development (UNCED) focussed on the need for sustainable management of global resources. Sustainability refers to the idea that "resources should be developed and used to meet the needs of the present generation in a way that does not compromise the ability of future generations to satisfy their needs" (World Commission on Environment and Development, 1987). While the sustainable use of resources is not a new concept, public concern regarding resource use has escalated considerably in recent years. The Montreal Process (Anon, 1995) resulted in the development of seven criteria and sixty-seven indicators from which to assess sustainability in managed forests. However, many of these criteria and indicators were not considered to be useful at a local level. It has been recognised that national laws and policies that take into consideration local ecological conditions, as well as encouraging individual, community and corporate responsibility for the protection of the environment, need to be developed to ensure the survival of species (World Commission on Environment and Development, 1987).

The view that forests need to be managed on a sustainable basis for both environmental protection and as a source of timber products is widely held (Whitmore and Sayer, 1992). However, the key to analysing sustainability is thought to lie in understanding ecosystem response to disturbance and the mechanisms of post-disturbance development (Kimmins, 1997).

Although New Zealand is a signatory to the principles outlined in both the UNCED (1992) and Montreal Processes (Anon, 1995), local definitions and measures of sustainability are still being developed. Recent changes to New Zealand's indigenous forestry legislation protect large areas of forest in the conservation estate and state that production forests are to be managed on a sustainable basis. Consequently, forest managers are required to prepare sustainable management plans and demonstrate sustainable management practices. Indigenous forest management in New Zealand is based on the need to preserve the forest in perpetuity and is based on international objectives such as those prepared by Brüenig (1996):
"...management should work toward a forest structure which keeps the ecosystem as robust, elastic, versatile, adaptable, resilient and tolerant as possible: canopy openings should be kept within the limits of natural gap formation; stand and soil damage must be minimised; felling cycles must be sufficiently long and tree marking so designed that selection forest canopy structure and a self regulation stand table are maintained, without or with very little, silvicultural manipulation; production of timber should aim for high quality and versatility. The basic principle is to mimic nature as closely as possible to make profitable use of the natural ecosystem dynamics and adaptability and reduce costs and risks."

The sustainable forestry practice adopted in New Zealand's indigenous forest involves uneven management, where single trees or small groups, are selected to mimic the type of disturbance patterns found in old-growth forests. International research indicates that selective tree harvest has a reduced impact on forest dynamics compared with more traditional forest management practices such as clear-felling (Kimmins, 1997; Tritton and Johnson, 1998). Though, the management techniques adopted in New Zealand are well intentioned, little is known about the impact of selective harvest on forest biota and it is not known whether timber harvest is sustainable in the short or long term. The research described in this thesis took place in the Maruia State Forest, South Island, New Zealand and areas of this forest are designated for the selective beech harvest scheme proposed by Timberlands West Coast Ltd.

**Invertebrates as indicators of sustainability.**

The primary concern with sustainable forest management is habitat destruction and the associated decline in diversity that has been demonstrated in some forests (Seastedt and Crossley, 1981; Hoekstra *et al.*, 1995; Niemelä *et al.*, 1995). Invertebrates comprise the largest component of diversity in forests (Southwood, 1985) and a better understanding of their function could lead to the selection of indicator species. Invertebrates are potentially good indicators of sustainability, largely due to their ubiquitous nature, their ability to respond quickly to changes in microhabitat and because of their involvement with many functional roles in the forest (Coulson and Witter, 1984). The presence of large numbers of invertebrates also means that it is relatively efficient and cost effective to obtain sufficient data sets to assess changes in their abundance and diversity (Coulson and Witter, 1984; Weaver,
However, any indicators have in the past been selected on the basis that they are of conservation value or are of significant economic importance and little regard has been given to whether they are of consequence to ecosystem maintenance (McGeoch, 1998; Rodriguez et al., 1998). Litter-dwelling invertebrates offer the opportunity to test experimentally the consequences of selective harvest since they are associated with ecosystem functions. Information regarding invertebrate responses to disturbance may therefore be used to better understand how ecosystems respond to disturbance and which ecosystem elements are vital for ecosystem maintenance.

**Effects of disturbance on environmental factors and litter resources.**

Small-scale disturbances such as windthrow play a critical role in maintaining forest communities (Ogden et al., 1996). Disturbances create changes in resources and local environmental conditions that may lead to changes in invertebrate community composition and ecosystem processes (Connell, 1978; Sousa, 1979). Determining the relationship between biodiversity and ecosystem function is, however, complicated by the confounding effects of environmental factors. It is therefore essential to quantify factors such as litter moisture, litter temperatures, litter pH, rainfall, litter fall and the quantity of ultraviolet light, which are considered to be major factors in determining invertebrate abundance.

Confounding environmental factors (or 'hidden treatments') make it difficult to ascertain the direct effect of a reduction in diversity on ecosystem processes. Litter temperature and moisture are critical in determining invertebrate colonisation rates of organic matter and the rate of decomposition (Wood, 1989; Tian et al., 1993; Couteaux et al., 1995). Temperature regulates the development of invertebrates (Wigglesworth, 1965; Kenagy and Stevenson, 1982; Curry, 1998) and microbial activity (Heal et al., 1997). In New Zealand, Moeed and Meads (1985, 1986 and 1987b) demonstrated that the abundance of invertebrates inhabiting the forest floor was correlated with seasonal fluctuations in temperature but not with rainfall. Litter pH also influences invertebrate community composition, in particular, earthworm and millipede abundances (Curry, 1998), which has implications for litter decomposition. Situations where pH is low, temperatures high and rainfall low, can result in slow decomposition and the accumulation of leaf litter for many years (Hopkins and Read, 1992; Hammel, 1997).

The amount of light entering the forest was also considered an important factor in the research
described in this thesis. Radiant energy can influence both litter temperature and moisture as well as the activity of invertebrates (Wigglesworth, 1965). It has also been suggested that ultraviolet light can change the fungal communities in leaf litter, which may result in reduced rates of decomposition (Heal et al., 1997). Assessing litter resources is also important when investigating invertebrate abundance (Alley et al., 1999). Leaf litter is a fundamentally important resource for invertebrates inhabiting the forest floor, and determining litter fall rates may be useful in understanding organic matter input and nutrient cycling in the forest ecosystem (Kenagy and Stevenson, 1982). Despite the importance of litter fall, few studies have compared invertebrate abundances with litter and seed-fall. Although beech trees (Nothofagus spp.) are evergreen, most species have high rates of litter fall (leaves and seeds) in autumn (Sweetapple and Fraser, 1992). Fitzgerald et al., (1996) recorded high proportions of lepidopteran larvae (Lepidoptera: Oecophoridae) when litter fall was high. Perhaps the most relevant work was that of Alley et al., (1999) who showed that lepidopteran larvae, spiders and amphipods were more abundant following beech flowering and seeding.

A study that did not involve assessing invertebrate abundance but investigated the impact of selective harvest on litter fall was carried out by Villela et al. (1998) in Brazil. Their study involved comparing litter fall, decomposition rates and carbon/nitrogen ratios in selectively logged and unlogged rainforest. Their results indicated that selective logging did not detrimentally affect litter fall, decomposition rates or carbon/nitrogen ratios.

It is apparent that studies of litter fall and environmental variables can be useful in explaining fluctuations in invertebrate abundance. In the present study, an attempt has been made to determine the influence of those environmental factors on invertebrate populations and communities and on litter decomposition.

**The impact of tree harvest on invertebrates.**

As selective harvest has only recently been adopted in New Zealand, no research has been published on its impact on invertebrate diversity or individual invertebrate groups. In fact, only a few studies have attempted to characterise the invertebrate fauna of New Zealand's indigenous forests. In New Zealand, most studies involving forest invertebrates have been limited by a lack of taxonomic information and by the vast richness of the invertebrate fauna. Early studies of the arthropods in beech forest include those of Grimmett (1926), McColl (1974, 1975) and Dugdale (1974). More recently, studies by Moeed and Meads (1984, 1985,
1986, 1987a, 1987b, 1992) comprehensively surveyed the seasonality and density of invertebrates inhabiting indigenous forest in the Orongorongo Valley, near Wellington, New Zealand. They used a range of sampling methods to study the vertical and seasonal distribution of airborne invertebrates, those active on the forest floor, as well as the number of emerging insects and the density of litter invertebrates.

These studies are the most comprehensive that have taken place in New Zealand’s indigenous forest and descriptions of the seasonality of litter-dwelling invertebrates are useful to the research outlined in this thesis. However, that research was predominantly conducted in a mixed forest (beech/podocarp) whereas this thesis describes research in a less botanically diverse beech forest. The research described in their studies did not investigate the impact of forestry practices such as harvest and did not evaluate the contribution of invertebrates to ecosystem processes.

Dugdale (1996) emphasised the importance of lepidopteran caterpillars in forest dynamics. In New Zealand, New Caledonia and Australia, a high proportion of the lepidopteran fauna (12-19%) is associated with the decomposition of leaf litter, whereas, only c. 5% of lepidopteran caterpillars occupy leaf litter in other countries (Hodges, 1983; Emmett, 1988). This may be related to deciduous trees being predominant in the northern hemisphere.

Dugdale (1996) described fully the lepidopteran fauna of a North Island beech forest and Alley et al. (1999) studied seasonal population fluctuations of lepidopteran larvae with litter fall and mouse populations. Both studies indicated that lepidopteran larvae were particularly abundant following beech-seed production. A minority of invertebrates in New Zealand’s indigenous forest have been identified (Kuschel, 1975) and nothing is known about the potential impact of selective beech harvest on the invertebrate fauna. Preliminary studies by Forest Research attempted to characterise the beetle fauna both within harvested sites (between 0.5 ha and 1 ha) and in adjacent forest, but these results have not as yet been published (Brockerhoff, pers. comm.).

In 1996, Timberlands West Coast Ltd contracted Lincoln University to compare the invertebrate fauna in an age series of managed forests. These included a 6 month old harvested site (0.5 ha), a clear-felled area with 15 years regeneration, a clear-felled area with 40 years regeneration (with pruned and thinned beech trees) and a clear-felled area with 40 years regeneration (no management). Each harvested site was also compared with adjacent unharvested forest. The results indicated that the invertebrate diversity was dependent on the level of forest habitat sampled (subcanopy or forest floor), the degree of forest regeneration
and the management techniques employed following harvest. It was also apparent from the results that the invertebrate fauna between different unharvested forests varied considerably (Evans et al., 1996). Unfortunately, this study was limited by the fact that invertebrates were identified only to a coarse taxonomic level and were monitored for only a short time. In summary, most New Zealand studies have looked only superficially at the invertebrate fauna in indigenous forests and have not attempted to investigate the responses of invertebrates to tree harvest. This is largely due to a prior focus on economic pests or endangered species. There has been inadequate attention paid to describing New Zealand's invertebrate fauna taxonomically and, as a result, characterising invertebrate communities in indigenous forest is extremely difficult. It has become important not only to characterise New Zealand's invertebrate fauna but to try to draw links between diversity and ecosystem function, so that key elements of the invertebrate fauna may be preserved and loss of biodiversity minimised.

Relevant studies in other forest types.

It is unclear whether the selective harvest of beech in New Zealand will lead to changes in the invertebrate fauna. Studies overseas indicate that the effects of tree harvest on invertebrate communities are variable. Several studies have demonstrated that invertebrates are detrimentally affected (Huhta, 1976; Seastedt and Crossley, 1981; Lenski, 1982; Chandler and Peck, 1992, Hill et al., 1995). Huhta (1976) studied the abundance, biomass and respiration rates of soil invertebrates in clear-felled areas of varying ages and uncut areas of forest in Finland. His results indicated that invertebrate families responded differently to clear-felling and that clear-felling is detrimental in the long term to most invertebrate groups. Earthworm (Annelida: Lumbricidae) and oribatid mite (Acari: Oribatida) abundances were higher in the newly harvested site compared with the control site yet lower in the older harvested sites. Tipulid (Diptera: Tipulidae) larvae were also considerably less abundant in the clear-felled area compared with the control area. This study provides useful background information on the likely responses of soil invertebrates to clear-felling, but it is hampered by a lack of site replication and by the acknowledged lack of baseline data on the study sites. Seastedt and Crossley (1981) investigated invertebrate responses following cable logging and clear-felling in the southern Appalachian Mountains, USA. Their results indicated that invertebrate densities declined in clear-felled areas compared with adjacent uncut forest and
they attributed this to an increase in temperature recorded on the soil surface. This study suggests that soil temperature may have an influence on invertebrate abundances and therefore is likely to play a role in determining rates of litter turnover.

Lenski (1982) described how forest cutting affected the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachian Mountains. His results indicated that the within-genus component of beetle diversity increased following tree harvest. He attributed this to a disruption of the competitive exclusion process where competition between species decreases following disturbance. The base for this conclusion is that there is congeneric species competition and that there is no emigration or immigration from the study area. The sampling method used to assess beetle diversity was pitfall trapping. This method provides estimates of relative abundance (since numbers depend on invertebrate activity) and is limited by a lack of defined catchment area (Halsall and Wratten, 1988). The conclusions of this study rely on the assumption that less beetle activity indicates less competition and greater diversity.

Chandler and Peck (1992) studied the diversity and seasonality of Leiodid beetles (Coleoptera: Leiodidae) in an old growth forest and a 40 year old forest that had previously been clear-felled in Britain. Their results indicated that species richness was similar in both forest types but that the species evenness differed. They attributed the difference in diversity to greater abundances of some Leiodid species in the old growth forest. Further evidence that some invertebrate populations may be modified by tree harvest was provided by Hill et al. (1995) who reported that the species richness and abundances of forest butterflies were lower in selectively harvested forest than unlogged forests in Indonesia.

Other international studies have shown that invertebrate populations have varying responses to harvest (Niemela et al., 1995; Hoekstra et al., 1995; Bengtsson et al., 1997; Watt et al., 1997).

Niemela et al. (1995) investigated the response of beetles to forest clear-felling in western Canada. In their study, they used pitfall traps to compare the abundance of beetle species in mature forest with those from five age classes of regenerating forest. Their results suggested that the species richness of Carabid beetles was higher in regenerating sites than in the mature forest site. The results also suggested that generalist species were no different between the sites, whereas species adapted to open habitats were more abundant in regenerating sites. Species commonly found in the mature forest sites declined in number in the regenerating sites. Although, this study illustrated how indicator species can be used to measure the impact of harvest, there was little indication of how other invertebrates may be responding to harvest.
or what role these beetles may play in maintaining ecosystem function.

Hoekstra et al., (1995) investigated the effect of selective redwood (Sequoia sempervirens (D.Don) Endl.) harvest on soil invertebrate abundance in a forest in coastal California, USA. Soil invertebrate abundances in harvested forest were compared with invertebrate abundances in uncut old growth forest and mature secondary growth forest. There was no significant difference in invertebrate abundance between old growth forest and secondary growth forest. However, there were significantly higher numbers of macrophytophage (larger plant feeders) and significantly lower numbers of predatory species in selectively harvested forest compared with the other treatments. The authors concluded that the observed results provided evidence that selective harvest had a long-lasting effect (15 yrs) on soil arthropod communities.

The impact of complete forest clearance and partial forest clearance on invertebrate abundance in west Africa was reported by Watt et al. (1997). They studied the damage caused by leaf-mining insects, the abundance of gall-forming mites and the number of trees affected by shoot borers. Their results indicated that several groups of insects were more abundant in partially cleared forest than in areas of total clearance. The authors conceded that the relevance of this research could have been improved by a detailed knowledge of the invertebrate community composition and an understanding of the functional roles of the invertebrates involved.

In 1997, a study was conducted in central Sweden to determine the long-term effects of logging residue on invertebrates (Bengtsson et al., 1997) (logging residue is the unmerchantable timber, branches and leaves that are left on site following harvest).

The study was completed in Scots pine, Pinus sylvestris (L.), almost 20 years after tree harvest. In sites that had received double the normal amount of logging residue, the composition of the invertebrate community was significantly different from sites that had logging residue removed. They concluded from this study that removal of logging residue may impact on the abundance of many soil invertebrates and attributed this to a reduction in nutrient availability.

Clearly, there are varying effects on invertebrate fauna from removing trees. Many of the studies outlined have reported that some families of invertebrates increase in diversity following harvest while others decline. A range of sampling methods has been used to quantify invertebrate abundance, which makes the studies difficult to compare with the present work. While the studies reported provide useful information on the probable responses of specific invertebrate groups to large-scale disturbance, few are useful in
determining the impact of selective harvest on invertebrate communities.

Many of the previous studies reviewed have neglected to:

- collect baseline data to ensure that treatments are comparable before intervention
- replicate their studies to enable robust statistical analysis
- use sampling techniques that provide representative samples of the invertebrate fauna
- standardise the sampling effort
- link invertebrate guilds with ecosystem functions.

**The effect of harvest on litter decomposition.**

Invertebrates play a vital role in the decomposition of plant material which is critical to nutrient cycling and primary productivity (Stout *et al.*, 1975; Anderson and Ineson, 1984; Verhoef and Brussard, 1990; Hoekstra *et al.*, 1995; Wardle and Lavelle, 1997).

Decomposition initially involves comminution of leaves by invertebrates whereas the latter stages of decomposition (mineralisation and immobilisation of nutrients) are largely completed by bacteria and fungi (microbial decomposition) (Wardle and Lavelle, 1997).

Attempts to quantify the role of invertebrates in the early stages of decomposition have previously involved reducing the mesh size of litter-bags to exclude certain groups of invertebrates or involved the use of insecticides. Excluding invertebrates using mesh litter-bags has had a measurable effect on the rate of decomposition (Swift *et al.*, 1979; Anderson, 1988). Santos and Whitford (1981) treated litter-bags with insecticide to exclude invertebrates and demonstrated that the rate of litter decay declined by 53%. Quantifying the rate of litter decay in the absence of invertebrates in this way confirms the importance of invertebrates in the decomposition process and nutrient cycling.

Despite constituting a large proportion of forest biodiversity and despite their importance in decomposition, litter-dwelling invertebrates have received relatively little research attention. A review of recent research by Setälä *et al.*, (1998) indicated that when the number of functional (or trophic) groups (e.g., detritivores, microbivores, predators, fungivores, etc.) was manipulated in decomposing material, microbial activity declined, reducing mineralisation of essential nutrients such as carbon and nitrogen. Studying the relationships within invertebrate communities and their role in the process of decomposition are imperative if the impacts of harvest are to be understood. Recognising which invertebrates are important for ecosystem function is fundamentally important for setting management and conservation priorities.
Grime, 1997). Clearly, there is an urgent need to determine how resilient invertebrate populations are and whether ecological processes are detrimentally affected by disturbances such as selective harvest.

### 1.2 Concluding remarks

It is apparent from the studies reviewed that invertebrates constitute a large proportion of forest biodiversity and play a vital role in the maintenance of forest processes. Loss of ecosystem function is of major concern and understanding which key elements of the biota are necessary to maintain ecosystems is critical to the preservation of forests (Craig, 1999). The research described in this thesis is intended to improve our understanding of how invertebrate communities respond to and recover from selective harvest and investigate what role litter-dwelling invertebrates play in maintaining ecological processes. It aims to identify which invertebrates (indicator species) are susceptible to the environmental changes resulting from selective harvest and artificial disturbances. In addition, it investigates whether current selective harvest regimes are within the ecological boundaries of natural disturbances such as windthrow and assists in the development of criteria for measuring sustainability. This information is largely required for the beech harvesting scheme proposed by Timberlands West Coast Ltd. and for management plans submitted by private forest owners. Although, the research was primarily designed to address forest management issues, some contemporary theories relating to the stability and functional significance of biodiversity in ecosystems are also explored.
1.3 Research Objectives

The research described in this thesis had the following objectives:

• To quantify changes in environmental factors due to selective harvest and determine whether these factors differ from those that occur following windthrow disturbance.

• To assess the impact of changes in environmental factors on seasonal abundances of litter-dwelling invertebrates and their responses to seasonal litter fall patterns in beech forest.

• To determine the potential impact of sustainable beech harvest and artificial windthrow on the abundance and diversity of litter-dwelling invertebrates and the rate of leaf litter decomposition.

• To investigate the links between invertebrate diversity and decomposition, and assess the efficacy of using litter-dwelling invertebrates as indicators of sustainable forest management.
Chapter 2

Site description and experimental design.

2.1 Research Area Description

The research described in this thesis was undertaken in the Maruia State Forest (42°13'S, 172°16'E), South Island, New Zealand. The forest is approximately 500 m above sea level and is dominated by two main tree species; red beech (*Nothofagus fusca*) (Hook.f.) Oerst. and silver beech (*Nothofagus menziesii*) (Hook.f.) Oerst. White pine (*Dacrycarpus dacrydioides*) (A.Rich.) Laubenf. and black pine (*Prumnopitys taxifolia*) (D.Don.) Laubenf. are also present but only in small numbers. Studies by Stewart and Burrows (1994) in the Maruia State Forest reported that undisturbed areas contained predominantly red beech trees (up to 250 stems/ha) and that most trees measured more than 20 cm diameter at breast height (DBH).

Plate 2.1: Maruia State Forest.
The mean rainfall in this region is c. 2000 mm (Tate et al., 1993; Hollinger et al., 1994). Rainfall recorded by local resident Beverly Blanche (Cave Stream Rd, Rappahannock Valley, Maruia) during this study (Figure 2.1 and Figure 2.2) was similar to those reported above.

![Figure 2.1: Rainfall in the Maruia District in 1997 (Blanche, unpubl.).](image)

![Figure 2.2: Rainfall in the Maruia District 1998 and in January and February 1999 (Blanche, unpubl.).](image)
Mean air temperatures at Maruia range between c. 3°C to 16°C during the year and can reach a maximum of 32°C in summer months (Hollinger et al., 1994). The geology of the region is varied due to movement of the alpine fault which runs the length of the South Island, but essentially consists of pre-quaternary strata where greywacke and schist are the main constituents (Mabin, 1983).

2.2 Experimental Design

The research described comprised two studies: a baseline study (February, 1997 - January, 1998) and an experimental study (February, 1998 - February, 1999).

The baseline study investigated the background abundance of litter-dwelling invertebrates and the rate of decomposition for one year before experimentation (preharvest).

The rationale for the baseline study was:

• to assess seasonal abundance of litter-dwelling invertebrates
• to assess the rate of leaf-litter decomposition relative to litter fall and abiotic factors
• to determine the level of variation between sites before harvest and artificial windthrow

(see page 18 for description of the treatments).

In the baseline study, nine 20 m x 20 m sites were established in old-growth forest. Each site was separated by at least 100 m of buffer zone forest. The sites were chosen to be similar in aspect, slope and floral composition of trees. The treatments were randomly allocated to the sites.

On 17 January, 1998 trees were selectively harvested from three randomly chosen sites (see Table 2.1). Harvesting was carried out by Timberlands West Coast Ltd, and followed their standard operating procedures. This involved directional felling of 2-3 trees in each site and removal of merchantable timber using a helicopter. The standard gap size created is approximately 0.05ha. The sites were labelled H1, H2, H3 (see Figure 2.3).
Plate 2.2: A Mil 17 helicopter lifting the harvested trees from one of the study sites.
Table 2.1: Inventory of trees harvested from three study sites.

<table>
<thead>
<tr>
<th>SITE</th>
<th>TREE SPECIES</th>
<th>DBH (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>H1</td>
<td><em>N. fusca</em></td>
<td>48.3</td>
</tr>
<tr>
<td></td>
<td><em>N. fusca</em></td>
<td>28.3</td>
</tr>
<tr>
<td>H2</td>
<td><em>N. fusca</em></td>
<td>33.3</td>
</tr>
<tr>
<td></td>
<td><em>N. fusca</em></td>
<td>31.8</td>
</tr>
<tr>
<td>H3</td>
<td><em>N. fusca</em></td>
<td>35.8</td>
</tr>
<tr>
<td></td>
<td><em>N. menziesii</em></td>
<td>28.8</td>
</tr>
<tr>
<td></td>
<td><em>N. menziesii</em></td>
<td>22.3</td>
</tr>
</tbody>
</table>

Tree harvest was carried out by Timberlands West Coast Ltd. and the recovery of logs followed guidelines outlined by the Civil Aviation code of practice (See Appendix 2.1). On 13 February, 1998 trees were manually winched over in three of the nine established sites (see Table 2.2). These sites were W1, W2, W3 (see Figure 2.3). Where the canopy opening was not comparable with those in harvested sites, additional trees were conventionally felled by Timberlands West Coast staff. Natural windthrow damage typically occurs during high wind episodes in beech forests and is exacerbated by factors such as tree health and soil stability (Ogden et al., 1996). The gap size created via natural windthrow can vary between beech forests although Stewart et al., (1991) demonstrated that the majority of gaps are less than 2 ha.
Table 2.2: Inventory of trees that were winched over or felled to simulate windthrow damage.

<table>
<thead>
<tr>
<th>SITE</th>
<th>METHOD OF FELLING</th>
<th>TREE SPECIES</th>
<th>DBH (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>W1</td>
<td>Winch</td>
<td><em>N. fusca</em></td>
<td>42.5</td>
</tr>
<tr>
<td></td>
<td>Winch</td>
<td><em>N. menziesii</em></td>
<td>10.0</td>
</tr>
<tr>
<td></td>
<td>Conventional</td>
<td><em>N. menziesii</em></td>
<td>43.0</td>
</tr>
<tr>
<td>W2</td>
<td>Conventional</td>
<td><em>N. fusca</em></td>
<td>80.0</td>
</tr>
<tr>
<td></td>
<td>Winch</td>
<td><em>N. menziesii</em></td>
<td>18.5</td>
</tr>
<tr>
<td></td>
<td>Winch</td>
<td><em>N. menziesii</em></td>
<td>22.0</td>
</tr>
<tr>
<td></td>
<td>Winch</td>
<td><em>N. menziesii</em></td>
<td>22.0</td>
</tr>
<tr>
<td></td>
<td>Winch</td>
<td><em>N. menziesii</em></td>
<td>30.5</td>
</tr>
<tr>
<td>W3</td>
<td>Conventional</td>
<td><em>N. fusca</em></td>
<td>67.5</td>
</tr>
<tr>
<td></td>
<td>Winch</td>
<td><em>N. fusca</em></td>
<td>61.5</td>
</tr>
</tbody>
</table>

Plate 2.3: Trees manually winched over to simulate windthrow damage.
The remaining three sites were undisturbed as comparative control sites. These were C1, C2, C3 (see Figure 2.3).

Figure 2.3: Placement of the nine sites at Station Creek.

2.3 Site Description

Floral Diversity

Several studies have demonstrated that leaf litter of varying composition and quality may affect invertebrate species composition (Seastedt and Crossley, 1984) and hence the rate of decomposition (Heal et al., 1997). To account for potential differences in litter quality and assess comparability of sites at baseline (before harvest or artificial windthrow), an inventory of floral diversity (Allen, 1993) was completed in each of the nine sites. All trees within each 20 m x 20 m plot that were > 5 cm DBH were identified and their diameter recorded (Table 2.3). Saplings (< 5 cm DBH) were also recorded but seedlings were not, as they were not considered to be contributing greatly to the basal area in each site. This method also resulted in a basal area measurement for each of the sites.
Table 2.3: The number of trees and saplings (>5 cm DBH) in the proposed control, harvest and artificial windthrow sites.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>H1</th>
<th>H2</th>
<th>H3</th>
<th>W1</th>
<th>W2</th>
<th>W3</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. menziesii</td>
<td>114</td>
<td>71</td>
<td>66</td>
<td>41</td>
<td>69</td>
<td>46</td>
<td>45</td>
<td>86</td>
<td>58</td>
</tr>
<tr>
<td>N. fusca</td>
<td>9</td>
<td>10</td>
<td>13</td>
<td>8</td>
<td>22</td>
<td>15</td>
<td>6</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>Coprosma foetidissima</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma parviflora</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma colensoi</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma microcarpa</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma propinqua</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma linearifolia</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma serrulata</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Myrsine divaricata</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>13</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Neomyrtus pendunculata</td>
<td>4</td>
<td>8</td>
<td>0</td>
<td>7</td>
<td>39</td>
<td>0</td>
<td>6</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Pseudopanax crassifolius</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Elaeocarpus hookerianus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Carpodetus serratus</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Griselinia littoralis</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Pseudowintera colorata</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Basal area

The basal area in each site was calculated so that it was possible to quantify trees felled in harvested and artificial windthrow sites. The following formula was used to calculate basal area:

\[
\text{Basal area (m}^2/\text{site}) = \left(\frac{\text{diameter at breast height}}{2}\right)^2 \times \pi / 10,000
\]

The average basal area was similar between the three treatment types; proposed control = 2.4 m\(^2\)/site, proposed harvest = 3.6 m\(^2\)/site, proposed windthrow = 3.4 m\(^2\)/site although there was a high variability in basal area within the treatments.
Soil Acidity

Previous studies have suggested that the chemical composition of soil has the potential to influence the abundance of some invertebrate groups (Maraun and Scheu, 1996), particularly earthworms (Curry, 1998) and millipedes (Hopkin and Read, 1992).

To determine whether acidity was consistent across all treatments in the present study, leaf-litter acidity was assessed both preharvest (6 April, '97) and postharvest (16 April, '98). Five samples of leaf litter each weighing 10 g (wet weight) were collected from the nine sites. Litter was then mixed with 50 ml distilled water for 24 h and assessed for acidity using an Orion electronic pH meter. The results indicated that mean acidity ranged between pH 4.05 and pH 4.66 and that mean acidity differed only slightly between the study sites (see Table 2.4). Similar values of between pH 3.7 - 4.7 have been reported by Ross and Tate (1993) in South Island Nothofagus spp. forests.

**Figure 2.4:** The basal area in each site- preharvest and postharvest.

**Table 2.4:** The mean acidity (pH) of leaf litter in nine sites - preharvest and postharvest.

<table>
<thead>
<tr>
<th></th>
<th>C1</th>
<th>C2</th>
<th>C3</th>
<th>H1</th>
<th>H2</th>
<th>H3</th>
<th>W1</th>
<th>W2</th>
<th>W3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preharvest</td>
<td>4.29</td>
<td>4.55</td>
<td>4.52</td>
<td>4.31</td>
<td>4.33</td>
<td>4.43</td>
<td>4.56</td>
<td>4.24</td>
<td>4.37</td>
</tr>
<tr>
<td>Postharvest</td>
<td>4.32</td>
<td>4.30</td>
<td>4.74</td>
<td>4.51</td>
<td>4.30</td>
<td>4.51</td>
<td>4.39</td>
<td>4.05</td>
<td>4.66</td>
</tr>
</tbody>
</table>
Summary
The study was conducted over a period of two years with the first year being a baseline (preharvest) study and the second, an experimental (postharvest) study. The three treatments consisted of proposed control, harvest and artificial windthrow sites in the preharvest study and control, harvested and artificial windthrow in the postharvest study. An assessment of the floristic composition indicated relatively low levels of species richness compared with New Zealand podocarp forests (Ogden et al., 1996; Poole, 1987). However, the botanical diversity was similar between the sites at baseline and was dominated by *N. fusca* and *N. menziesii* (Table 2.3). An estimate of basal area following harvest and artificial windthrow enabled quantification of the disturbance in those sites. The average basal area of proposed control, proposed harvest and proposed windthrow sites varied slightly between the sites but the canopy openings were considered to be comparable (see Chapter 3). The results from the litter pH study indicated that the sites were similar at baseline and between the treatments in the postharvest study.
Chapter 3

Abiotic and biotic changes following selective harvest and artificial windthrow.

3.1 Introduction

Studying the interactions between abiotic and biotic factors can be important when addressing issues related to ecosystem function and preservation. Abiotic factors can influence invertebrate populations in disturbed forests and this can impact on ecosystem functioning (Didham et al., 1996). Many studies report considerable changes in the abundance and distribution of forest insects at stand edges adjacent to clear-cut forest (Huhta, 1976; Klein, 1989; Peltonen et al., 1997; Watt et al., 1997). This is often attributed to changes in temperature and light conditions which occur adjacent to harvested forest (Likens et al., 1978; Kapos, 1989; Matlack, 1993). The complexity of ecosystem processes often makes it difficult to determine which factors provoke environmental responses. In many situations, the problem of "hidden treatments" arises, where the observed ecosystem response is due to an unrecognised cause (Huston, 1997). Rigorous experimentation is required to produce results that pinpoint the causal factors that contribute to ecosystem dysfunction and biodiversity loss.

In this study, the establishment of harvested and windthrow sites has resulted in abiotic changes which may have an impact on the invertebrate fauna. The factors most likely to influence invertebrates are; the quantity of light reaching the forest floor, the quantity of litter fall, and leaf litter temperature and moisture (water content). Litter temperature and moisture influence decomposer activity and therefore rates of organic matter decomposition (Swift et al., 1979; Tian et al., 1993). The quantitative impacts of selective harvest on these factors have never been investigated in beech forest. However, it is essential that environmental changes resulting from tree harvest and natural disturbances are quantified so that forest managers can adjust management practices to mimic natural disturbance patterns.
Light Intensity

It is well known that beech seedling recruitment and growth is dependent on light and moist growing conditions which are provided by windthrow disturbance (Ogden et al., 1996). A study by Franklin (1976) indicated that red and silver beech seedlings had better growth and survival rates if they were situated under an open canopy as opposed to a closed canopy. Disturbances such as windthrow, that result in opening the canopy, are considered to be necessary for seedling recruitment and therefore essential for forest renewal. Excessively high levels of light however, can increase temperature and decrease moisture on the forest floor, potentially resulting in the desiccation of some invertebrates or in changes to their vertical distribution in the litter layers (Klein, 1989; Tian et al., 1997).

In this study the amount of light was measured in each of the sites. This was initially done to verify comparability between sites at baseline and repeated later to compare the amount of light entering the canopy openings in harvested and artificial windthrow sites.

Litter fall

The quantity of litter fall in a forest has important implications for energy flow, primary production and nutrient cycling (Lisanework and Michelsen, 1994). In addition, the leaf litter provides a sheltered and relatively stable habitat for invertebrates to pupate and over-winter (Alley et al., 1998). Several studies have investigated the timing of beech forest litter fall. Sweetapple and Fraser (1992) report that in a mixed red and silver beech forest, peaks in litter fall were during late spring and late summer and that annual litter fall was c. 4927 kg ha⁻¹ yr⁻¹. Burrows and Allen (1991) also reported peaks in silver beech litter fall during late summer, but indicate that the timing of peak litter fall can vary between years. Following peaks in litter fall, particularly those with high seed content, increases in lepidopteran larvae and other invertebrates have been reported (Moeed and Meads, 1986; Dugdale, 1996; Fitzgerald et al., 1996, Alley et al., 1999). The implication from these studies is that litter-dwelling invertebrates may be influenced by potential changes in litter fall that can result from selective harvest.
Temperature and Moisture

Temperature and moisture are in most cases considered together as they are inextricably linked in their effect on invertebrate phenology and growth (Wigglesworth, 1965). The growth rate of invertebrates has been shown to be related to temperature (Gilbert, 1988) and it is considered one of the main limiting factors for invertebrate survival globally (Brown and Gange, 1990). The effective temperature range (range of temperatures over which normal functions take place) for invertebrates can vary between invertebrate families (McColl, 1975) and invertebrate preferences for specific temperature and moisture regimes have been clearly demonstrated (Erlich et al., 1980; Gilbert and Raworth, 1996). While, high temperatures combined with low moisture can result in desiccation of some litter-dwelling invertebrates, others are detrimentally affected by excessive soil moisture. Studies by Christiansen (1964) and Ashraf (1971) indicated that the activity of litter-dwelling invertebrates is optimised at temperatures of 10-18°C and relative humidity of >85%. Changes in temperature and soil moisture as a consequence of tree harvest have been reported to change soil invertebrate abundance (Seastedt and Crossley, 1981; Kenagy and Stevenson, 1982; Klein, 1989). Some studies suggest that harvested areas can influence the microclimate creating greater extremes in temperature e.g. creating frost pockets in the winter and reductions of moisture in the summer (Kimmins, 1997; Benecke, pers.comm.).

The temperature and relative humidity on the litter surface of a Nothofagus truncata (Col.) Ckn. forest in Kaitoke, North Island, New Zealand was investigated by McColl (1975). Her results indicated that Collembola were adversely affected by high rainfall but were not inhibited by temperatures of <5°C. She also found that Diptera larvae abundance peaked when temperatures were <5°C while the occurrence of Lepidoptera larvae was highest when temperatures were between 10 °C and 15 °C, although, her findings were confounded by seasonal effects.

Extreme changes in moisture levels within leaf litter have also been shown to influence the survival (Regniere et al., 1981) and the vertical distribution of some invertebrates within litter layers (McBrayer et al., 1997). Hartman and Hynes (1977) found that the larvae of some Diptera families such as Tipulidae for example, require very moist conditions to survive.

In the research described in this chapter, dataloggers were placed in each of the sites, before
and following harvest, to determine whether selective harvest or artificial windthrow resulted in changes to the litter temperatures compared to unharvested forest. The moisture of the leaf litter was assessed at two-monthly intervals by calculating the apparent mass loss from litter samples.
3.2 Methods

Light Intensity
The percentage of foliage cover was measured in all study sites before harvest and to verify comparability between selective harvest and artificial windthrow sites following harvest. The amount of relative foliage cover in each site was assessed using a Licor photometer (LAI-2000, Li-cor Inc, USA.). The photometer was used to assess light interception by the vegetative canopy. Four readings per site were made from randomly chosen positions and one per site was made outside of the forest canopy at least 20 m from the forest edge. The positions were marked to enable postharvest readings to be taken from the same positions. The mean percent radiation interception (Table 3.1) was calculated for each site using the following formula:

\[
\text{Percent radiation interception} = (1 - \text{diffusion}) \times 100.
\]

(\text{where diffusion = the fraction of sky visible to the sensor})

Litter fall
Three litter-funnels were randomly placed in each of the nine 20 x 20 m sites. This number of funnels allowed for variation in litter fall between funnels and was considered to give sufficient statistical power for data analysis. These consisted of a metal cone with a diameter of 0.8 m at the widest point, suspended by three wooden stakes. A plastic tube with a mesh base was attached to the base of the funnel to collect the leaves. The funnels were removed during the harvesting operation and replaced in the same positions. The funnels were emptied at two month intervals. The litter was then dried at 70°C for 72 hrs to obtain a dry weight measurement. The mean dry weight of leaf litter (kg ha\(^{-1}\) day\(^{-1}\)) was then compared between the treatments using a repeated measures ANOVA.
Temperature

Leaf litter temperature was measured at all nine sites for the duration of the field-work (February, 1997 - February, 1999). One data logger was placed in each of the sites with the temperature probe buried 2-3 cm below the surface of the leaf litter (Plate 3.2). The probes were left in the same position to reduce variation between recordings. ‘Tinytag’ data loggers (Gemini Data Loggers (U.K.) Ltd.) are capable of recording temperatures between -40°C and
+125°C and took readings at one hour intervals. After c.60 days the loggers were downloaded using the software package Orion tiny logger manager (OTLM) on a laptop computer. The recordings were summarised to produce mean temperatures from a two-week period (bimonthly), as were the maximum and minimum temperatures recorded at the same time period.

Plate 3.2: A datalogger used to monitor leaf litter temperature.

Water Content

The water content in the leaf litter was determined using the gravimetric method (McLaren and Cameron, 1990). This involved collecting by hand ten 100g (wet weight) samples of leaf litter from each site (these samples were also used for the study described in Chapter 4) in preweighed muslin bags. The leaf litter was then oven dried at 70°C for 72 hrs and reweighed to obtain a dry weight measurement. The mean water content of the leaf litter was then compared between the treatments using ANOVA.
3.3 Results

Light

The light intercepted by the canopy in the preharvest study was similar in all nine sites at baseline, ranging between 91% and 96% radiation interception. The amount of light intercepted by the canopy declined following harvest and artificial windthrow, however, the two treatments were comparable. Harvested sites had radiation interception ranging between 72% - 88% and artificial windthrow ranged between 79% - 88%. See Appendix 3.1 for photos of the canopy openings.

<table>
<thead>
<tr>
<th>Preharvest Sites</th>
<th>Diffusion</th>
<th>% Radiation Interception</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>0.065</td>
<td>94</td>
</tr>
<tr>
<td>C2</td>
<td>0.043</td>
<td>96</td>
</tr>
<tr>
<td>C3</td>
<td>0.052</td>
<td>95</td>
</tr>
<tr>
<td>H1</td>
<td>0.070</td>
<td>93</td>
</tr>
<tr>
<td>H2</td>
<td>0.086</td>
<td>91</td>
</tr>
<tr>
<td>H3</td>
<td>0.056</td>
<td>94</td>
</tr>
<tr>
<td>W1</td>
<td>0.089</td>
<td>91</td>
</tr>
<tr>
<td>W2</td>
<td>0.069</td>
<td>93</td>
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<tr>
<td>W3</td>
<td>0.059</td>
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<tr>
<th>Postharvest sites</th>
<th>Diffusion</th>
<th>% Radiation Interception</th>
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<tbody>
<tr>
<td>C1</td>
<td>0.053</td>
<td>95</td>
</tr>
<tr>
<td>C2</td>
<td>0.050</td>
<td>95</td>
</tr>
<tr>
<td>C3</td>
<td>0.038</td>
<td>96</td>
</tr>
<tr>
<td>H1</td>
<td>0.220</td>
<td>78</td>
</tr>
<tr>
<td>H2</td>
<td>0.282</td>
<td>72</td>
</tr>
<tr>
<td>H3</td>
<td>0.118</td>
<td>88</td>
</tr>
<tr>
<td>W1</td>
<td>0.211</td>
<td>79</td>
</tr>
<tr>
<td>W2</td>
<td>0.182</td>
<td>82</td>
</tr>
<tr>
<td>W3</td>
<td>0.124</td>
<td>88</td>
</tr>
</tbody>
</table>
Litter fall
The mean total litter fall (derived from control sites) recorded in preharvest and postharvest years was 4649 kg ha\(^{-1}\) yr\(^{-1}\) and 5194 kg ha\(^{-1}\) yr\(^{-1}\) respectively. The amount of litter fall in each site during the preharvest and postharvest years is reported in Figure 3.1.

![Chart showing litter fall in control, harvested, and windthrow sites](image)

**Figure 3.1**: The mean litter fall recorded in control, harvested and windthrow sites during the preharvest and postharvest years (Arrow indicates the start of the postharvest year).

A repeated measures ANOVA indicated that there was no significant difference in the rate of litter fall between the treatments in either the preharvest or postharvest years \((P>0.05)\). However, there was a trend for less litter fall in the selective harvest and artificial windthrow sites during the postharvest year.

Temperature
The maximum, minimum and mean litter temperatures recorded in preharvest (baseline) and postharvest years are shown in Figures 3.2 - 3.5. Temperatures differed between years. In the preharvest year, they ranged from \(-3.5^\circ\)C to \(34.1^\circ\)C (Figure 3.2), whereas in the postharvest year, temperatures in the control sites were less extreme ranging between \(0.1^\circ\)C and \(31^\circ\)C (Figure 3.3).
Figure 3.2: Mean, minimum and maximum bimonthly leaf litter temperatures from all nine sites in the preharvest year (7 February, 1997 - 17 January, 1998).

Figure 3.3: Mean, minimum and maximum bimonthly leaf litter temperatures from the control sites in the postharvest year (13 February, 1998 - 15 February, 1999).
Figure 3.4: Mean, minimum and maximum bimonthly leaf litter temperatures from the harvested sites in the postharvest year (13 February, 1998 - 15 February, 1999).

Figure 3.5: Mean, minimum and maximum bimonthly leaf litter temperatures from the windthrow sites in the postharvest year (13 February, 1998 - 15 February, 1999).
Mean temperatures were similar in the treatments during the postharvest study (Figure 3.6). There was a small trend for higher temperatures in harvested sites particularly during the winter.

**Water content of leaf litter.**

The water content of leaf litter samples taken at two-monthly intervals in the preharvest and postharvest years are shown in Figures 3.7 and 3.8. Water content varied from 150% in a proposed control site (12 Jan, 98) to 419% in proposed harvest sites (7 Oct, 97). There was no significant difference ($P>0.05$) in the water content of leaf litter between the proposed treatments during the preharvest study. The water content of the leaf litter during the postharvest study varied between 15% in control sites (16 Feb, 1999) and 423% in control sites (16 Oct, 1998). There was no significant difference ($P>0.05$) in the water content of leaf litter between the three treatments during the postharvest year.
Figure 3.7: Mean water content of leaf litter samples at two monthly intervals: preharvest.

Figure 3.8: Mean water content of leaf litter samples at two monthly intervals: postharvest.
3.4 Discussion

Light
The amount of light in an area can differ depending on the slope and aspect or on factors such as the latitude, time of the year or atmospheric conditions (Kimmins, 1997). The results indicated that the nine study sites used in this research received similar levels of light during the preharvest year, which will reduce the chance of variation in light availability confounding the results in the preharvest study. The level of light following harvest and artificial windthrow was also comparable, which suggested that selective harvest resulted in similar-sized light wells to those in artificial windthrow sites. This is important from a management perspective since selective harvest is intended to mimic windthrow disturbance. As a product of increased light, enhanced seedling production would be expected in the harvested and artificial windthrow sites compared with unharvested control sites in the coming decade.

Litter fall
The results support those of Sweetapple and Fraser (1992) and Burrows and Allen (1991) which indicated that peaks in litter fall occurred during late spring and late summer. Similar overall rates of litter fall per hectare were also reported in this study to those reported by Sweetapple and Fraser (1992) from a red and silver beech forest. The data collected in this study will have important implications for understanding how invertebrate abundances (reported in Chapter 4) change in relation to selective harvest and artificial windthrow.

Temperature
Temperature is considered to be a major factor influencing insect activity, development and distribution (Wigglesworth, 1965). Invertebrate species differ in their ability to tolerate extreme temperatures and have thresholds beyond which development ceases or death ensues (Gilbert and Raworth, 1996). Earthworms, for example, can function only within a narrow range of temperatures (Curry, 1998). In this study, litter temperatures ranged from \(-3^\circ\text{C}\) in the winter months to approximately \(34^\circ\text{C}\) in summer months. The temperature varied only slightly between the years and between the study sites. Following harvest and artificial windthrow, minimal differences in temperatures were noted, with slightly higher temperatures during the winter months in selective harvest sites compared to artificial
windthrow and control sites. Higher temperatures during the winter months in harvested sites are likely to have a small impact on invertebrate activity but little or no effect on invertebrate development since a majority of invertebrates enter a period of 'quiescence' during winter months (Wigglesworth, 1965). Removal of the forest canopy can result in greater temperature extremes on the litter-surface of the forest floor (Seastedt and Crossley, 1981). However, this was not apparent from the results reported in this study and is likely to be a result of the low intensity of tree harvest conducted in this study. Several forest ecologists have indicated also that canopy closure is rapid in forest gaps of this size suggesting that any increases in temperature are likely to be short term (Stewart, pers.comm.; Allen, pers.comm.).

In conclusion, it is generally thought that the climatic conditions in New Zealand are not extreme enough to curtail invertebrate activity (Moeed and Meads, 1986). The effect of temperature fluctuations will be discussed further in Chapters Four and Five when seasonal abundances of detritivore families and decomposition rates are reported.

Water content

Moisture content of leaf litter has an influence on the numbers of invertebrates on the forest floor, and for most invertebrates, higher moisture levels result in higher invertebrate abundances (Crossley and Hogland, 1962). Contrary to suggestions in the literature (Seastedt and Crossley, 1981; Kenagy and Stevenson, 1982; Klein, 1989), the removal of canopy trees in this study did not result in dehydration of the leaf litter. There was no difference in the water content of leaf litter between the treatments over time. This is perhaps not surprising since there were minimal differences in temperatures reported. Extremely dry conditions were however recorded on 16 February, 1999 in all treatments which is coincident with low rainfall.

Summary

Forest processes such as the decomposition of litter are regulated by environmental variables such as climate, temperature and moisture (Meentemeyer, 1978). Attempts to evaluate the role of invertebrates in decomposition in the past have largely neglected to assess such environmental variables. Assuming a direct link between biodiversity and function may be
dangerous in the absence of environmental monitoring of abiotic factors (Didham et al. 1996). i.e., environmental variables can confound observed associations between biodiversity and ecosystem function. Quantifying the effects of both selective harvest and windthrow will help forest managers determine to what extent their harvesting practices mimic natural disturbances.

In this study, an attempt was made to quantify the level of light in the study sites and assess the temperature and moisture of the leaf litter. Although the results indicated there was more light entering the forest following harvest and artificial windthrow, there was little difference in either the temperature or water content of leaf litter between the three treatments. It is possible that the small size of the harvested and artificial windthrow sites (approximately 20 m x 30 m) reduced the likelihood of changes to litter temperature and moisture. The implications of abiotic changes are discussed further in Chapter Four where invertebrate abundances are compared with temperature and moisture levels.
Chapter 4

Responses of litter-dwelling invertebrates to selective harvest and artificial windthrow.

4.1 Introduction

It is evident that invertebrates are susceptible to adverse biotic and abiotic conditions created by clear-felling (Huhta, 1976; Seastedt and Crossley, 1981; Lenski, 1982; Chandler and Peck, 1992). Less severe harvesting techniques may have a negligible effect on forest invertebrates (Wolda, 1987) or may even result in an increase in diversity as resources change (Lenski, 1982; Schowalter, 1995; Spitzer et al., 1997). However, the effect of low-impact management techniques such as selective harvest on invertebrates have seldom been assessed thoroughly.

A lack of entomological research in New Zealand has meant that only c. 50% of invertebrates have been described and only a small proportion are understood ecologically (Kuschel, 1975). This has made it difficult to provide a full inventory of all species and made it difficult for forest managers to predict how invertebrates might respond to selective harvest or associated environmental changes. Sustainable use of forest resources requires information based on sound ecological studies which will enable forest managers to adopt low impact management techniques.

During the 1980’s Moeed and Meads (1986) studied the invertebrate fauna of a North Island beech forest. Their results present the seasonal abundances of invertebrates in beech forest and suggest that the invertebrate fauna is diverse but dominated by a few groups such as mites. They also found that almost all invertebrates had higher abundances in the spring (October-December) which is coincident with litter fall peaks reported by Sweetapple and Fraser (1992). Since then, investigations into the beetle (Klimaszewski and Kuschel, 1997) and lepidopteran fauna (Dugdale, 1996; Alley et al., 1999) have been completed which suggest that invertebrate diversity on the forest floor is high and that abundances are high during peak litter fall. Evans et al., (1996) compared the diversity of invertebrates in an age-series of West
Coast beech forests. Invertebrate orders were sampled from the sub-canopy and forest floor of harvested areas and adjacent unharvested forest. Harvested areas had been clear-felled 6 months, 15 years and 40 years (with and without postharvest management) earlier. The key conclusions from this study were:

- invertebrates responded differently to harvest depending on their functional guild.
- invertebrate diversity differed between harvested and unharvested forest in all sites except the 40 year old site which had been managed (pruned and thinned).
- that different sampling methods suggested different levels of diversity
- there was no clear relationship between invertebrate diversity and the age of the site
- the most diverse invertebrate fauna was on the forest floor.

Although this investigation was useful for studying invertebrate interactions between different forest habitats, it was limited by a lack of temporal replication and was also hampered by difficulties in comparing diversity derived from multiple sampling methods.

Current management of indigenous forests attempts to mimic natural disturbance patterns, using them as a template for sustainable forest management. However, there is a lack of detailed knowledge about the impact of natural disturbances on the forest ecosystem (Hunter, 1999). Disturbance, whether it is naturally occurring or not, results in environmental changes and changes in habitat heterogeneity. Invertebrates have an intricate relationship with their habitat and they respond in different ways to disturbance. The most probable environmental changes following windthrow or selective harvest include an increase in light intensity, a decline in the amount of litter fall as well as changes in temperature and moisture on the forest floor (Likens et al., 1978). All these factors are likely to impact on invertebrate communities but whether this leads to a loss of diversity is unknown. Some studies have reported an increase in invertebrate diversity following disturbance and this has been attributed to a reduction in competition for resources (Niemelä et al., 1988; Lenski, 1995; Wootton, 1998). Studies by Niemelä et al. (1988) and Lenski (1995) for example, reported an increase in carabid beetle diversity following tree harvest. Other studies report a loss of invertebrate diversity in response to clear-felling (Huhta, 1976; Schowalter et al., 1981; Klein, 1989; Hill et al., 1995; Watt et al., 1997). Huhta (1976) reports that oribatid mite abundance declined
after an initial increase, as did dipterous larvae. He also concluded that invertebrate groups responded differently to tree harvest and that this was partly explained by their degree of dependence on different litter resources. Watt et al., (1997) demonstrated that the abundances of some invertebrates in a southern Cameroon lowland forest declined following clear-felling. A decline in diversity can be associated with outbreaks of pest species which can be detrimental to regenerating trees and to remaining mature trees. This was partly demonstrated by Schowalter et al. (1981) who showed that regenerating trees were damaged by an increase in aphid and ant populations following the harvest of hardwood trees in the Coweeta watershed, USA. Similarly, an increase in wood-boring beetles such as Platypus spp., which damage live adjacent beech trees has been reported in New Zealand (Litchwark, 1978). The challenge for sustainable forest management is to define the ecological effects of natural disturbances and to design a harvesting regime that works within those limits. The underlying assumptions are that invertebrates (and other biota) are adapted to natural disturbances and that populations are perpetually in a state of ‘disequilibrium’ (Kimmins, 1987; Tritton and Johnson, 1998).

This chapter addresses the following questions:

• What are the relationships between seasonal abundances of litter-dwelling invertebrates and litter fall?
• How does disturbance (selective harvest and artificial windthrow) impact on the abundance/diversity of litter-dwelling invertebrates?
• Does the effect of selective harvest differ from the impact of wind throw disturbance?
• Is invertebrate community composition related to environmental gradients associated with selective harvest or artificial windthrow?

To address these questions, invertebrates from the detritivore guild were extracted from leaf litter samples and identified where possible to family level. Using families as a surrogate for species is not ideal but some research has indicated that there is often a good relationship between higher taxa and species richness (Gaston et al., 1995; Hodge and Frampton, 1999). Only functionally similar invertebrates were chosen for this study because they are likely to be affected by forest disturbance in similar ways. Studying functionally similar groups may also improve the understanding of the links between invertebrate abundance and the
maintenance of ecosystem processes (Walker, 1992). The detritivore guild was chosen because of its associations with the process of litter decomposition.

Species-abundance studies such as this are useful for monitoring invertebrate responses to forest disturbance whereas studies of diversity are more useful in classifying or comparing different sites in replicated studies (Basset, 1998).

4.2 Methods

A pilot study was conducted to ensure that samples were representative of the invertebrate fauna. This involved collecting 15 litter samples, each weighing 100 g from three forest sites on 7 February, 1997. Monte-Carlo analysis of invertebrate abundances involved resequencing the order in which samples were collected and generating faunal accumulation curves. This analysis indicated that ten samples provided approximately 80-85% representation of the total fauna (non-oribatid detritivores and oribatid mites) caught using this sampling method (see Appendix 4.1).

Ten 100 g litter samples were collected at approximately two month intervals from the nine forest sites which comprised three control sites, three harvested sites and three windthrow sites (see Chapter 2, Figure 2.3). Sampling took place at approximately two month intervals on: 6 April, 5 June, 8 August, 7 October, 5 December, 1997 and 12 Jan, 1998 during the preharvest year. (The last sampling interval in the preharvest study was shortened due to timing of harvest operations). In the postharvest year the same number of samples were collected on: 16 April, 16 June, 16 August, 16 October, 16 December, 1998 and 16 February, 1999. Once collected, each litter sample was placed in a cotton bag (30 x 20 cm) and stored in an ice-box. In the laboratory, the samples were either immediately placed into Tullgren funnels (Kempson et al., 1963) or were stored at 3°C for up to 6 days depending on funnel availability. (The samples chosen for immediate placement on the funnels were randomly selected). This procedure was necessary because of limited funnel availability.
Each sample remained on a funnel for 3 days, which according to a funnel efficiency test, was sufficient to extract c. 80% of all invertebrates from the leaf litter (see Appendix 4.2). Once invertebrates had been extracted, the remaining leaf litter from ten samples was hand searched for invertebrates which may have been too large to pass through the 6 mm sieve. On no occasion were large invertebrates found.

Plate 4.1. The Tullgren funnels used to extract invertebrates from leaf litter.

Extracted invertebrates were sorted into non-oribatid detritivores, oribatid mites and others. The non-oribatid detritivores were subsequently identified to family level and oribatid mites were identified to recognisable taxonomic units (RTUs). The use of RTUs is justified because of the diverse nature of the fauna and a lack of taxonomic expertise on this group in New Zealand (voucher specimens have been placed in the Lincoln University Entomological Museum). Oliver and Beattie (1996) report that the use of RTUs provides similar estimates of diversity to species. For the remainder of this thesis non-oribatid detritivores will be referred
to as ‘detritivores’ and oribatid mites are referred to as Oribatid A - U.

The invertebrates chosen to represent the detritivore guild were:

- Diplopoda (millipedes) - Polyzoniidae, Schedotrigonidae, Dalodesmidae, Habrodesmidae, Sphaerotheridae.
- Lepidoptera larvae (moths and butterflies) - Oecophoridae, Noctuidae, Tortricidae and Psychidae.
- Crustacea (Amphipoda) - Talitridae
- Diptera (Flies) - Tipulidae
- Coleoptera (weevils and beetles) - Curculionidae, Cerambycidae
- Oligocheata (earthworms) - Megascolecidae
- Isopoda (slaters) - Styloniscidae
- Acarina (mites) - Cryptostigmata (oribatid mites).

Few Sphaerotheridae (millipedes) or Noctuidae (lepidopetran larvae) were found and for that reason these families were excluded from the results. While it is acknowledged that Collembola and some beetle larvae are also involved with litter decomposition (Wardle and Lavelle, 1997; Emberson, pers.comm.), uncertainty regarding their identity and their preference for leaf material or soil microbes, resulted in their exclusion.

The results reported in this chapter describe both relative abundance and the diversity (species richness + evenness) of invertebrates. Invertebrate abundance data were also interpreted using Canonical Correspondence Analysis (CCA) to determine whether invertebrate composition changes in response to selective harvest and artificial windthrow.

The following keys were used to identify detritivores and oribatid mites:
- Millipedes: Johns (1962)
- Lepidoptera larvae: Dugdale (1996)
- Amphipoda: Duncan (1994)
- Tipulidae: Smith (1989)
- Curculionidae and Cerambycidae: Klimaszewski and Watt (1997)
- Earthworms: Lee (1959)
Statistical Analysis

The Shannon-Wiener diversity index was used as a measure of invertebrate diversity (Pielou, 1975; Magurran, 1986). This index was considered the most useful index of diversity since it considers the number of families (richness) as well as the evenness with which individuals are distributed among families (relative abundance) (Magurran, 1986).
The Shannon-Wiener diversity index was calculated using the function:

\[
H' = \sum_{i=1}^{s} (p_i)(\log p_i)
\]

where: \(H'\) = Index of family diversity  
\(s\) = Number of families/ RTU’s  
\(p_i\) = Proportion of total sample belonging to the \(i\) th family.

A repeated measures ANOVA was used to explore the effects of time and treatment on invertebrate diversity in the preharvest and postharvest years. (Although, in the preharvest years, all sites were the same (unharvested) it was important to test whether the proposed sites differed at this stage).

Ordination was used to describe how invertebrate abundances were arranged along environmental gradients. A direct gradient analysis technique - Canonical correspondence analysis (CCA) was completed using the statistical package - Canoco (ter Braak, 1998). This analysis involves multivariate regression between species and environmental data (ter Braak, 1986). The advantage of using CCA is that it does not depend on normally distributed species data and is not influenced by ‘noise’ in environmental variables (Palmer, 1993). Specifically, CCA was used in this study to explore the possibility that invertebrate community composition was influenced by variables such as litter fall, temperature and moisture. Invertebrates that are grouped together on the ordination axis are considered to occur together under similar environmental conditions. The direction of the arrows represents an increase in the strength of the relationship with environmental variables and provides an indication of the influence of the variable on the invertebrate distribution. Data from preharvest and postharvest years were combined for these analyses.
4.3 Results

The results from the Monte Carlo analysis and the Tullgren efficiency tests are reported in Appendix 4.1 and 4.2.

Invertebrate abundance

The total abundances (expressed as a proportion of total detritivores collected) of each detritivore family on six sampling dates during the preharvest years are reported in Figure 4.1. The purpose of this figure is to demonstrate how the detritivore community is constituted. The oribatid mites occupy more than 80% of the detrital fauna (for brevity, mite RTUs have been pooled in Figures 4.1 and 4.2). The next most abundant groups were Curculionidae, Oecophoridae, Megascolecidae and Styloniscidae. In this study, high abundances of Schedotrigonidae, Oecophoridae and Tortricidae coincided with the spring peak in litter fall whereas the abundance of Styloniscidae (slaters), Curculionidae (weevils) and Talitridae (amphipods) coincided with autumn peaks in litter fall. Figure 4.2 shows the proportion each family occupies in control, harvested and windthrow sites on similar dates during the preharvest and postharvest years. The purpose of this figure is to demonstrate that there are fluctuations in the proportions occupied by invertebrate families (e.g., Curculionidae, Tipulidae) between the preharvest and postharvest years.
Figure 4.1: The proportion of each family in the detritivore guild collected in all nine sites during the preharvest study.

Figure 4.2: The proportion of each family in the detritivore guild collected on 5 December, 1997 during the preharvest study and 16 December, 1998 during the postharvest study.
The proportions of each detritivore on each sampling date are shown in Appendix 4.3. Seasonal changes in the abundance of individual detritivores in beech forest leaf litter from the postharvest year are reported in Appendix 4.4. 
P-values derived from a repeated measures ANOVA showed that there was no significant difference in detritivore or oribatid mite abundances as a result of selective harvest or artificial windthrow (Appendix 4.5 (year * harvest)). However, there was a significant sampling date (season) effect on a majority of the detritivores and oribatid mites, indicating that abundances differed seasonally.

**Family richness**

The richness of detritivores and oribatid mite RTU's in preharvest and postharvest years are compared between the three treatments in Figures 4.3 - 4.6. Similar numbers of mite RTUs and detritivore families were found in both the preharvest and postharvest years. In the preharvest year the number of detritivore families and mite RTUs remained relatively constant between the treatments and between the sampling dates (Fig. 4.3 and 4.4). A similar trend was shown in the postharvest year, with little difference between the treatments and sampling dates except on 16 June, 98 when the number of mite RTUs in the harvested sites was considerably less than the other sites (Fig. 4.5 and 4.6).

**Figure 4.3:** Detritivore family richness in control, harvest and windthrow sites during the preharvest and postharvest year (Arrow indicates the start of the postharvest year).
Figure 4.4: Oribatid mite richness in control, harvest and windthrow sites during the preharvest and postharvest years (Arrow indicates the start of the postharvest year).

Invertebrate diversity

Total numbers of invertebrates found in the 10 litter samples taken from each site were used to calculate diversity. The diversity of detritivore families and oribatid mite RTU's in preharvest and postharvest years are shown in figures 4.7 - 4.10. Similar levels of diversity were reported in the preharvest and postharvest years. While there were significant differences in detritivore and oribatid mite abundances within preharvest and postharvest years ($P<0.05$), there was no significant difference in detritivore or oribatid mite diversity between the treatments in either the preharvest or postharvest years ($P>0.05$).
**Figure 4.5**: Detritivore diversity in the proposed control, proposed harvest and proposed windthrow sites during the preharvest year. \( I = \) standard error. Arrow indicates the start of the postharvest year.

**Figure 4.6**: Oribatid mite diversity in the proposed control, proposed harvest and proposed windthrow sites during the preharvest year. \( I = \) standard error. Arrow indicates the start of the postharvest year.
Invertebrate Community Composition

Canonical correspondence analysis indicated that detritivore and oribatid mite abundances from both preharvest and postharvest studies were influenced by; litter fall, temperature and moisture.

Figure 4.7: Biplot showing how invertebrate families were influenced by temperature, moisture and litter fall in the preharvest and postharvest years combined.

Figure 4.7 represents all invertebrates from the preharvest and postharvest leaf litter study and shows how the invertebrate community might be distributed in relation to the variables tested irrespective of season or year. Mites B, I, K, L, and T are more abundant at higher temperatures (and therefore low moisture), as are millipedes, Schedotrigonidae and Habrodesmidae. In contrast, Tipulidae (diptera larvae), Megascolecidae (earthworms), Taltridae (landhoppers), and oribatid mites G are more abundant where moisture is high (and therefore temperature is low).
Figure 4.8: Biplot showing how invertebrates in the preharvest study sites (No. 1-9) and postharvest study sites (No. 10-18) are influenced by temperature, moisture and litter fall two months after selective harvest and artificial windthrow.

Figure 4.8 shows a biplot of the relative positions of the nine sites in equivalent seasons preharvest (No. 1-9) and postharvest (No. 10-18) during April. Yearly changes in invertebrate composition are indicated by this biplot, i.e., sites 1-9 were aggregated and sites 10-18 were all dispersed. In general sites 10-18 (postharvest data) shifted to the right along the temperature and moisture gradients. This suggests that invertebrates collected during April in the postharvest year were found in sites with higher temperatures and with more moisture than the previous year. If this was a response due to selective harvest and artificial windthrow, it would be expected that the control sites (10-12) would move differently to the other sites (13-18). Although the invertebrates in sites 11 and 12 appeared to be responding to litter fall gradients rather than to temperature and moisture, site 10 follows the movement of sites 13-18, suggesting that the trends shown are due to differences in the variables between the years. In summary, there was no consistent change in invertebrate composition as a consequence of
the treatments two months after harvesting. Figure 4.9 shows changes in site placement 12 months following selective harvest and artificial windthrow. It appears that there is a more pronounced treatment effect in the postharvest year where harvested and windthrow sites appear to be characterised by low litter fall (13-18) and control sites appear to be characterised by higher moisture (10-12).

![Biplot showing how invertebrates in the preharvest study sites (No. 1-9) and postharvest study sites (No. 10-18) are influenced by temperature, moisture and litter fall 12 months after selective harvest and artificial windthrow.](image)

**Figure 4.9:** Biplot showing how invertebrates in the preharvest study sites (No. 1-9) and postharvest study sites (No. 10-18) are influenced by temperature, moisture and litter fall 12 months after selective harvest and artificial windthrow.
4.4 Discussion

This study has shown that the effects of selective harvest on the abundance, diversity and community composition of litter dwelling invertebrates has been negligible. Instead it appears that macroclimatic variations unrelated to the treatments may be influencing the abundance and diversity of litter-dwelling invertebrates. These results have important implications for forest processes such as litter decomposition and for forest management.

Invertebrate abundance.

A high proportion of invertebrates extracted from leaf litter samples were oribatid mites. Mites also dominated the samples collected from beech forest in the Orongorongo valley by Moeed and Meads (1986,1987). These authors estimated that >75% of all invertebrates extracted from leaf litter were mites and that abundances were highest during the spring. There were other similarities between the results here and the results reported by Moeed and Meads (1987) and Klimaszewski and Kuschel (1996), suggesting that the composition of litter-dwelling invertebrates is broadly similar between different beech forests and that most invertebrates are in highest abundance during the spring and summer. In this study, high lepidopteran larval abundance coincided with the spring peak in litter fall whereas other high detritivore abundances coincided with autumn peaks in litter fall. This supports the findings of Dugdale (1996) and Fitzgerald et al., (1996) who also found peaks in the numbers of lepidopteran larvae in response to periods of high litter fall. The results also support those of Moeed and Meads (1986) who found Talitridae and Styloniscidae abundant in the autumn. Although in this study, temperatures were higher in selective harvest sites than control sites particularly during the winter months, there was no evidence that invertebrate densities were affected by this. Overall temperatures during the preharvest and postharvest years did not exceed those recorded in artificial windthrow sites. There was a definite seasonal effect in invertebrate abundances during the preharvest and postharvest years in this study but there were no significant changes in abundances between the treatments i.e., the nine sites contained similar invertebrate abundances prior to harvest and neither harvesting or windthrow had a significant impact on these abundances (Appendix 4.5).
**Invertebrate diversity**

Selective harvest and artificial windthrow did not result in coarse changes to detritivore or oribatid mite family richness. The richness and diversity of oribatid mites was higher than the diversity of other detritivores, demonstrating their dominance in litter fauna. Similar numbers of oribatid mite RTUs were present on all sampling dates indicating that there was a low turnover in the RTUs studied i.e., similar combinations of RTUs were present throughout the study. Despite large fluctuations in environmental conditions due to seasonal differences, the richness and the diversity of the oribatid mites and the detritivores remained similar throughout the preharvest and postharvest year.

**Invertebrate community composition**

A canonical correspondence analysis was undertaken to explore the effects of factors such as litter fall, temperature, and litter moisture on the composition of litter-dwelling invertebrates, and the extent to which the selective harvest or artificial windthrow affected invertebrate composition. Results from samples collected two months following harvest differed slightly to those collected 12 months following harvest, suggesting that there may not be an immediate effect on invertebrates resulting from disturbance. Some invertebrates in the control sites were influenced by litter fall, temperature and moisture in the postharvest year, suggesting that the timing of the seasons may have been different between the years. The CCA also indicated that invertebrates were responding to changes in litter fall even though litter fall was found not to be significantly different (Chapter 3). Invertebrate composition (how invertebrate abundances were arranged along the variable gradient) in each of the treatments did not change consistently in the postharvest year suggesting that harvest and windthrow were not as important as seasonal effects in determining invertebrate composition. Both the results in figures 4.12 and 4.13 are however unusual in that moisture and temperature appear to be correlated. This is possibly due to declining temperatures during April and due to an increase in temperatures in December coinciding with high rainfall.
Concluding remarks

Determining the effect of disturbances, whether they are natural or induced by humans, on forest biota is critical to understanding how biodiversity is maintained in forest ecosystems (Connell, 1978; Sousa, 1984). Disturbance typically occurs on a range of temporal and geographical scales and varies in intensity, creating a range of environmental changes (Likens et al., 1978). How these changes impact on invertebrate communities is not well understood. Current ecological theories suggest that rare species, which may appear functionally redundant, maintain ecosystem processes during extreme environmental conditions (Lawton and Brown, 1993). There is some evidence from the results reported in this chapter, to support the theory that particular invertebrate groups are favoured by some environmental variables. Results from this study also indicated that selective harvest and artificial windthrow had little effect on invertebrate abundances. However, CCA analyses suggested there were subtle changes in invertebrate abundances in response to environmental variables but that the changes in abundance were generally consistent between the treatments. The indication that invertebrate abundances changed between seasons (between sampling dates) in both years suggests that invertebrates are responding to seasonal/temporal cues to a greater extent than they do to small changes in resources or environment. Therefore, the changes created by selective harvest may not be extreme enough to supersede seasonal changes in abundance. One explanation for this could be the small size of the harvested areas. Typically, natural windthrows vary in size from 2 or 3 trees up to areas 2 ha in size (Stewart et al., 1991). Selective harvest is intended to mimic small windthrows, which may have little or no effect on invertebrate populations. Certainly there were no apparent increases or decreases in diversity following harvest as were reported in previous studies following clear-felling (Huhta, 1976; Seastedt and Crossley, 1981; Lenski, 1982; Chandler and Peck, 1992). The results from this study indicated that the invertebrate fauna in windthrow sites is no different from that in selectively harvested or control areas. It is unlikely that windthrow would result in coarse changes to the invertebrate community, given that disturbance is a part of beech forest ecology and produces similar small scale variations in environmental factors (Chapter 3) that are considered to be ‘normal’ fluctuations. Therefore, providing the impacts of selective harvest are within the environmental limits imposed by windthrow, it is unlikely that there will be coarse changes in the densities of litter-dwelling invertebrates.
Although invertebrate abundances differed between sampling dates, diversity remained relatively constant. i.e., the number of families present were similar but the evenness with which individuals were distributed among them changed. It has been suggested that there may be ecological mechanisms or 'feed-back mechanisms' acting on diversity to keep it at a constant level (Wardle and Lavelle, 1997). For example, the diversity of litter material entering the organic matter or interactions between tree roots and the soil interface may influence the diversity of litter-dwelling invertebrates. It is also likely that inter-trophic interactions such as predation help to maintain a constant level of diversity but this will be discussed in more detail in Chapters 5 and 6.

The results from this study support the findings from previous research which indicates that some of the litter-dwelling invertebrates studied do have preferences for specific temperature and moisture regimes (Seastedt and Crossley, 1981; Gilbert and Raworth, 1996) while other invertebrate abundances tend to be correlated with litter fall (Dugdale, 1996; Fitzgerald et al., 1996; Alley et al., 1999).
Chapter 5

The effect of selective harvest and artificial windthrow on litter-dwelling invertebrates and litter decomposition.

5.1 Introduction

This study investigates the links between invertebrate diversity and the process of decomposition in harvested and artificial windthrow sites. Invertebrates regulate the breakdown of organic matter by their feeding action (Visser, 1985), but the interactions between invertebrates and decomposition are poorly understood. Decomposition depends on a combination of factors including litter quality (chemical properties), climate and the activity of soil fauna acting at different spatial and temporal scales (Wardle and Lavelle, 1997). When litter fauna are removed from decomposer food webs, a decline in soil microbial activity often occurs (Setälä et al., 1988). Changes in microbial activity have important implications for nutrient turnover and primary production (Anderson, 1988) as well as the long-term storage of carbon in terrestrial ecosystems (Heal et al., 1997). Loss of invertebrate diversity may therefore have important implications for processes such as decomposition as well as ecosystem-level properties which are dependent upon the decomposer subsystem (Wardle and Giller, 1996).

Theories relating to the functional significance of litter-dwelling invertebrates.

Ecologists are divided over whether below-ground ecosystems follow a classical “Linnean” pattern (where every species plays a unique and essential role) (Linnaeus, 1760) or whether a number of substitutable species and a few ‘keystone’ species (whose removal is detrimental to other species) maintain ecosystem processes (May, 1973). Springett (1976) compared invertebrate diversity and litter decomposition in an age series of Pinus pinaster (Ait.) plantations. Her results suggested an asymptotic relationship between the rate of decomposition and invertebrate diversity where the decomposition rate reached a plateau at a particular level of diversity. Springett (1976) suggests that there may be a
minimum number of species required for ecosystem function and that additional species may act as a type of ecosystem 'insurance' against disturbance (Hobbs, 1992). Lawton and Brown (1993) suggested that there is a degree of redundancy in ecosystems whereby loss of some invertebrate species does not affect decomposition. If this is the case, it is important to understand how many and which species are necessary for ecosystem function and what degree of disturbance an ecosystem can sustain. Andren et al., (1995) investigated the relationships between soil fauna and barley straw decomposition. Their results demonstrated that decomposition was unaffected by the diversity and composition of soil fauna and that decomposition was instead correlated with external temperature and moisture conditions. They suggested that there was a high degree of redundancy in the soil fauna and that the biota involved with barley straw decomposition responded to changes in temperature and moisture in similar ways. Bengtsson et al. (1997) studied the effects of tree harvest residues (unmerchantable timber, branches and leaves) on invertebrates and found that the stability of higher taxa and functional groups were not affected by removal of residues, but concluded that removal of residues may result in long-term (15-18yrs) decreases in the abundances of invertebrates. Their study followed indications from an earlier publication (Bengtsson, 1994) which reported that the temporal variability of soil communities in forests was low in the absence of substantial environmental impacts such as those resulting from clear-felling. It is generally thought that changes in invertebrate community structure and loss of specific groups of decomposer organisms result in reduced rates of decomposition (Hobbs, 1992). The question is - what level of disturbance results in species loss and at what point does species loss result in ecosystem breakdown? It is in the context of these theories and investigations that this study analyses the links between invertebrate diversity and decomposition rates.

**Impacts of tree harvest on decomposition.**

The direct impact of tree harvest on decomposition was investigated by Black and Harden (1995). They demonstrated that tree harvest resulted in a reduction in carbon storage and changes to carbon:nitrogen ratio as vegetation regenerated. They also suggested that decomposition is likely to vary depending on the harvest method and post harvest management. Villela et al., (1998) studied the impact of selective tree harvest in a Brazil rainforest on litter decomposition and found no differences in decomposition rates between
selectively harvested and unharvested forest. Goh and Phillips (1991) compared forest floor biomass and nutrient turnover in clear-felled and unharvested beech forest and found that clear-felled areas were detrimentally affected by tree harvest. However, the impacts of selective beech harvest on decomposition have not been investigated.

In this chapter, litter-bags were used to explore the effects of different invertebrate diversities on decomposition. Litter-bags are commonly used to quantify litter decomposition rates and to analyse carbon and nitrogen ratios (Bocock and Gilbert, 1957). Although this method is considered to underestimate actual decomposition (because it excludes some invertebrate fauna), it is assumed that the results reflect general decomposition trends of unconfined leaf litter and can therefore be frequently used to compare decomposition rates between sites (Wieder and Lang, 1982). The carbon:nitrogen ratio is frequently used as an index of litter quality and is considered to be an important regulator of decomposition rates (Heal et al., 1997). As litter decomposes, carbon declines and nitrogen increases resulting in a decline in the carbon:nitrogen ratio. Carbon is utilized by soil organisms as an energy source (Blair et al., 1997) and nitrogen is liberated by mineralisation making it available for plant uptake (Fenton, 1958; Anderson et al., 1985). Several investigations indicate that role of invertebrates appears to be greater when the carbon:nitrogen ratio is high (i.e., at the early stages of decomposition) and when the substrate quality is low (Parnas, 1975; Aber and Melillo, 1979; Bosatta and Staaf, 1982). Data collected from litter-bags in this study were also used to determine the rate of invertebrate succession in decomposing leaves. Succession is a predictable and orderly process of community development that results from habitat modification and occurs at a range of temporal scales (Odum, 1969). As decomposition advances, the physical and chemical properties of leaf particles change and can result in changes to invertebrate community composition. The invertebrate fauna inhabiting litter-bags was assessed at varying stages of decomposition to determine whether there was a predictable pattern to litter colonisation and if so, whether this pattern was affected by selective harvest or artificial windthrow.
The main objectives of this study were to:

- determine whether changes in invertebrate diversity had a consequential effect on the process of litter decomposition. An understanding of the functional significance of invertebrate diversity may help to determine what levels of disturbance an ecosystem can sustain before important processes are affected.

- identify which ecological variables are responsible for controlling rates of decomposition, so that forest managers can adjust harvesting methods to minimise them.

The development of an indicator-based monitoring scheme, based on an ecological understanding of the forest ecosystem, could be used to predict whether current harvesting regimes are within the level of natural disturbance patterns such as windthrow i.e., as a measure of sustainable forest management.

5.2 Methods

Litter-bags containing a known quantity of leaf litter were placed in control, selective harvest and artificial windthrow sites. Subsets of the bags were retrieved at two-month intervals for one year prior to harvest and for one year following harvest to monitor invertebrate colonisation in the bags and to assess weight loss and carbon:nitrogen ratios of the remaining leaf litter.

A total of 30 plastic litter-bags (30 cm x 15 cm) each containing 25 g (dry weight) of insect free leaf litter were randomly placed in each of the nine sites on 7 February, 1997 (preharrow study) and on 16 February, 1998 (postharvest study). Fresh leaf litter collected on 3 February, 1997 was used in all litter-bags to minimise differences in litter quality between the pre and postharvest studies. A large mesh size (5 mm) was chosen so that only large invertebrates were excluded from entering the bags but that leaves were retained in the bags. The bags were pinned to the forest floor using a bicycle spoke to ensure that a good interface
with lower soil horizons was established. At two-month intervals, five of the bags were retrieved from each site.

Plate 5.1. One of the litter-bags used in this study.

On each sampling occasion, invertebrates were extracted from the leaf litter for 3 days (see Chapter 4, Plate 4.1) using Tullgren funnels (Kempson et al., 1963). These comprised a 60 watt light bulb placed over a mesh sieve (6 mm) containing leaf litter above a collection tube. Invertebrates were stored in 70% ethanol and the leaf litter from each litter-bag was dried at 70°C for 3 days to obtain dry weight measurements. The leaf litter was then ground to a fine powder using a Cyclotec grinder and the carbon and nitrogen content was assessed using an elemental analyser carbon:nitrogen:sulphur analyser - 2000 (LECO Corporation, Michigan, USA). Detritivores were separated from other litter-dwelling invertebrates and identified to family level or RTU as described Chapter 4.
Statistical Methods
The abundance data for comparisons between sampling dates were adjusted to a weight constant (25g) since over time the amount of leaf litter in litter-bags declined. A repeated measures ANOVA was used to explore the effect of treatments and sampling date on invertebrate abundances.

A canonical correspondence analysis (CCA) was conducted using the statistical package Canoco (ter Braak, 1998) to determine whether invertebrate composition changed over time as a consequence of selective harvest and artificial windthrow.

Analysis of variance was used to compare the coefficients of variation calculated for each of the treatments to determine if the amount of temporal variation in invertebrate abundances during the postharvest year differed between control, selective harvest and artificial windthrow sites.

The Shannon-Wiener Diversity Index Function (Pielou, 1974; Magurran, 1986) was used to calculate diversity. Total numbers of invertebrates found in litter-bags at each site were used in diversity calculations.

\[
H' = \sum_{i=1}^{s} (p_i)(\log p_i)
\]

\(H'\) = Index of family diversity
\(s\) = Number of families
\(p_i\) = Proportion of total sample belonging to the \(i\)th family.

The evenness of individuals between the detritivore families and oribatid mite RTU’s was calculated using the following equation:
E = Diversity (Shannon-Wiener) 
\[ \frac{\text{Log} (s)}{\text{Log} (s)} \]

where: \( E = \) evenness
\( s = \) the number of families

A repeated measures ANOVA was also used to compare diversity indices between the treatments during preharvest and postharvest years.

Decomposition rates and changes in the carbon:nitrogen ratio were estimated from the slopes of a linear-log regression of weight remaining in litter-bags and carbon:nitrogen ratio against time. These rates were then compared between control, selective harvest and artificial windthrow sites using ANOVA.
5.3 Results

**Abundance of invertebrate families**

A repeated measures ANOVA compared the changes in abundances between the treatments and between the preharvest and postharvest years (Appendix 5.1). The analysis indicated that there was no significant difference ($P>0.05$) in any detritivore family abundances or oribatid mite abundances between the treatments in either the preharvest or the postharvest years ($A \times \text{Tmt}$). There was a significant seasonal (within year) effect ($B$ - Appendix 5.1) on the abundance of most oribatid mites ($P<0.05$). However, only the detritivores Schedotrigonidae (millipedes), Dalodesmidae (millipedes), Oecophoridae (lepidopteran larvae), Curculionidae (weevils) and Styloniscidae (slaters) were significantly affected by season ($P<0.05$).

The CCA results suggest that Oecophoridae (lepidopteran larvae) and oribatid mites B, G, H and K are most abundant when the litter decomposition is more advanced (i.e., at the time at which litter weight and carbon:nitrogen ratio are low). Whereas, Polyzoniidae (millipedes) occurred at early stages of decomposition consistently in the preharvest and postharvest years (Figures 5.1 and 5.2). To verify that this trend was consistent across all sites, the sites and environmental variables were plotted (Figures 5.3 and 5.4). No.s 1-9 were aggregated on the ordination axes, indicating that invertebrates in the litter-bags collected after two months of decomposition occurred when the carbon:nitrogen ratio and litter-bag weight were high. This trend was consistent in the preharvest and postharvest data.
Figure 5.1: Canonical Correspondence Analysis ordination of the detritivore families in each of the nine sites in relation to environmental variables following two months' and 12 months' decomposition in the preharvest year.
Figure 5.2: Canonical Correspondence Analysis ordination of the detritivore families in each of the nine sites in relation to environmental variables following two months' and 12 months' decomposition in the postharvest year.
Figure 5.3: Canonical Correspondence Analysis ordination of the nine sites in relation to environmental variables following two months (Nos. 1-9) and 12 months (Nos. 10-18) decomposition in the preharvest year.
Examination of the coefficients of variation in the preharvest and postharvest years indicated that selective harvest and artificial windthrow had no consistent effect ($P > 0.05$) on the temporal variability of either detritivore or oribatid mite abundance (Appendix 5.2).

**Family richness**

The detritivore family richness data indicated little difference in the number of detritivore families between the treatments and a trend for fewer detritivore families present during the winter months (June/August) and on 16 February 1999 (Figure 5.5). The richness of oribatid mite RTU’s remained relatively constant over time (Figure 5.6). There were no consistent differences in the number of RTU’s between the treatments over the sampling dates in either the preharvest or postharvest years.
Figure 5.5: The richness of detritivore families in litter-bags collected at two monthly intervals from control, harvested and artificial windthrow sites (Arrow indicates end of preharvest year).

Figure 5.6: The richness of oribatid mites in litter-bags collected at two monthly intervals from control, harvested and artificial windthrow sites. (Arrow indicates end of preharvest year).
Evenness of invertebrate families

The evenness with which individuals were distributed among the families and RTUs is shown in Figures 5.7 and 5.8. The results indicated that detritivores were less evenly distributed in windthrow sites during June in both preharvest and postharvest years and in all sites on 16 February, 1999. The evenness of oribatid mites showed a trend to be lower in proposed harvested sites but during the postharvest year this trend was not as apparent, except on 16 February, 1999, when evenness was lower in harvested sites.

Figure 5.7: The evenness of detritivore distributions in control, harvested and windthrow sites in preharvest and postharvest years. (Arrow indicates end of preharvest year).
Figure 5.8: The evenness of oribatid mite distributions in control, harvested and windthrow sites in preharvest and postharvest years. (Arrow indicates end of preharvest year).

Diversity of invertebrate families

A repeated measures ANOVA indicated that there was no significant difference in the diversity of detritivore families or oribatid mite RTUs (Figures 5.9 and 5.10) between the treatments in the preharvest or postharvest years ($P>0.05$). However, there was a trend for lower detritivore diversity in all treatments during the winter (June).
Figure 5.9: The mean diversity of detritivore families in litter-bags collected at two month intervals from control, harvested and artificial windthrow sites (I = standard error), (arrow indicates end of preharvest year).

Figure 5.10: The mean diversity of oribatid mites in litter-bags collected at two month intervals from control, harvested and artificial windthrow sites (I = standard error), (arrow indicates end of preharvest year).
Decomposition

There was no significant difference ($P>0.05$) in the rate of weight loss from litter-bags between the control, harvested and artificial windthrow treatments in either the preharvest or postharvest years (Figure 5.11 and 5.12). The weight of leaf litter in litter-bags decreased from 25.0 g to 17.1 g (32 % reduction) in control sites, 16.3 g (35 % reduction) in harvested sites and 16.7 g (33 % reduction) in windthrow sites in the preharvest year. The total weight loss in the postharvest year was significantly lower than that in the preharvest year ($P<0.05$). The rate of change in the carbon:nitrogen ratio did not differ between the treatments in either the preharvest or the postharvest year (Figure 5.13 and 5.14). Weight loss from litter-bags was highly correlated ($r = 0.87$) with the carbon:nitrogen ratio which suggests that there was also no significant difference ($P>0.05$) in the carbon:nitrogen ratio between treatments over time. However, when the carbon and nitrogen are expressed as a percentage of the litter weight in the litter-bags, it is apparent that while the carbon concentration is declining over time, the nitrogen concentration remains constant (Figure 5.15).

![Graph](image)

**Figure 5.11:** The percentage weight remaining in litter-bags collected at two-monthly intervals from control, harvested and artificial windthrow sites in the preharvest year (Exponential curves were fitted to the data points).
Figure 5.12: The percentage weight remaining in litter-bags collected at two-monthly intervals from control, harvested and artificial windthrow sites in the postharvest year (Exponential curves were fitted to the data points).

Figure 5.13: The mean carbon:nitrogen ratio of leaf litter in litter-bags in control, harvested and artificial windthrow sites at two-monthly intervals during the preharvest year (Exponential curves were fitted to the data points).
Figure 5.14: The mean carbon:nitrogen ratio of leaf litter in litter-bags in control, harvested and artificial windthrow sites at two-monthly intervals during the postharvest year (Exponential curves were fitted to the data points).

Figure 5.15: The percentage of carbon and nitrogen per litter-bag in control, harvest and windthrow sites during the preharvest study.
5.4 Discussion

The results from this study suggest that neither selective harvest or artificial windthrow impacted on the abundance or diversity of invertebrates in litter-bags. Neither invertebrate abundances or diversity were affected. The rate of decomposition was also not affected. i.e., there was no change in the rate of weight loss and no difference in the rate of carbon:nitrogen ratio change in litter-bags between the treatments. These results are discussed in relation to contemporary theories on ecosystem maintenance.

The effects of selective harvest and artificial windthrow.
While there was no effect on invertebrates or decomposition attributable to selective harvest and artificial windthrow, the results are useful in understanding the links between invertebrates and decomposition processes. Examination of the ‘coefficient of variation’ between treatments and sampling dates enables a prediction of the variability in a population and how resilient it is to disturbance (Pimm, 1991). In an ecosystem that has populations with low temporal variation (and therefore high stability), it would be expected that disturbances might cause instability. This study compared the temporal variability of invertebrates in preharvest and postharvest years and found low variability between the two years. If the impact of selective harvest and artificial windthrow was large enough to cause an impact on the invertebrate fauna, we would have expected high variability in invertebrate abundances between the treatments in the postharvest year. As this was not the case, it suggests that the invertebrate population studied were stable despite the impact of selective harvest and artificial windthrow and that the beech forest ecosystem is sufficiently buffered against the fluctuations in environmental variables studied here so that processes remain unaffected. Similar results were reported by Bengtsson (1994) who reported that the temporal variability of soil communities in forests was low in forests that were subject to high-impact harvesting. A later study by Bengtsson et al. (1997) which compared the invertebrate fauna in areas with and without logging residue, reported similar levels of stability for higher taxa and functional groups. However, Collembola and some mite families were found to differ between the treatments.
In this study, family richness and diversity remained relatively constant throughout the preharvest and postharvest years. This supports the above discussion which suggests that the environmental conditions created by selective harvest and artificial windthrow did not result in changes to invertebrate community composition in the postharvest study. The results from this study were consistent with the results from Chapter 4 where richness and diversity did not vary greatly between the preharvest and postharvest years. Diversity may be maintained by buffering or ‘feedback’ mechanisms which hold it at a relatively constant level. Feedback mechanisms are likely to involve interactions with other trophic levels such as soil microbes - particularly fungi (Setälä et al., 1998). Additionally, community changes such as an increase in the size of organisms, longevity and interspecific competition for resources may maintain diversity (Odum, 1969). It is probable that in beech forests similar mechanisms occur to keep litter-dwelling invertebrate diversity constant over time. These mechanisms could also include ‘competitive exclusion’, where disturbances of intermediate intensity prevent competitively superior species from dominating the fauna (Wootton, 1998), although there was no evidence of this occurring in these results.

**Effects of seasonal patterns on invertebrates and decomposition.**

Invertebrate abundances in litter-bags differed between the sampling dates in both the preharvest and postharvest years. This suggests that either there is a predictable successional pattern in invertebrate colonisation occurring in the litter-bags or that the observed results are due to seasonal effects. Such information is extremely valuable in understanding how invertebrates are involved in litter decomposition and helps to predict how changes in diversity might affect ecosystem processes (Huston, 1994). A successional trend was observed following the CCA analysis which indicated that some invertebrates occurred when the litter-bag weight and carbon:nitrogen ratio were high (indicating early stages of decomposition) while other invertebrates occurred when litter-bag weight and carbon:nitrogen ratio were low.

However, examination of the invertebrate abundances reported in Chapter 4 (from unconfined leaf litter) indicated that the observed successional trends were better explained by seasonal effects rather than the stage of litter decay. i.e., abundances of Oecophoridae, OB
and OK had increased in abundance between April and February in both years. Similarly, Polyzoniidae had decreased in abundance between these months in unconfined leaf litter. While the abundance of invertebrates differed between sampling dates, the rate of decomposition remained relatively constant and appeared to be independent of changes in abundance. This is consistent with the findings of several earlier investigations which demonstrate that decomposition rate was independent of invertebrate abundance and is largely a product of microbial activity in the leaf litter (Springett, 1976; Petersen and Luxton, 1982; Seastedt and Crossley Jr, 1984; Andren et al., 1995; Hasegawa and Takeda, 1996; Poinso-Balaguer, 1996). While the rate of decomposition was independent of invertebrate abundance and treatment there was a difference in the rate of decomposition between the preharvest and postharvest years. This suggests that climatic variables such as rainfall, temperature and the timing of the seasons may have had a greater effect than small scale disturbances e.g., selective harvest and artificial windthrow on the rate of decomposition. A number of earlier studies have noted that decomposition occurs faster in regions where there is a high rainfall (e.g., tropical regions) than in regions where drier conditions predominate (Wood, 1974). Conejo et al. (1994) found irrigation of decomposing leaf litter resulted in increases in the rate of mass loss and biological activity. Similarly, Springett (1976) and Seastedt and Crossley Jr. (1984) suggested that seasonality of temperature and moisture regimes have important influences on decomposition rates. In this study, rainfall was higher in the preharvest year than the postharvest year and this may help to explain the faster rate of decomposition observed in the preharvest year (see Chapter 2).
Concluding remarks.

This study assumed that the presence of litter-bags did not alter invertebrate composition. Similar levels of diversity were found in litter-bags as in unconfined leaf litter (Chapter 4), suggesting that confining leaf litter to litter-bags with large mesh (5 mm) has a minimal effect on invertebrate diversity. Other studies have similarly reported only small effects on species richness and abundance of individuals from using large mesh (>1 mm) litter-bags (Nieminen and Setälä, 1998).

Seasonal factors are likely to have confounded the results describing successional patterns. It is difficult to control for these factors when doing field studies but further research would benefit from using more than one series of litter-bags and starting the studies at different times during the year. A seasonal effect could also be verified by leaving litter-bags in the forest for at least two years to verify whether abundance patterns occurred at similar times of the year and not in response to decomposition.

Although, the leaf litter used in each litter-bag was standardised as much as possible in the preharvest and postharvest years to control for differences in litter quality, a number of additional factors could have influenced the observed rates of decomposition. These include interactions between fauna at the same trophic level e.g., competition for resources and changes in population dynamics as well as interactions between different trophic levels of soil fauna (‘top-down : bottom-up’ effects - as described by De Ruiter et al., 1995 and Hairston et al., 1960). These ecosystem mechanisms affecting decomposition are likely to be responding to similar biotic and abiotic cues (Wardle et al., 1997) which lends support to the suggestion that climatic factors are largely responsible for the results observed in this study.

In conclusion, understanding the ecological mechanisms that maintain an ecosystem and how disturbance affects those mechanisms is extremely difficult. This study has given a short-term indication that selective harvest and artificial windthrow have a minimal effect on litter-dwelling invertebrates and the associated process of decomposition. This study has emphasised the difficulties associated with studying ecosystem processes but has clearly demonstrated that variables such as litter fall, temperature, moisture and climatic differences between seasons and years play a role in determining invertebrate abundance. Invertebrate
diversity however, appears to be maintained at a relatively constant level possibly by a range of ecosystem level feedback mechanisms. The role that invertebrates play in decomposing leaf litter remains unclear but is likely to involve comminution of the litter material and the timing of nutrient release from decomposing leaves (Beare et al., 1992). It appears that a majority of litter decomposition is completed by soil microbes and that the links between invertebrates and decomposition rates are relatively weak. Instead it appears that climatic variables and ecosystem mechanisms act together at varying scales to maintain to the reported levels of diversity and function. In addition, feedback mechanisms operating at varying temporal and spatial scales make it difficult to pinpoint the factors determining decomposition rates. There remains an urgent need to test at what point of species loss does ecosystem process breakdown occur, which “keystone” species are vital for ecosystem maintenance and what level of disturbance jeopardises the maintenance of forest ecosystems.
Chapter 6

The effect of excluding invertebrates on decomposition rate and
the effect of selective harvest on microbial respiration.

6.1 Introduction

In Chapter 5, it was established that selective harvest resulted in no loss of invertebrate
diversity and no changes to the rate of decomposition. There were however, changes in
invertebrate abundance during the year which could have potentially changed the rate of
decomposition. However, despite changes in invertebrate abundance, the rate of
decomposition remained relatively constant during the preharvest and postharvest years. This
providing an indication that invertebrates play only an indirect role in decomposition and that
compensatory mechanisms might counteract the loss of invertebrate abundance. Several
studies have demonstrated that when soil fauna is absent, litter disappearance is retarded
(Witkamp and Ausmus, 1976; Macauley, 1975; Santos and Whitford, 1981). However, the
mechanisms behind this observation are not well understood. It is extremely difficult to assess
the contributions of the invertebrates involved in decomposition (Peterson and Luxton, 1982)
and there is little evidence describing how changes in species diversity might alter ecosystem
properties or function (Wardle et al., 1997). Studies by Tilman (1996) and Naeem et al.
(1994) suggest that a reduction in plant diversity threatens primary production and ecosystem
sustainability. However, the effects on below-ground processes were unclear. Studies that
have investigated the effects of increased soil biota on below-ground processes have failed to
find simple cause and effect relationships (Andren et al., 1995; Huston, 1997; Wardle et al.,
1997).

This chapter addresses two objectives. The first was to test experimentally the consequences
of reduced invertebrate diversity on litter decomposition. The underlying assumption is that
leaf litter with reduced invertebrate abundance and diversity will decompose more slowly than
that with intact invertebrate communities. The second objective was to investigate whether selective harvest or artificial windthrow affected other trophic levels of the decomposer subsystem i.e., microbial activity in the leaf litter.

**Excluding invertebrates from the decomposer food web.**

It is thought that invertebrates influence microbial activity by increasing the surface area of leaves and by stimulating microbial growth via their feeding activity (Anderson, 1988). Attempts to evaluate the role of invertebrates in litter decomposition have involved using chemicals or different mesh sizes to exclude invertebrates. Several studies have found that by excluding invertebrates from litter-bags, the rate of decomposition declined (Macauley, 1975; Santos and Whitford, 1981; Heneghan et al., 1998). Macauley (1975) compared the rate of *Eucalyptus* spp. leaf decomposition using 5 mm, 1 mm and 0.5 mm mesh bags as well as a range of insecticides and fungicides. His results suggested that the rate of weight loss (decomposition) did not differ between the mesh sizes but by treating litter-bags with insecticide and/or fungicide the rate of weight loss from litter-bags declined. He concluded that invertebrates had a minimal role in decomposition but that their presence affected the pattern of nutrient release from the leaves. Santos and Whitford (1981) also found that litter-bags treated with insecticide lost less organic matter than did untreated bags. A similar study by Heneghan et al., (1998) demonstrated that by excluding invertebrates from litter-bags using insecticide, the rate of decomposition declined, but that this effect was more pronounced in tropical regions than in temperate ones. Exclusion experiments by Beare et al., (1992) studied trophic relationships between invertebrates and soil microbes and found that invertebrates determined the nitrogen dynamics and rates of litter decomposition.

This chapter reports on a study which excluded invertebrates using small mesh litter-bags (0.5 mm) and insecticide to determine whether the rate of weight loss was reduced in the absence of invertebrates. It was expected that the rate of weight loss would be reduced in the absence of invertebrates but that this effect would be minimal given that a large proportion of litter breakdown is completed by soil microbes.
Assessing microbial biomass

Although the interactions between invertebrates and microbes are fundamentally important in regulating the decomposition process (Wardle and Lavelle, 1997), most chemical breakdown is completed by soil dwelling bacteria and fungi (Anderson, 1988). Some studies have demonstrated that microbial activity is reduced by disturbance or stress but enhanced following a period of regeneration (Anderson and Domsch, 1978; Insam and Domsch, 1988). In this study, the level of soil microbial respiration was assessed in unconfined leaf litter, to determine at one point in time, whether selective harvest or artificial windthrow reduced the level of microbial activity. It was expected that given that there were no significant differences in invertebrate abundances between control, harvested and windthrow sites (indicated in the results reported in Chapters 4 and 5) there would be no difference in microbial respiration rates between the treatments. The amount of microbial activity in leaf litter samples was estimated by substrate induced respiration (SIR) which determines the amount of CO$_2$ produced by microbial activity. This method was developed by Anderson and Domsch (1978) and first used to measure carbon in the living microbial biomass of soils. West and Sparling (1986) improved the methods by standardising the moisture content of the leaf litter, allowing accurate estimation of induced microbial respiration using gas chromatography.

Several assumptions were made in order to complete the two studies reported in this chapter. The first two assumptions relate to the exclusion of invertebrates from litter-bags. It was assumed that the insecticide used did not reduce the level of microbial activity in the litter-bags. This would have made it difficult to attribute changes in litter mass to invertebrate absence only. The second assumption was that the insecticide maintained its effectiveness between reapplications which occurred at two month intervals. The third assumption relates to measuring microbial respiration rates. An assumption was made that CO$_2$ produced by respiration in the leaf litter was primarily from soil microbes rather than from invertebrates that may have been in the leaf litter. This assumption was based on the findings of Petersen and Luxton (1982) who found that invertebrates are responsible for less than 5% of total decomposer respiration.
In summary, it is thought that both invertebrates and soil microbes are necessary to recycle the nutrients in leaf litter, making them readily available for plant uptake. The experiments reported in this chapter were conducted to investigate further the relationships between invertebrates and decomposition and to complete an investigation into the possible effects of disturbance on microbial activity.

6.2 Methods

Insecticide study
Two pilot studies were conducted to test invertebrate susceptibility to three different synthetic pyrethroid insecticides for use in this study; 0.57 ml/l lambdacyhalothrin (Karate, 50 g/l, EC), 0.72 ml/l deltamethrin (Decis, 25 g/l, EC) and 0.40 ml/l taufluvalinate (Mavrik, 240 g/l, SC). The results indicated that lambdacyhalothrin (50 g/l) was the most effective insecticide for litter-dwelling invertebrates in beech forest (See Appendix 6.1).

Twenty litter-bags made from nylon material (mesh size 0.5 mm) and containing 25g of oven-dried leaf litter were initially soaked in a solution of 0.57 ml/l lambdacyhalothrin (concen. 0.57 ml/l). Subsequent insecticide application was carried out in the field at two-month intervals using a back-pack sprayer. One naphthalene ball (paradichlorobenzene) weighing approximately 5 g was also added to each of the litter-bags to deter invertebrates before they were placed in control and harvested sites on 16 February, 1998 (windthrow sites were not used due to the limited availability of Tullgren funnels). Twenty identical litter-bags, without insecticide were also placed in each of the six sites on 16 February, 1998 to determine the effect of using small mesh only on litter-dwelling invertebrates and decomposition. In addition to the forty small mesh litter-bags that were placed in control and harvested sites, two additional small mesh bags treated with insecticide were placed in each site as ‘sacrificial bags’ to verify that the insecticide remained effective after one month. These bags were retrieved on 15 March, 1998 and checked for invertebrate colonisation (Appendix 6.2).
All litter-bags were placed in the forest on 16 February, 1998 to coincide with the timing of the litter-bag study described in Chapter 5. Subsets of five insecticide treated and five untreated litter-bags were collected from each site on 16 April, 1998, 16 June, 1998, 16 October, 1998 and on 16 February, 1999. Once collected, the contents of all litter-bags were emptied into Tullgren funnels and left for 3 days to extract invertebrates (as described in Chapters 4 and 5). Following this, the leaf-litter was oven-dried for 72 hrs at 70°C and reweighed to determine the amount of weight loss from litter-bags.

The results from small mesh litter-bags with and without insecticide were compared with the results from large mesh litter-bags reported in Chapter 5.

**Microbial Respiration Study**

Five litter samples weighing 100 g were randomly collected by hand from control, harvested and windthrow sites on 16 February, 1999 and stored in an ice box. A subset of each sample was weighed and dried at 70°C for 2 days to determine the gravimetric moisture content (McLaren and Cameron, 1990).

Two leaf litter subsamples of approximately the same size, were adjusted (by adding water) to a standard moisture level (150%) and to a weight of 7.5 g. Glucose (0.1 g) was then added to one of the two subsamples to optimise the initial respiratory response by the microbes. Each study site was therefore represented by 10 samples: 5 subsamples with glucose and 5 subsamples without glucose. The subsamples were then placed in sterile flasks (125 ml) and incubated for four hours at 21°C. The amount of CO₂ produced by the microbes in the leaf litter was measured after 1 hour and 4 hours of incubation using a gas chromatograph.
6.3 Results

Insecticide experiment

The results from two pilot studies indicated that lambdacyhalothrin (50 g/l) was the most effective insecticide against invertebrates in beech forest leaf litter but that some oribatid mites were not killed by it (Appendix 6.1). Virtually no invertebrates were found in the ‘sacrificial bags’ treated with insecticide. This verified that the insecticide remained active for at least one month after application (Appendix 6.2).

The total number of invertebrates found in five small mesh litter-bags with and without insecticide and results from large mesh litter-bags (see Chapter 5) are reported in Table 6.1 and 6.2.

Table 6.1: The total abundance of detritivore families from five small mesh litter-bags with insecticide, five small mesh litter bags without insecticide and five large mesh litter-bags collected from harvested and control sites.

<table>
<thead>
<tr>
<th>Detritivore families</th>
<th>Large mesh (no - I)</th>
<th>Small mesh (no - I)</th>
<th>Small mesh (plus I)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Harvest</td>
<td>Control</td>
<td>Harvest</td>
</tr>
<tr>
<td>Polyzoniidae</td>
<td>9</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Schedotrigonidae</td>
<td>28</td>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td>Dalodesmidae</td>
<td>17</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>Habrodesmidae</td>
<td>4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Oecophoridae</td>
<td>32</td>
<td>49</td>
<td>47</td>
</tr>
<tr>
<td>Psychidae</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tortricidae</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Talitridae</td>
<td>60</td>
<td>52</td>
<td>1</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Curculionidae</td>
<td>85</td>
<td>66</td>
<td>0</td>
</tr>
<tr>
<td>Cerambycidae</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Megascolecidae</td>
<td>111</td>
<td>69</td>
<td>131</td>
</tr>
<tr>
<td>Styloniscidae</td>
<td>103</td>
<td>123</td>
<td>0</td>
</tr>
</tbody>
</table>

87
Table 6.2: The total abundance of oribatid mites from five small mesh litter-bags with insecticide, five small mesh litter-bags without insecticide and five large mesh litter-bags collected from harvested and control sites.

<table>
<thead>
<tr>
<th>oribatid mite (RTU's)</th>
<th>Large mesh (no - I)</th>
<th>Small mesh (no - I)</th>
<th>Small mesh (plus I)</th>
</tr>
</thead>
<tbody>
<tr>
<td>OA</td>
<td>17</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>OB</td>
<td>158</td>
<td>244</td>
<td>37</td>
</tr>
<tr>
<td>OC</td>
<td>399</td>
<td>296</td>
<td>1</td>
</tr>
<tr>
<td>OD</td>
<td>167</td>
<td>21</td>
<td>4</td>
</tr>
<tr>
<td>OE</td>
<td>154</td>
<td>51</td>
<td>6</td>
</tr>
<tr>
<td>OF</td>
<td>90</td>
<td>51</td>
<td>2</td>
</tr>
<tr>
<td>OG</td>
<td>1</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>OH</td>
<td>21</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>OD</td>
<td>234</td>
<td>543</td>
<td>472</td>
</tr>
<tr>
<td>OA</td>
<td>7</td>
<td>10</td>
<td>23</td>
</tr>
<tr>
<td>OB</td>
<td>60</td>
<td>74</td>
<td>3</td>
</tr>
<tr>
<td>OC</td>
<td>42</td>
<td>62</td>
<td>36</td>
</tr>
<tr>
<td>OD</td>
<td>730</td>
<td>459</td>
<td>163</td>
</tr>
<tr>
<td>OA</td>
<td>79</td>
<td>137</td>
<td>43</td>
</tr>
<tr>
<td>OR</td>
<td>31</td>
<td>40</td>
<td>43</td>
</tr>
<tr>
<td>OP</td>
<td>9</td>
<td>16</td>
<td>1</td>
</tr>
<tr>
<td>OQ</td>
<td>195</td>
<td>108</td>
<td>2</td>
</tr>
<tr>
<td>OR</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>OS</td>
<td>205</td>
<td>62</td>
<td>11</td>
</tr>
<tr>
<td>OT</td>
<td>21</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>OU</td>
<td>0</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

ANOVA indicated that there was a significant difference in the abundance of invertebrates between the three types of litter-bags ($P<0.05$) but that there was no significant difference in invertebrate abundances between control and harvested sites ($P>0.05$).

ANOVA also indicated that the rate of decomposition in litter-bags was not significantly different between the three bag types ($P>0.05$). However, the weight did vary significantly between the sampling dates ($P<0.05$). There was no significant difference in the weight of the bags placed in control or harvested sites ($P>0.05$).
Figure 6.1: The mean weight remaining in large mesh litter-bags, small mesh litter-bags and small mesh litter-bags treated with insecticide after 0, 2, 4, 8 and 12 months litter decomposition.

Microbial respiration results
ANOVA indicated that microbial respiration rates did not differ significantly between control, harvested and windthrow sites ($P>0.05$). Table 6.3 reports the basal respiration (no glucose added) and substrate induced respiration rates (addition of glucose) for samples collected on 16 February, 1999.
Table 6.3: The mean (± SE) for microbial substrate induced respiration for litter collected from control, harvested and windthrow sites (n = 15 samples/treatment).

<table>
<thead>
<tr>
<th></th>
<th>Mean CO₂ - C μg g⁻¹ h⁻¹</th>
<th></th>
<th>Mean CO₂ - C μg g⁻¹ h⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Basal Respn.</td>
<td>Substrate Induced Respn.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(- glucose)</td>
<td>(+ glucose)</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>21.8 ± 3.66</td>
<td>35.3 ± 6.20</td>
<td></td>
</tr>
<tr>
<td>Harvested</td>
<td>24.0 ± 3.66</td>
<td>43.6 ± 6.20</td>
<td></td>
</tr>
<tr>
<td>Windthrow</td>
<td>17.2 ± 3.66</td>
<td>33.6 ± 6.20</td>
<td></td>
</tr>
</tbody>
</table>

6.4 Discussion

Insecticide study

More invertebrates were found in large mesh litter-bags than small mesh ones. Small mesh litter-bags that were not treated with insecticide contained more invertebrates than small mesh litter-bags treated with insecticide. If decomposition rates are reduced in the absence of invertebrates (Santos and Whitford, 1981; Seastedt, 1984), the addition of insecticide to small mesh bags should result in reduced rates of decomposition. In this study, the application of insecticide altered invertebrate abundances but not the rate of decomposition i.e., decomposition rates did not vary between the different bag types despite differences in invertebrate abundance.

There was also no difference in the rate of decomposition between litter-bags in harvested or control sites, suggesting that selective harvest had no apparent impact on decomposition processes. The results support those of Macauley (1975) who found that there was no difference in the rate of decomposition between bags of differing mesh sizes. However, he found that insecticide application reduced the rate of decomposition. One explanation for his
results could be that the DDT (dichlorodiphenyltrichloroethane) insecticide he used to exclude invertebrates also affected microbial activity (Mellanby, 1992). This could account for the decline in decomposition rates seen in his insecticide treated litter-bags. The results from the present study do not support those of Santos and Whitford (1981) who demonstrated that the exclusion of invertebrates resulted in a 53% reduction in mass loss from litter-bags. The results observed in the present study where there was change in the rate of decomposition could be due to the presence of a few oribatid mites (Table 6.2) or more likely, compensation for the lack of invertebrate activity by microbial activity in the small mesh litter-bags. This suggestion is based on the findings of Beare et al. (1992) who found that invertebrates played an important role in decomposition by grazing on litter-dwelling bacteria and fungi. Assuming there were no invertebrates present in the litter-bags, soil microbes may have increased in number and in so doing increased their ability to decompose leaf litter. Another possible explanations for the observed results is that the duration of the study was not sufficiently long to detect differences between the three litter-bag types. Future studies might benefit from studying decomposition over a longer period of time and using smaller initial quantities of leaf litter in litter-bags.

**Microbial respiration**

The results from this study do not support those of Insam and Domsch (1988) who found that disturbance affected the level of CO₂ production. Instead, the level of CO₂ produced by microbes in this study was similar between the treatments. This suggests that the impact of selective harvest and artificial windthrow was not sufficiently large to affect the microbial activity in leaf litter. The results were consistent with predictions that selective harvest would have no impact on microbial activity, given that selective harvest had no impact on invertebrates (Chapters 4 and 5) and given that there is evidence that invertebrates influence the level of microbial activity in decomposing matter. The overall rates of respiration were slightly lower than those reported by Wardle (1993) from beech forest, but this is thought to be due to the unusually dry conditions at the time of sampling (Couteaux et al., 1995; Wardle, pers. comm.). A lack of temporal replication, restricted this study and the results have given only an indication at one point in time of the impact of disturbance.
Concluding remarks

In conclusion, these studies experimentally investigated the role of invertebrates in the process of decomposition and investigated the impact of small scale disturbances on microbial activity. The results from the first study provide support for the findings reported in Chapter 5 that invertebrates have only a small and indirect role to play in the decomposition of leaf litter and that most decomposition is completed by soil microbes. The second study provided some evidence to suggest that the microbial fauna is not affected by small-scale disturbances such as selective harvest but further research is needed to confirm this.
Chapter 7

General Discussion

7.1 Addressing the research objectives.

This thesis has investigated the responses of litter dwelling invertebrates to selective harvest and artificial windthrow disturbance in New Zealand’s indigenous *Nothofagus* forests. The need for this information stems from a global trend for sustainable use of forest resources and a desire to conserve biodiversity. New Zealand is signatory to international agreements such as the Montreal Process (Anon, 1995) that aim to ensure that natural resources such as forests are managed on a sustainable basis. That is, that forests are managed in perpetuity without compromising forest resources for future generations. While sustainability has become a widely used term in forestry circles, there is little agreement about how to define sustainability or how to measure it (Kimmins, 1997). Much discussion has centred around the best way to minimise species loss and retain ecosystem integrity. However, most ecologists agree that the key to analysing sustainability lies in understanding which aspects of diversity are critical for maintaining ecosystems and how ecosystems respond to disturbance (Odum, 1969; May, 1973; Walker, 1992; Lawton, 1994; Andren *et al.*, 1995; Grime, 1997; Huston, 1997; Kimmins, 1997; Wardle and Giller, 1997; Wootton, 1998).

The research described in this thesis is based on the need to develop an indicator-based monitoring system to demonstrate whether selective beech harvest is ecologically sustainable and whether disturbance patterns resulting from selective harvest resemble those created by natural windthrow disturbance. Determining which invertebrates and ecological variables are susceptible to the environmental changes caused by selective harvest and natural disturbance is vital for ecosystem maintenance (Wootton, 1998).

Invertebrates comprise the largest component of diversity in forests (May, 1973) and a large number of invertebrates occupy the forest floor (Stork, 1988). Despite their importance, forest invertebrates have received relatively little research attention, particularly those involved in
maintaining below-ground processes such as the decomposition of organic matter (Wardle and Giller, 1997). Recently however, there has been a realisation that these invertebrates offer opportunities to test ecological theories, allow for more robust statistical analysis and are potentially suitable as indicators of forest well-being (Wardle and Giller, 1997; Weaver, 1995). This thesis reports on a series of individual studies which investigated the impact of selective beech harvest on litter-dwelling invertebrates and evaluated the prospect of using invertebrates as indicators of sustainable forest management. Litter-dwelling invertebrates were selected because of their association with decomposition processes and because of their potential as indicator species. The results are discussed in the context of ecological theories, particularly those relating to the functional significance of diversity and how diversity relates to ecosystem stability. Both of these are relevant to biodiversity maintenance and the allocation of conservation resources (Grime, 1997).

The results reported in Chapter 3 described changes in environmental factors such as light, temperature and litter moisture as well as biotic variables such as litter fall. Biotic and abiotic elements of an ecosystem are inextricably linked and therefore should be studied together. However, the interactions between biotic and abiotic elements make it difficult to distinguish causal factors (Huston, 1997). Results in Chapter 3 suggest there was an increase in light following selective harvest and artificial windthrow, which has implications for beech seedling establishment and for the temperature and moisture of the forest floor (Ogden et al., 1996). Small increases in litter temperature were recorded during the winter months in harvested sites but essentially the temperature and moisture did not differ between the treatments. While there is considerable evidence that the forest floor is subjected to more extreme temperatures and associated changes in moisture following tree harvest, this is largely generated from studies involving high-impact harvesting techniques such as clear-felling (Seastedt and Crossley, 1981; Kenagy and Stevenson 1982; Klein, 1989; Kimmins, 1997). Litter fall was measured to investigate the influence of selective harvest and artificial windthrow on litter resources and on invertebrate populations. The results reported show a trend for less litter fall in selective harvest and artificial windthrow sites compared with unharvested forest. However, this was considered to be a short-term phenomenon only since canopy closure occurs rapidly in beech forest gaps created by windthrow (R.Allen, pers. comm.).
Chapter 4 investigated whether there were changes in invertebrate abundance as a consequence of changes to abiotic and biotic factors reported in Chapter 3. There was a definite seasonal effect on invertebrate abundances during the preharvest and postharvest years, but there were no significant differences in abundances between the treatments in this study. The presence of a seasonal effect suggests that invertebrates are responding to climatic changes rather than to small changes in microclimate that may have resulted from selective harvest or artificial windthrow. Litter fall is the primary resource for litter-dwelling invertebrates and the hypothesis that invertebrate abundances may be detrimentally affected by declines in litter fall was tested. Although, invertebrate abundances in relation to litter fall have been investigated in New Zealand by Moeed and Meads (1986), Dugdale (1996) Fitzgerald et al. (1996) and Alley et al. (1999), the impacts of a potential reduction in litter fall resulting from selective harvest and windthrow were not known. In this study, some invertebrate numbers were correlated with the spring peak in litter fall whereas others coincided with autumn peaks. This supports the findings of Dugdale (1996), Fitzgerald et al., (1996) and Moeed and Meads (1986) who also found coincident peaks in invertebrate abundance during periods of high litter fall.

Chapter 5 investigated the relationship between invertebrate diversity and ecosystem process in selectively harvested, artificial windthrow and unharvested forest. Specifically this chapter determined whether potential changes in invertebrate diversity resulted in changes to the rate of decomposition. In addition, this chapter addressed contemporary ecological theories relating to stability and resilience of invertebrate communities as well as the consequences of reduced stability for ecological function (Lawton and Brown, 1993). The results suggested that selective harvest and artificial windthrow did not affect invertebrate diversity and therefore did not affect the rate of decomposition supporting the findings of Andren et al., (1995) who found that decomposition was largely controlled by temperature and moisture conditions. The results also indicated that invertebrate abundances changed seasonally, yet the rate of decomposition remained constant, suggesting the presence of compensatory mechanisms such as inter-trophic interactions, changes in interspecific competition or phenology which can influence invertebrate communities as well as effect decomposition (Odum, 1969; Setälä et al., 1998; Wootton, 1998).
Examination of the 'coefficient of variation' between treatments and sampling dates demonstrated that the variability in invertebrate abundances between the two years did not differ, implying that the invertebrate community was relatively stable despite the occurrence of selective harvest and artificial windthrow (Pimm, 1991). The results did not enable conclusions regarding the presence of redundant (or substitutable) species to be made and successional patterns were confounded by seasonal effects on invertebrates. In conclusion, it appears that ecosystem-level mechanisms such as interactions within and between trophic levels regulate decomposition and that these respond to similar biotic and abiotic cues such as rainfall, timing of the seasons and associated temperature fluctuations. Finally, it is concluded that climatic factors were of greater significance to litter-dwelling invertebrates than the effects of selective harvest and artificial windthrow.

Chapter 6 tested experimentally whether the exclusion of invertebrates retarded decomposition rates. Several studies have demonstrated that when invertebrates are excluded from litter-bags the amount of litter decomposed declines (Macauley, 1975; Santos and Whitford, 1981; Heneghan et al., 1998). In this study invertebrates were excluded from litter-bags by using small-mesh material and by applying insecticide to leaf litter. While there were differences in the abundances and diversity of invertebrates between the different bag types, there were no differences in the rate of decomposition. This supports theories discussed in Chapter 5 which suggest that decomposition rates may be indirectly related to invertebrate abundance (Seastedt and Crossley Jr, 1984; Andren et al., 1995; Poinsot-Balaguer, 1996) and that compensatory mechanisms exist which decompose litter when particular invertebrate groups are less abundant (Setälä et al., 1998). A possible explanation for the observed results is that in the absence of invertebrates, soil microbial decomposition was enhanced, thus compensating for the lack of invertebrates. While there is no experimental evidence of this occurring, litter-bags can influence microclimatic variables such as temperature and moisture and this increases microbial activity (D. Wardle, pers.comm). An additional study investigated whether microbial respiration rates in leaf-litter were detrimentally affected by the effects of selective harvest and artificial windthrow. The results suggested that neither selective harvest or artificial windthrow detrimentally effected microbial respiration. However, this study was not replicated temporally and was conducted at a time of extremely low moisture levels which may have lowered the overall CO₂ respiration rates.
Key results from this thesis have demonstrated that environmental factors and litter fall were not significantly affected by selective harvest and artificial windthrow. These factors were, however, important in determining invertebrate abundances seasonally. Consistent with these results was the finding that there was no detectable effect of selective harvest or artificial windthrow on invertebrate abundance and diversity. Despite seasonal changes in invertebrate abundance the process of decomposition remained relatively constant, suggesting there were compensatory mechanisms counteracting for changes in invertebrate abundance. When invertebrates were deliberately excluded from the decomposer food-web, there was still no detectable effect on the rate of decomposition. Either compensatory mechanisms engaged or the methods used were not sensitive enough to detect changes in the rate of decomposition. Also, the study may have been too short to detect whether decomposition had been retarded or not as a consequence of changes in diversity.

In conclusion it appears that neither selective harvest nor artificial windthrow had a sufficiently large impact to cause detectable changes to litter-dwelling invertebrates or to their interacting abiotic elements. Instead, it appears that macroclimatic conditions were of greater magnitude than the effects of selective harvest and played a dominant role in influencing ecosystem diversity and function. Variability in invertebrate diversity and abundance did not differ between the preharvest and postharvest years, suggesting a degree of constancy in invertebrate populations despite disturbance. This conclusion is supported by the lack of an invertebrate successional pattern in the results from Chapter 5. Had there been a significant perturbation of the invertebrate community, an associated successive temporal pattern would have been expected.

7.2 Limitations of this research.

Although this thesis has reported no short-term impacts on invertebrate densities resulting from selective harvest, the long-term impacts are not known. Studies by Huhta (1976), for example, reported an initial increase in invertebrate diversity resulting from clear-felling, followed by a long-term decline which he attributed to a decline in litter resources. Bengtsson
et al. (1997) also demonstrated that the presence of logging debris resulting from clear-felling had significant long-term effects on invertebrates, particularly those in higher trophic levels.

A lack of published research on invertebrates and their associations with forest processes has made it difficult to put the results from this study in context. This study was also hampered by the fact that few of New Zealand's estimated 20,000 invertebrates have been formally identified and even fewer are ecologically understood (Kuschel, 1975). The use of RTU's as a surrogate for taxonomic descriptions allows rapid estimation of diversity provided that the morphospecies are easily recognised (Oliver and Beattie, 1996). This method has been advocated in this thesis on the basis that Oribatid mites were easily divided into morphospecies and that voucher specimens have been placed in the Lincoln University Entomological Museum. The disadvantage with using this method was an inability to distinguish between juvenile and adult stages.

The design of this study was also slightly confounded due to the lack of true control sites. Ideally, to compare the effect of selective harvest and artificial windthrow sites on invertebrate densities, control sites would need to have experienced no natural disturbances. This is, however, extremely difficult to achieve in beech and other forest types because of the high level of background disturbance.

Assessing decomposition rates has traditionally involved confining leaf litter to litter-bags or measuring the disappearance of cotton from cloth strips. Both methods are restricted in that they underestimate decomposition rates and quantify only the organic matter that has not been decomposed (Wieder and Lang, 1982). Alternative methods that could have been used involve labelling leaves with radioisotopes such as C\(^{14}\) labelling and monitoring their movements through the soil processes. Litter-bags were chosen since they were a simple, inexpensive method that enabled a range of quantitative data to be extracted from them and because comparisons with other studies were possible. The results from the decomposition study (Chapters 5 and 6) would have been more beneficial if they were carried out over a longer period of time so that the potential effect of reduced invertebrate diversity on decomposition rates was more obvious.
7.3 Concluding Remarks

Although selective harvest is considered to be 'low-impact', research into the long-term effects are essential. Apart from the obvious need for taxonomic studies in New Zealand, there needs to be a greater understanding of which species modulate the availability of resources to other species or which are 'keystone' species whose removal could have implications for other taxa and ecosystem functions (Lawton, 1994). There is also an opportunity in beech forests to investigate how disturbance interacts with ecological processes and affects invertebrate successional patterns. Although the selectively harvested areas are small and are not expected to result in long-term abiotic or biotic changes, the effect of selectively removing logs may also have long-term implications for litter-dwelling invertebrates and carbon storage on the forest floor (Tate et al., 1993; Clinton et al., 1992). The effect of selective harvest on microbial respiration could also be researched more thoroughly by including measurements over a range of time periods and over a range of disturbance intensities. The development of an indicator-based monitoring system for sustainable harvest requires further research to demonstrate a consequential effect of invertebrates on the process of decomposition. Research has recently been initiated to study the long-term consequences of log removal on invertebrate populations and nutrient retention in beech forest. Logs form a large proportion of the coarse woody debris on the forest-floor and may be important as a mechanism to reduce nitrogen loss from the forest ecosystem (Stewart and Allen, 1998). If this is so, it would be expected that decomposer communities and decomposition rates would differ in the vicinity of logs.

One of the main objectives of this research was to gain an understanding of how litter-dwelling invertebrates respond to disturbance and how they contribute to ecological processes, so that indicator species might be selected to monitor environmental stress in selectively harvested forests. The prerequisites for selecting indicators are: that they occur ubiquitously throughout the forest; that they are sensitive to the environmental changes brought about by selective harvest and natural disturbance; that they are ecologically well understood and taxonomically described; they are independent of sample size; easily sampled and that they predict the diversity of other fauna (Weaver, 1995; McGeoch, 1998; Rodriguez et al., 1998). In the past, indicator species have been selected on the basis that they are of
conservation value or are of significant economic importance and little regard has been given to whether they are of consequence to ecosystem maintenance (McGeoch, 1998; Rodriguez et al., 1998). While the invertebrates studied in this thesis clearly offer potential as indicators of forest health because of their association with ecosystem processes and because of their ubiquitous nature, none of those studied were obviously susceptible to the impacts of selective harvest. More importantly there was no clear evidence of direct links between the particular invertebrates and ecosystem function. It is therefore difficult to select with confidence invertebrates that would be suitable indicators of sustainable forest management. Some of those studied were, however, more suitable candidates than others. The first of these was Lepidoptera larvae. These are relatively well described taxonomically (Dugdale, 1996) and are well represented in the leaf litter fauna. They also have a wide distribution in New Zealand beech forests and play an important role in decomposition as well as the population dynamics of stoat (Mustela erminea (L.)) which is a predator of endangered birds (Fitzgerald et al., 1996). Other potential candidates are Amphipoda (Talitridae) and Isopoda (Styloniscidae) since they have been relatively well described and are susceptible to desiccation in higher litter temperatures (Hurley, 1950; Duncan, 1994). However, the robustness of these invertebrates as indicators would need to be more thoroughly tested before implementing them as a measure of sustainable forest management. The selection and testing of bioindicators is a difficult and slow process, and there are few examples of research that have provided decision-makers with robust indicators (McGeoch, 1998). The urgency for conservation of diversity and the need for indicators of sustainable practices should not however be allowed to compromise the research needed to select suitable indicators of sustainable forest management practices.
References


History of Aerial Harvesting

Aerial harvesting was first trialed in Scotland in 1956. Numerous further trials were conducted during the late 1950s and 60s in Russia, North America and Scandinavia. By 1972 the use of helicopters had become an accepted practice in a number of countries. In New Zealand, helicopter harvesting trials since the late 1970s have included extraction of kauri and rimu pole thinnings, sawn timber and logs, as well as Pinus radiata thinnings and posts.

On the West Coast, the recognition that sustainable rimu management would require low impact harvesting methods, resulted in trials commencing in 1978. However, commercial operations remained constrained, undermined by the log prices of the day. To implement sustainable management in rimu forests and remove the impacts of conventional operations, Timberlands West Coast Limited introduced this technique on a large commercial scale for the first time in New Zealand in 1993. Expressions of interest were received from 40 companies in six different countries.

The Operation

Harvesting logs by helicopter follows a defined and strict operational structure. Timberlands West Coast Limited runs a “cold deck” operation where every stage is completed before the next stage starts.
- ground crews fell and prepare logs to exact weights
- a remotely actuated grapple on the helicopter longline grasps the logs which are then lifted and delivered to the landing site before being released
- logs are loaded out and transported to mills

Why Aerial Harvest?

Environmental Advantages

The nature of the operation limits the environmental impact of harvesting on the surrounding forest.
- the helicopter enables “true” selective harvesting where only those trees suitable for extraction are taken
- the elimination of any cable or ground based systems ensures minimum damage to soil and water values and remaining forest
- a substantial reduction in roadning reduces one of the major potential causes of soil erosion
- by lifting logs to the landing site there is no concentration of damage around the area
- the scenic views of the forest are maintained
- environmental risk under the Resource Management Act is reduced
- the helicopter is the only extraction technique currently suitable for some sensitive forest types.

Appendix 2.1

Operational Advantages

- logs arrive at mill relatively free from stones, mud and other contamination
- ease of transfer between locations increases operational flexibility
- operation is not greatly influenced by volume per hectare or block distribution
- roadng requirements are signifIcantly reduced
- minimum lead in time is required for unexpected supply demands, i.e. “just in time” inventory capability
- ability to operate in most weather conditions
- economic if machine is tailored to scale of operation.

...sustaining our forestry future
Appendix 3.1: An example of a canopy gap in a selectively harvested site (above) and artificial windthrow (below).
Appendix 4.1: The mean number of invertebrate families collected in leaf litter with each additional sample (95% Confidence Intervals are also shown).
Appendix 4.2: The percentage of detritivore individuals that were extracted from leaf litter using Tullgren funnels over a period of ten days.
Appendix 4.3a: Invertebrate proportions in detritivore guild from leaf litter samples taken in control sites during the preharvest year.

Appendix 4.3b: Invertebrate proportions in detritivore guild from leaf litter samples taken in harvested sites during the preharvest year.
Appendix 4.3c: Invertebrate proportions in detritivore guild from leaf litter samples taken in windthrow sites during the preharvest year.

Appendix 4.3d: Invertebrate proportions in detritivore guild from leaf litter samples taken in control sites during the postharvest year.
Appendix 4.3e: Invertebrate proportions in detritivore guild from leaf litter samples taken in harvested sites during the postharvest year.

Appendix 4.3f: Invertebrate proportions in detritivore guild from leaf litter samples taken in windthrow sites during the postharvest year.
Appendix 4.4a: Millipede families in control, harvested and windthrow sites - postharvest.
Appendix 4.4b: Lepidopteran families in control, harvested and windthrow sites - postharvest.
Appendix 4.4c: Remaining detritivore families in control, harvested and windthrow sites - postharvest.
Appendix 4.4d: Abundance of oribatid mites in control, harvested and windthrow sites - postharvest.
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<th>Season (B)</th>
<th>Year<em>Season (A</em>B)</th>
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Appendix 4.5: P-values resulting from a repeated measures ANOVA testing for effects of treatment, season (sampling date) and year on the abundance of invertebrates in leaf litter during the preharvest and postharvest years.
### Detritivores (Families) | Year (A) | Harvest (A*Tmt) | Season (B) | Year Season (A*B) | Season Year Harvest (B*A*Tmt)
--- | --- | --- | --- | --- | ---
Polyzonidae | 0.430 | 0.460 | 0.558 | 0.232 | 0.223
Schedotrigonidae | 0.000 | 0.148 | 0.000 | 0.002 | 0.187
Dalodesmidae | 0.252 | 0.151 | Insufficient data | Insufficient data | 0.292
Habrodesmidae | 0.029 | Insufficient data | Insufficient data | 0.026 | 0.178
Sphaerotheriidae | Insufficient data | Insufficient data | Insufficient data | Insufficient data | Insufficient data
Oecophoridae | 0.280 | 0.343 | 0.021 | 0.354 | 0.171
Phyldidae | 0.148 | 0.152 | 0.000 | 0.000 | 0.000
Tortricidae | 0.236 | 0.718 | 0.000 | 0.108 | 0.963
Tipulidae | 0.002 | 0.131 | 0.001 | 0.007 | 0.105
Dorculanidae | 0.017 | 0.125 | 0.000 | 0.003 | 0.672
Cerambycidae | Insufficient data | Insufficient data | Insufficient data | Insufficient data | Insufficient data
Megascolecidae | 0.100 | 0.152 | 0.280 | 0.007 | 0.340
Styloniscidae | 0.056 | 0.567 | 0.002 | 0.000 | 0.242

### Oribatid mites (RTU's) | Year (A) | Harvest (A*Tmt) | Season (B) | Year Season (A*B) | Season Year Harvest (B*A*Tmt)
--- | --- | --- | --- | --- | ---
OA | 0.280 | 0.343 | 0.021 | 0.354 | 0.171
OB | 0.088 | 0.152 | 0.000 | 0.000 | 0.000
OC | 0.320 | 0.725 | 0.000 | 0.000 | 0.579
OD | 0.236 | 0.718 | 0.000 | 0.108 | 0.963
OE | 0.002 | 0.131 | 0.001 | 0.007 | 0.105
OF | 0.017 | 0.125 | 0.000 | 0.003 | 0.672
OG | Insufficient data | Insufficient data | Insufficient data | Insufficient data | Insufficient data
OH | 0.795 | 0.326 | 0.010 | 0.933 | 0.937
OI | 0.125 | 0.208 | 0.163 | 0.104 | 0.633
OJ | 0.119 | 0.542 | 0.162 | 0.077 | 0.490
OK | 0.033 | 0.640 | 0.007 | 0.006 | 0.016
OL | 0.356 | 0.733 | 0.000 | 0.876 | 0.992
OM | 0.031 | 0.182 | 0.000 | 0.000 | 0.807
ON | 0.341 | 0.759 | 0.202 | 0.023 | 0.737
OO | 0.045 | 0.655 | 0.127 | 0.002 | 0.992
OP | 0.014 | 0.397 | 0.458 | 0.266 | 0.451
OQ | 0.745 | 0.280 | 0.354 | 0.129 | 0.853
OR | Insufficient data | Insufficient data | Insufficient data | Insufficient data | Insufficient data
OS | 0.677 | 0.233 | 0.052 | 0.251 | 0.620
OT | 0.020 | 0.234 | 0.002 | 0.081 | 0.416
OU | Insufficient data | Insufficient data | Insufficient data | Insufficient data | Insufficient data

**Appendix 5.1:** P-values resulting from a repeated measures ANOVA testing for effects of treatment, season (sampling date) and year during the preharvest and postharvest years. (Abundances were adjusted to a weight constant of 25 g since the quantity of leaf litter declined in litter-bags over time).
<table>
<thead>
<tr>
<th>CVb/CVa</th>
<th>Control</th>
<th>Harvest</th>
<th>Windthrow</th>
<th>P-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schedotigonidae</td>
<td>1.26</td>
<td>0.94</td>
<td>1.45</td>
<td>0.50</td>
</tr>
<tr>
<td>Dalodesmidae</td>
<td>1.04</td>
<td>0.98</td>
<td>1.55</td>
<td>0.57</td>
</tr>
<tr>
<td>Habrodesmidae</td>
<td>5.55</td>
<td>1.28</td>
<td>2.76</td>
<td>0.05</td>
</tr>
<tr>
<td>Oecophoridae</td>
<td>1.41</td>
<td>1.05</td>
<td>2.01</td>
<td>0.52</td>
</tr>
<tr>
<td>Taldridae</td>
<td>10.94</td>
<td>0.88</td>
<td>0.40</td>
<td>0.26</td>
</tr>
<tr>
<td>Tiptulidae</td>
<td>0.93</td>
<td>0.47</td>
<td>0.25</td>
<td>0.11</td>
</tr>
<tr>
<td>Curculionidae</td>
<td>2.20</td>
<td>1.86</td>
<td>0.71</td>
<td>0.28</td>
</tr>
<tr>
<td>Megascolecidae</td>
<td>0.65</td>
<td>0.47</td>
<td>0.57</td>
<td>0.76</td>
</tr>
<tr>
<td>Styloischidae</td>
<td>1.05</td>
<td>1.54</td>
<td>1.45</td>
<td>0.78</td>
</tr>
<tr>
<td>OA</td>
<td>1.78</td>
<td>1.45</td>
<td>1.60</td>
<td>0.95</td>
</tr>
<tr>
<td>OB</td>
<td>0.51</td>
<td>1.42</td>
<td>1.22</td>
<td>0.05</td>
</tr>
<tr>
<td>OC</td>
<td>4.12</td>
<td>2.04</td>
<td>0.78</td>
<td>0.28</td>
</tr>
<tr>
<td>OD</td>
<td>2.74</td>
<td>0.87</td>
<td>0.32</td>
<td>0.04</td>
</tr>
<tr>
<td>OE</td>
<td>1.44</td>
<td>0.37</td>
<td>0.43</td>
<td>0.11</td>
</tr>
<tr>
<td>OF</td>
<td>0.72</td>
<td>0.89</td>
<td>0.78</td>
<td>0.58</td>
</tr>
<tr>
<td>OH</td>
<td>2.18</td>
<td>1.55</td>
<td>0.62</td>
<td>0.63</td>
</tr>
<tr>
<td>OI</td>
<td>0.80</td>
<td>3.15</td>
<td>0.39</td>
<td>0.16</td>
</tr>
<tr>
<td>OJ</td>
<td>0.18</td>
<td>0.04</td>
<td>1.50</td>
<td>0.25</td>
</tr>
<tr>
<td>OK</td>
<td>0.60</td>
<td>0.79</td>
<td>2.25</td>
<td>0.06</td>
</tr>
<tr>
<td>OL</td>
<td>2.65</td>
<td>2.57</td>
<td>0.45</td>
<td>0.25</td>
</tr>
<tr>
<td>OM</td>
<td>1.72</td>
<td>1.04</td>
<td>1.04</td>
<td>0.08</td>
</tr>
<tr>
<td>ON</td>
<td>0.63</td>
<td>0.90</td>
<td>2.84</td>
<td>0.36</td>
</tr>
<tr>
<td>GO</td>
<td>2.37</td>
<td>1.01</td>
<td>0.42</td>
<td>0.23</td>
</tr>
<tr>
<td>OP</td>
<td>2.60</td>
<td>0.46</td>
<td>0.22</td>
<td>0.07</td>
</tr>
<tr>
<td>OQ</td>
<td>0.74</td>
<td>0.11</td>
<td>0.20</td>
<td>0.39</td>
</tr>
<tr>
<td>OS</td>
<td>7.53</td>
<td>0.55</td>
<td>0.22</td>
<td>0.14</td>
</tr>
<tr>
<td>OT</td>
<td>1.46</td>
<td>4.90</td>
<td>1.42</td>
<td>0.31</td>
</tr>
</tbody>
</table>

Appendix 5.2: Coefficients of variation, calculated on invertebrate abundances, from litter-bags in control, harvested and windthrow sites in the preharvest and postharvest year. P-values are reported from an ANOVA using three replicated sites (CVb = postharvest and CVa = preharvest; ratio determined separately for each replicate).
### Study One:

<table>
<thead>
<tr>
<th>Mean number of invertebrates</th>
<th>Control</th>
<th>Lambda cyhalothrin (Karate, 50 g/l, EC)</th>
<th>Deltamethrin (Decis, 25 g/l, EC)</th>
<th>trifluvalinat (Mavrik, 240 g/l, SC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diplopoda (millipedes)</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Lepidopteran larvae</td>
<td>8.3</td>
<td>0.3</td>
<td>0.3</td>
<td>3.0</td>
</tr>
<tr>
<td>Orbital mites</td>
<td>89.7</td>
<td>16.3</td>
<td>40.7</td>
<td>19.3</td>
</tr>
<tr>
<td>Coleoptera (weevils)</td>
<td>4.7</td>
<td>0.3</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Megascolecida (earthworms)</td>
<td>0.7</td>
<td>0.0</td>
<td>0.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Stylonychidae (slaters)</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Talitridae (amphipods)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

### Study Two:

<table>
<thead>
<tr>
<th>Mean number of invertebrates</th>
<th>Control</th>
<th>Lambda cyhalothrin (Karate, 50 g/l, EC)</th>
<th>Deltamethrin (Decis, 25 g/l, EC)</th>
<th>trifluvalinat (Mavrik, 240 g/l, SC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diplopoda (millipedes)</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.7</td>
</tr>
<tr>
<td>Lepidopteran larvae</td>
<td>1.3</td>
<td>0.0</td>
<td>0.7</td>
<td>1.3</td>
</tr>
<tr>
<td>Orbital mites</td>
<td>73.7</td>
<td>14.0</td>
<td>34.0</td>
<td>5.3</td>
</tr>
<tr>
<td>Coleoptera (weevils)</td>
<td>0.0</td>
<td>0.7</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Megascolecida (earthworms)</td>
<td>0.3</td>
<td>0.0</td>
<td>0.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Stylonychidae (slaters)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Talitridae (amphipods)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Tipulid larvae</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

### Appendix 6.1: The number of invertebrates in leaf litter after treatment with insecticide: study one and two.

<table>
<thead>
<tr>
<th>Mean number of invertebrates</th>
<th>(N = 12)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diplopoda (millipedes)</td>
<td>0</td>
</tr>
<tr>
<td>Lepidopteran larvae</td>
<td>0</td>
</tr>
<tr>
<td>Orbital mites</td>
<td>0.5</td>
</tr>
<tr>
<td>Coleoptera (weevils)</td>
<td>0</td>
</tr>
<tr>
<td>Megascolecida (earthworms)</td>
<td>0</td>
</tr>
<tr>
<td>Stylonychidae (slaters)</td>
<td>0</td>
</tr>
<tr>
<td>Talitridae (amphipods)</td>
<td>0</td>
</tr>
<tr>
<td>Tipulid larvae</td>
<td>0</td>
</tr>
</tbody>
</table>

### Appendix 6.2: The number of invertebrates in sacrificial litter-bags after treatment with insecticide one month prior.